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THE DIVERSE TURTLE FAUNA (TESTUDINES, CRYPTODIRA: TESTUDINIDAE, GEOEMYDIDAE) FROM THE NEOGENE OF MAKRYGIALOS AND AGIANNIS, PIERIA, THERMAIKOS GULF, N. GREECE

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ΜΑΡΙΑ ΣΑΛΤΣΙΔΟΥ
Πτυχιούχος Γεωλόγος

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Chapters

PROLOGUE

This dissertation was prepared within the framework of the Inter-Institutional Postgraduate Studies Program in "Palaeontology-Geobiology", specializing in Macropalaeontology. The supervising researcher is Dr. Evangelos Vlachos from CONICET and Museo Paleontológico Egidio Feruglio whom I sincerely thank for the assistance and guidance he provided me and the excellent cooperation during my studies.

I sincerely thank the members of the committee, Professor Evangelia Tsoukala and Professor Dimitrios Kostopoulos for the valuable help and advice they provided me with during the course of my studies and the writing of this thesis.

The aim of this thesis is the study of the new material of giant tortoises of the species *Titanochelon bacharidisi* from two localities of the western part of Thermaikos Gulf, Makrygialos and Agiannis, Pieria, the systematic description of the specimens their comparison with published material from Greece, Europe and Asia Minor and the contribution of this new material to the more detailed description of the species, the local stratigraphy, paleogeography, and paleoecology. In addition, new elements of the osteology and general morphology of these tortoises are presented that contribute to the better systematic study of these giants. Lastly, the importance of the turtle fauna of the general area is discussed.

I thank the School of Geology and especially the Department of Structural, Historical & Applied Geology for the infrastructure I was provided with during the preparation of my thesis and my postgraduate studies.

The particularly important material presented in this thesis has been discovered and preserved by some people whom I would like to thank for their significant contribution to the research of giant tortoises in Greece:

Mr. Nikolaos Bacharidis, who discovered and excavated the first giant tortoise of the species in the eastern side of the Thermaikos Gulf, in Epanomi, that initiated the research of these giant reptiles in the wider area, but also participated in the excavation and preparation of the rest of the specimens from that area, as well as from Makrygialos and Agiannis. Mr. Vassileios Makridis for his valuable help in the excavation and preservation of the specimens from Makrygialos and Agiannis, and his contribution to the exhibition of the giant tortoises in the Dinosaur Park - Mammoth Museum of Nouvelle (Oreokastro-Thessaloniki). Mr. Vassileios Michailidis for the granting of the appropriate space for the preservation of the fossils and their temporary exhibition in the Dinosaur Park - Mammoth Museum in Nouvele. I would also like to thank all my colleagues that helped with the excavation and preservation of the specimens studied herein.

The recent renewed interest in the fossilized turtles of Makrygialos is due to the actions and efforts of Mr. I. Poimenidis, who discovered many of the finds, as well as Mrs. M. Avramidou and Mr. M. Mavridis, who representing the local community did everything possible to help us. An important role in the recovery of some specimens was played by Mr. K. Koutoupas and his staff, who provided equipment and boats without which it would have been impossible to remove the specimens from the field. Several of the photos were taken by drone by Mr. K. Kavouras to whom I am deeply grateful.

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CHAPTER 1. INTRODUCTION

1.1 The giant tortoise record

1.1.1 The giant tortoises of Europe

Giant tortoises roamed Europe since the beginning of the Eocene. Back then though, they were not so giant. In the beginning, during the Eocene to Pliocene, their size varied from 30 cm almost 70 cm. Some of the first taxa of large sized tortoises that initially appeared are *Pelorochelon eocaenica* (Hummel, 1935) from the middle Eocene, Lutetian, of Germany and Austria, which barely reached 70 cm in shell length (Karl, 1996; Pérez-García et al. 2015), *Pelorochelon soriana* Pérez-García, Ortega and Jimenez Fuentes, 2015, from the middle Eocene of Spain, which also barely reached 70 cm in shell length, *Cheirogaster maurini* Bergounioux, 1935, from the Late Eocene, Priabonian, of France, which was almost 40 cm in shell length (Pérez-García and Vlachos, 2014), and *Taraschelon gigas* (Bravard, 1844) from the Early Oligocene of France, which almost reached 80 cm in shell length.

Because it was believed that European tortoises were derived from North American taxa, and their taxonomy was not that well known in the past; several large sized specimens found in various localities of Europe were attributed to the genera *Hadrianus* and *Achilemys* known from the Eocene of North America. It was believed that these testudinids reached Europe and then diversified in different parts of the continent, giving different genera and species (Lapparent de Broin, 1977). The same European specimens were later attributed to other species and genera and the taxa were proposed as *nomina dubia* (Pérez-García et al., 2015).

Initially, all the large sized tortoises of Europe and Asia Minor were attributed to the genus *Testudo*, along with most of the turtles and tortoises, extinct or extant, around the world. The genus *Cheirogaster* was erected by Bergounioux in 1935, to describe its type species *Cheirogaster maurini* from France. However, that description was problematic because Bergounioux added as a diagnostic character the absence of the entoplastron (among other problematic interpretations). Lapparent de Broin (1977) redescribed the same material and redefined the genus *Cheirogaster* stating that it is more derived than *Hadrianus.* As a result, she placed all the medium and large-sized continental tortoises from the Eocene to Pliocene of Europe and Asia Minor in the genus *Cheirogaster* (Lapparent de Broin, 2001; 2002). Later though, all the giant tortoises from the Neogene of Europe were separated from the more primitive forms and were reattributed to the new genus *Titanochelon* by Pérez-García and Vlachos (2014) leaving *Cheirogaster* to be represented only by its type species. Other species of giant tortoises of the Paleogene that were included in the genus *Cheirogaster* were attributed to different genera.

After that reevaluation of the giant tortoises of Europe other concerns about their taxonomy arose. The tortoises that once belonged to the *Cheirogaster* group are believed to not be a monophyletic group but consist of many different tortoise lineages that arrived somehow in Europe. Answers to these concerns were given by Vlachos and Rabi (2018) where, the cladistic analysis clearly showed that the more primitive tortoises make up several different lineages. *Fontainechelon cassouleti* (Claude & Tong, 2004) for example, is one of the most primitive tortoises to be found in Europe and is outside the crown clade of Testudinidae (Fig. 1). This species along with *Pelorochelon soriana* and *Pelorochelon* or *“Testudo” eocaenica* are the three representatives of the stem Testudinidae that existed in Europe. The rest of the tortoises of Europe are inside the crown lineage of today’s Testudinidae (Vlachos & Rabi, 2018).

Another important result of the study discussed above is the separation of a more primitive group, from the Paleogene, that includes *Cheirogaster* from the more derived group, from the Neogene, that includes *Titanochelon* (Fig. 1). These two clades are distinct which implies two separated dispersal events in Europe, one in Paleogene and another in Neogene (Vlachos & Rabi, 2018).

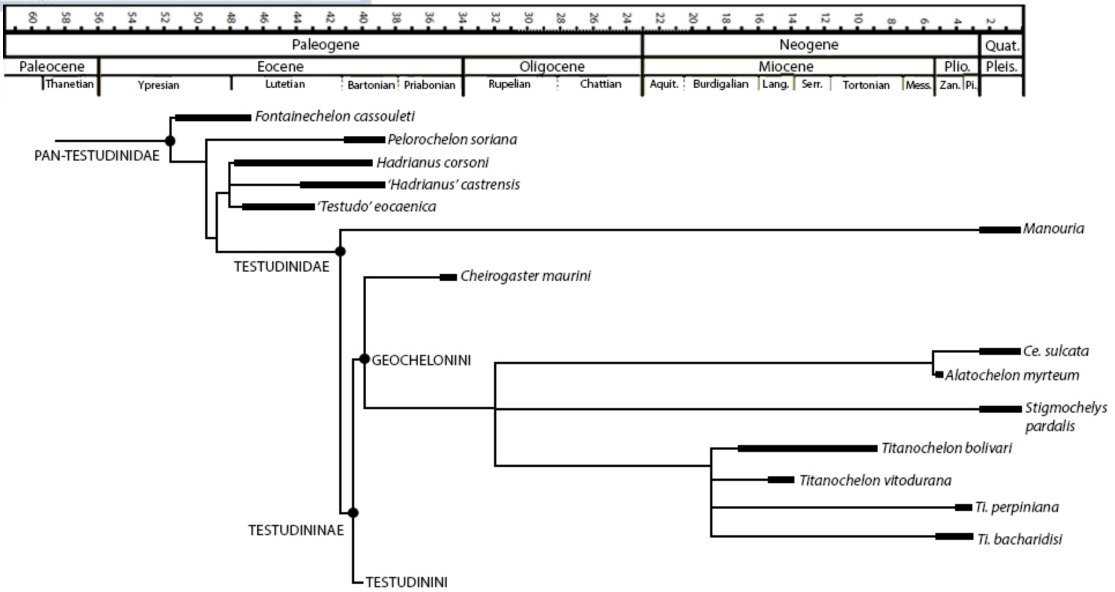

Figure 1: Simplified cladogram of the large sized extinct tortoises of Europe and several extinct and extant taxa from other continents. (Vlachos & Rabi, 2018; Pérez-García et al. 2020)

The genus *Titanochelon* has a wide distribution in Europe. Specimens of the genus have been found in Portugal, Spain, France, Switzerland, Germany, Austria, Greece, Bulgaria and Asia Minor and is represented by various species (Fig. 2). It survived from the Early Miocene to the Early Pleistocene of Europe. Its type species is *Titanochelon bolivari* (Hernández-Pacheco, 1917a) found in Spain and Portugal. Other species of the genus are *Titanochelon bacharidisi* Vlachos, Tsoukala and Corsini 2014 from various localities of Greece, *Titanochelon perpiniana* (Depéret, 1885) from the locality of Perpignan, France, *Titanochelon schafferi* (Szalai, 1931) from the Island of Samos, Greece, *Titanochelon kayadibiensis* Karl, Staesche & Safi, 2020 from various localities of Turkey, *Titanochelon ginsburgi* (Lapparent de Broin, 1977) from the locality of Artenay, France, *Titanochelon vitodurana* (Biedermann, 1862) from the localities Winterthur and Veiltheim of Switzerland, *Titanochelon eurysternum* (Gervais, 1848–1852) from the locality of Saint-Gerard-le-Puy, France, and lastly *Titanochelon leberonensis* (Depéret, 1890) from France.

However, with every new discovery of material that belongs to giant tortoises in Europe, the taxonomy becomes even more complicated. There are more species and specimens that were suggested to be attributed to the genus *Titanochelon,* but new findings and data have changed the narrative. One of them is "*Testudo*" *gymnesica* Bate, 1914, a large testudinid from the Early Pliocene of Menorca in the Gymnesic Islands of the eastern Balearics, Spain that was proposed as a member of *Titanochelon* by Pérez-García and Vlachos (2014), Rhodin et al. (2015) and later supported by Pérez-García et al. (2017). Specimens of large sized tortoises were also found in Malta, dated to the Middle Pleistocene but their taxon was not determined (Rhodin et al., 2015, Pérez-García et al., 2017). In 2022 however, it was suggested that *"Testudo" gymnesica* along with *"Testudo" robusta* Leith-Adams, 1877 from Malta, the unnamed material from Monte Pellegrino, Sicily, and the material from Zubbio di Cozzo San Pietro Cave that was attributed to the species *Solitudo sicula* Valenti et al., 2022 form a distinct evolutionary lineage that consists of tortoises that inhabited the Mediterranean islands from Pliocene to Pleistocene. All these specimens were placed in the new genus *Solitudo* (Valenti et al., 2022). It is obvious, therefore, that the history of the giant tortoises of Europe is long and complex and may change with every new discovery (Fig. 2).

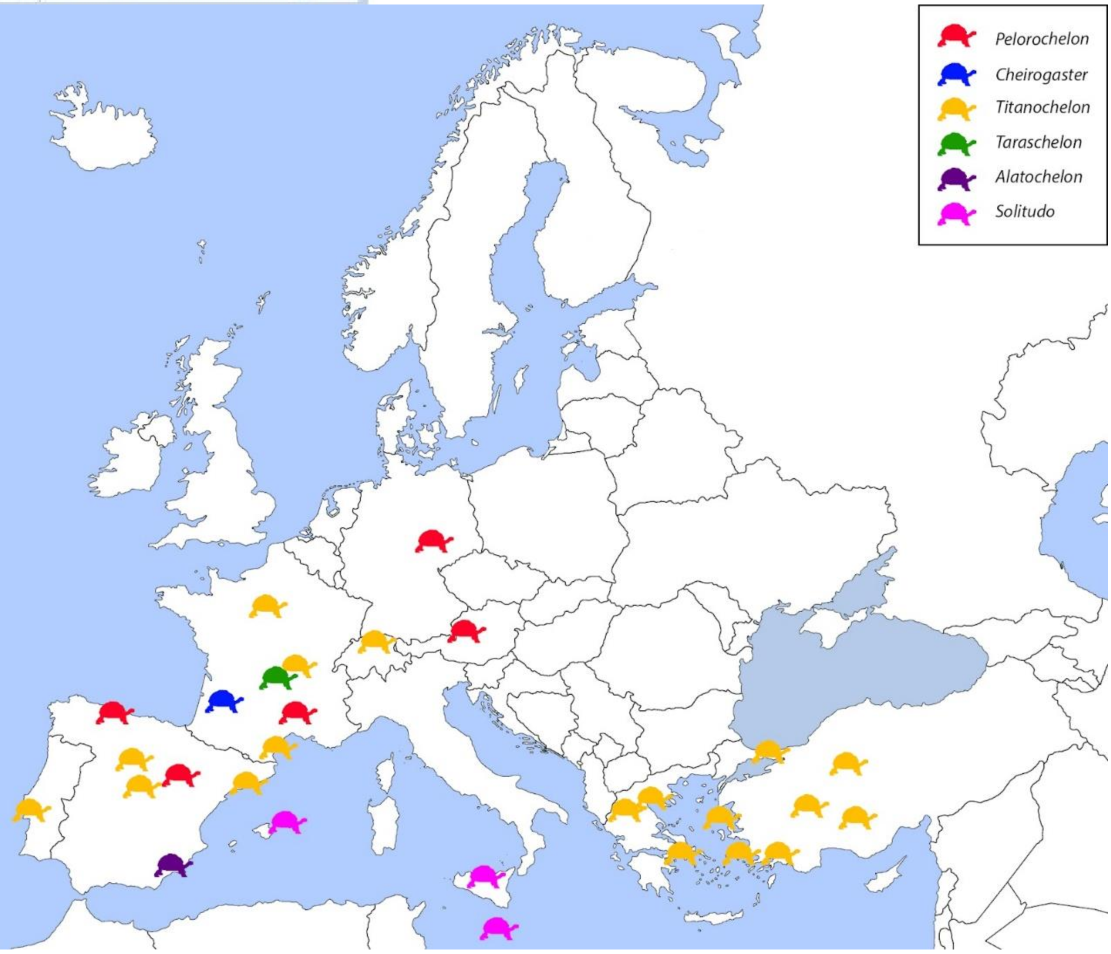

Figure 2: Distribution of large-sized tortoises in Europe. Distribution of large-sized tortoises in the Cenozoic of Europe, including the Paleogene genera *Pelorochelon*, *Cheirogaster*, *Taraschelon*, the Neogene *Titanochelon* and *Alatochelon*, and the Quaternary *Solitudo* (see text).

The present work is placed within this complex systematic concept and aims to offer new insights in a timely manner. This is because the giant fossil tortoises from Greece have only received specific interest in recent, but they nevertheless proved to be crucial in forming the current taxonomic consensus on the European giant tortoises. This thesis expands the renewed interest on the Neogene giant tortoises from the circum-Thessaloniki region to the region of Pieria, presenting new fossils and revising the latest new species of a giant tortoise described in Greece.

1.1.2 The giant tortoises of Greece

In Greece, the genus *Titanochelon* has a wide distribution and is represented by two species: *Titanochelon bacharidisi* and *Titanochelon schafferi* (Fig. 3). A complete skull and a complete femur of “*Testudo*” *schafferi* were initially found in the Late Miocene of the island of Samos and described by Szalai (1931). It was later reattributed to the genus *Cheirogaster* by Lapparent de Broin (2002) and finally to the genus *Titanochelon* along with the other giant tortoises from the Neogene of Europe by Pérez-García & Vlachos (2014). More specimens of giant tortoises from the island of Samos were discovered from old collections, that include plastral and several appendicular remains, and were described by Vlachos et al. (2019a). This material triggered discussions concerning its potential origins, which up to now is only found in Samos Island. It is believed that *Titanochelon schafferi* had biogeographic links with Asia Minor because more similarities in terms of morphology have been observed with specimens found in that region compared to the taxa from the Balkan area (Vlachos et al., 2019a).

The most widely distributed species of giant tortoises in Greece is *Titanochelon bacharidisi*. The locations where this species is found are the Late Miocene to the possibly Pliocene locality of “Salonique” (Arambourg & Piveteau, 1929), the Pliocene localities of Nea Kallikratia, Nea Michaniona, and Epanomi (Vlachos et al., 2014; Vlachos, 2015), all located along the coastal exposures of the eastern side of Thermaikos Gulf. The new material described herein was discovered in similar and coeval, stratigraphically related coastal outcrops from the western side of the Thermaikos Gulf (Fig. 4). Previous studies of the small-sized turtle and tortoise taxa showed important taxonomic differences between the chelonofaunas on the western and eastern side of Thermaikos (Vlachos, 2015; Saltsidou et al., 2022). It is therefore intriguing to investigate how the giant tortoises fit into this scheme.

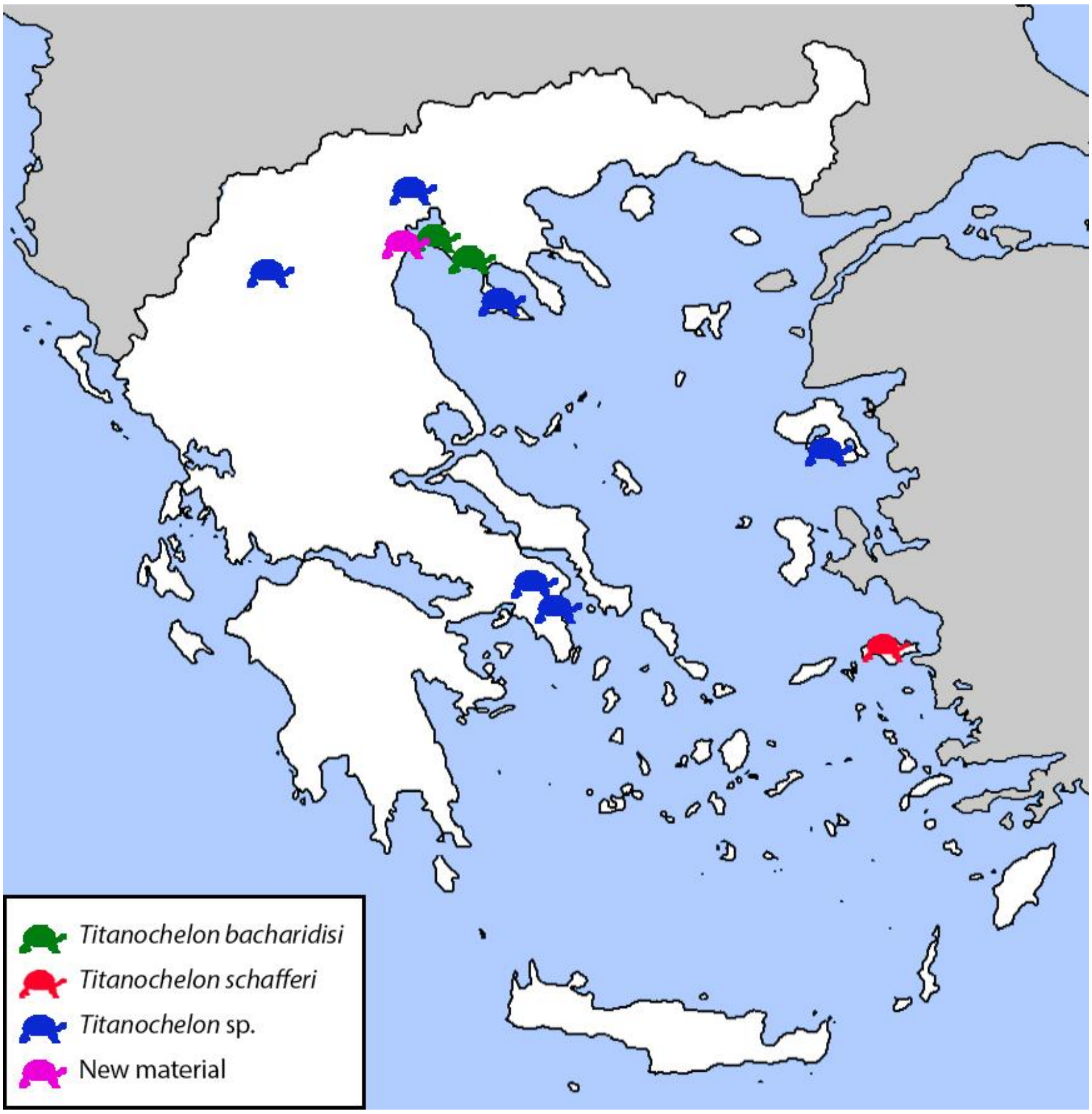

Figure 3: Distribution of the genus *Titanochelon* in the Neogene of Greece. It includes the taxa *Titanochelon bacharidisi*, *Titanochelon schafferi*, and *Titanochelon* sp. The pink figure indicates the new material from Makrygialos and Agiannis (see text).

The first reported material of a giant tortoise that can be associated with the species *Titanochelon bacharidisi* was mentioned in 1929 by Arambourg and Piveteau, where they described several specimens from the locality "Salonique", but in reality, they were found in two different locations, Axios Valley, more specifically Vathylakkos, and Cape Megalo Emvolon of Northern Greece (Vlachos et al., 2014; Vlachos, 2015). They were initially mentioned as *Testudo* sp. but were later allocated to *Titanochelon bacharidisi* (Vlachos et al., 2014). Later, a giant tortoise from Megalo Emvolon, near Thessaloniki is described by Bachmayer et al. (1979) that was also later attributed to the species *T. bacharidisi* (Vlachos et al., 2014; Vlachos, 2015). More recently, in 2014, four new specimens of giant tortoises were discovered in three localities that had not been mentioned in previous studies but are relatively close to Megalo Emvolon, Epanomi, Nea Kallikratia and Nea Michaniona. Those specimens were initially attributed to the species *Cheirogaster bacharidisi* but were later classified as *Titanochelon bacharidisi* (Vlachos et al., 2014; Pérez-García and Vlachos, 2014; Vlachos, 2015).

There are more specimens of giant tortoises found in other localities around Greece that have been attributed to the genus *Titanochelon* but did not provide enough information and diagnostic characters to attribute them to a species. The material from Pikermi and its close locality Liossati (Kiourka), Attika, is dated in the Late Miocene and consists mainly of fragments of the carapace and plastron, and several postcranial elements (Vlachos, 2015; Vlachos et al., 2019a). They were initially attributed to *Testudo* cf. *schafferi* by Bachmayer (1967) as it was the only known species of large sized tortoises in Greece at the time. Later, they were referred to as *Cheirogaster* cf. *schafferi* by Lapparent de Broin (2002) but finally identified as *Titanochelon* sp. by Vlachos (2015).

The material from the Early Pleistocene locality of Vatera of the island of Lesvos consists of several postcranial elements of a giant tortoise. They are the youngest known giant tortoise remains that are found in Greece, and until 2017 it was considered the youngest known tortoise of the genus *Titanochelon* in Europe (Pérez-García et al., 2017). Lapparent de Broin (2002) identified it as *Cheirogaster* aff. *schafferi* due to the similarities in size, morphology of the femur and the geographic proximity with the Samos taxon. However, the preserved information was not enough for this material to be placed in a specific species, so it was referred to as *Titanochelon* sp. by Vlachos (2015). While Lesvos is an island, the material was attributed to a continental form and not to an insular one. This happened because during the Pliocene and Pleistocene Lesvos was connected to the Anatolian Peninsula and became an island again during the Holocene (Drinia et al., 2002; Vlachos et al., 2014; Pérez-García et al., 2017).

In the Upper Pliocene site of Milia, Grevena two fragmentary specimens that belong to a giant tortoise were found, but they did not preserve any diagnostic features to allow their attribution to a species (Vlachos, 2015; Vlachos and Tsoukala, 2016). Lastly, four specimens were found in total in the two Late Miocene localities of the Kassandra peninsula of Chalkidiki, Kryopigi and Fourka. The material is really scarce, so the identification of the species was impossible, but those localities are close in geographical proximity with Epanomi, Nea Michaniona and Nea Kallikratia.

There is more material that needs to be conserved and studied like the partially complete specimen from the Late Miocene of Nikiti, Chalkidiki (Fig. 4). It is of great importance because it broadens the distribution of the *Titanochelon* genus in the general area of Chalkidiki (Vlachos, 2018).

1.1.3 The giant tortoises of Makrygialos and Agiannis

The presence of fossil giant tortoises in Makrygialos has been known since the beginning of the 21st century, when specimens were identified by a group of paleontologists from France (University of Poitiers), who explored the area. However, the team did not proceed to excavate the giant fossils but only collected two small-sized tortoises that have been studied in Saltsidou et al. (2022). In 2015, the giant tortoises came back to light by a resident of the area, who contacted the Aristotle University of Thessaloniki about the finding of specimens on the coast between Makrygialos and Agiannis. This specimen was immediately removed from the beach in May of 2015 as its preservation was poor due to marine erosion. Later surveys were organized by E. Tsoukala and E. Vlachos with funding from National Geographic, in order to excavate and preserve the rest of the specimens, which lasted until August 2019. Seven giant tortoises and four small-sized ones were found, in the Makrygialos and Agiannis coastlines. Only the four small-sized turtles, two *Chersine hermanni* (Gmelin, 1789) individuals and two *Mauremys* sp. Gray, 1869, have been studied so far (Saltsidou et al., 2022). Five of the seven giant tortoises have been properly excavated, collected and prepared and form the specimens that will be studied herein. This is the richest material of giant fossil tortoises collected from a broader locality in Greece.

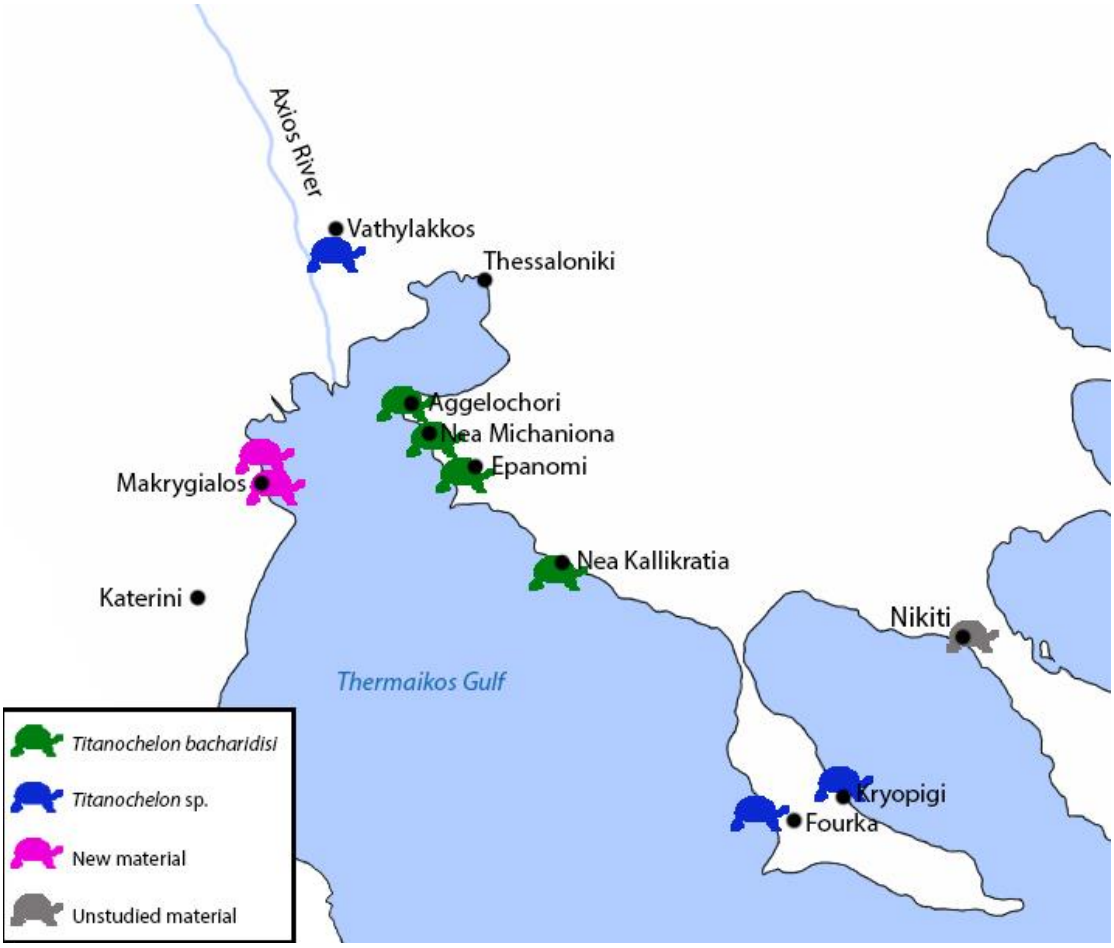

Figure 4: Distribution of giant tortoises in Thermaikos Gulf. It includes the taxa *Titanochelon bacharidisi*, and *Titanochelon* sp. The pink figure indicates the new material from Makrygialos and Agiannis.

1.2 Geological Setting

1.2.1 Geology of the general area

The area of study is located in the coastal slopes of Makrygialos and the neighboring settlement of Agiannis. Makrygialos is a large settlement, on the northern coast of the regional unit of Pieria, Greece. It is located in the western part of

Thermaikos Gulf, south of the Axios river delta. South of Makrygialos is the city of Katerini, at a distance of 21 km, as well as Mount Olympus. North of Makrygialos is located the small-sized settlement called Agiannis and to the south the settlement of Ancient Pydna. Directly across the sea from Makrygialos, on the eastern side of Thermaikos gulf, the beach of Epanomi is located. The coasts of Makrygialos and Agiannis face to the East.

The study area, from a geological point of view, belongs to the Katerini Basin. It comprises the western part of the wider elongated depression of the Axios-Thermaikos basin which has been formed upon the older Axios trench that evolved after the end of the Eocene orogenetic period of Northern Greece (Sylvestrou, 2002; Paschalidou, 2020; Saltsidou et al., 2022). Tectonic systems that were activated during the Oligocene-Miocene period created horsts and basins of NW-SE directions. In this geotectonic frame the Axios-Thermaikos basin was originally created and was filled up with mostly terrestrial to brackish sediments up to 1,000-1,500 m (Doutsos & Ferentinos, 1984; Lalechos, 1986; Psilovikos & Syrides, 1984). The basement in the western border of the basin consists of rocks of the Almopia Subzone, mostly of flysch-phyllitic series with semi-metamorphic clasts, recrystallized limestones, and ophiolite appearances. Furthermore, rocks of the Pelagonian continental margin are found in the basin, mostly schists, gneiss-schists as well as, in the upper parts, marbles (Mountrakis, 2010; I.G.M.E 2002, Kolindros sheet).

According to Sylvestrou (2002), the western section of the wider basin was divided into eight Neogene - Quaternary formations which are the following: (a) the Elatochori Formation, of Lower Miocene age, which consists of mixed conglomerates and clay layers in its upper parts; (b) the Moschopotamos Formation, of Lower to Middle Miocene age, which consisting of clays, marls with intercalations of sands and layers of lignite; (c) the Sykea Formation, of Middle Miocene age, which consists of brown-reddish clays-silty clays and layers of gray-green sands-sandstones; (d) the Riakia Formation, of middle Miocene age, which consists of brown to yellow sands including lenses of sandstones and gray to green clay layers with calcrete concretions; (e) the Lagorachi Formation, of Upper Miocene age, which consists of off-white fine to coarse sands and local appearances of loose conglomerates and cobbles; (f) the Sfendami Formation, of Upper Miocene age, which consists of brackish fossiliferous layers of clays, marls and sands with characteristic Paratethyan fauna (Late Miocene, Pontien); (g) the Makrygialos Formation, of Upper Miocene to Early Pliocene age, which consists of alternations of sands, clays, layers of marl and lenses of loose conglomerates with pebbles of volcanic material; and (h) the Lophos Formation, of Pliocene to Lower Pleistocene age, which consists of sands and cobbles in the lower horizons and extensive layers of marls and marly limestones in alternations with sands and sandstones in its upper parts but without any volcanic material.

1.2.2 The Makrygialos Formation

The Makrygialos Formation, to which our study area belongs and where the fossils studied herein were located, has a thickness up to 200-220 m, and stretches in the northern part of the basin. It has an Upper Miocene to Lower Pliocene (latest Turolian-Ruscinian) age. The formation can be found in three geological maps of I.G.M.E but with a different name. In the geological map of I.G.M.E. Katerini sheet (1986), it is referred to as fluvioterrestrial deposits of Methoni-Makrygialos. In the Plati and Alexandria sheets the sediments of the Palianela locality that belong to the Makrygialos Formation, are included in the underlying Sfendami Formation. Between the Makrygialos Formation and the overlying Quaternary deposits an unconformity is observed. The large contribution of volcanic material in the formation is believed to originate from the volcanic center of Almopia (Syrides, 1990; Sylvestrou, 2002). The presence of a white tuff horizon in the wider area is considered to originate from the first explosive event that took place between 5.6 and 5.0 Ma from the volcanic centers of Voras (Vougioukalakis, 2002). There is a remarkable presence of similar volcanic material in the eastern part of the wider Axios basin in the areas of Aggelochori, Epanomi and in the Gonia Formation of the Chalkidiki peninsula (Syrides, 1990; Sylvestrou, 2002; Paschalidou, 2020; Saltsidou et al., 2022). The discovery of the similar volcanic material and fossil tortoises in the Gonia Formation are two similarities that could help us correlate the two locations from the opposite sides of Thermaikos Gulf.

On the coasts of Makrygialos and Agiannis, there are generally coarse-grained layers alternating with thin clay and silty clay horizons with lenses of marls and marly sandy limestones. According to several depositionary models (Miall, 2006; Soares et al., 2018), it looks like river systems were predominant in the area. The coarse-grained materials, mostly sands, lenses of gravels with cross-bedded, abrupt or corrosive base contacts and grading of material to the upper parts, indicate active channel filling with gradually decreasing capacity of the channel flow from high energy conditions to low energy conditions up to the suspension of fine sand.

Thin clay-silty layers, with a high percentage of calcareous concretions and rootlets residues, indicate mainly a stable basic level, immature old soils and deposits mostly in floodplains or abandoned areas of active channels in periods of low water level (Miall, 2006). Pedogenous calcifications, found in several horizons, appear in the form of vertical and branching irregular veins, thin horizontal forms (laminar calcrete) and finally, as nodules (Alonso-Zarza & Tanner, 2010). These are usually secondary accumulations of calcium carbonate in a variety of soils through soil processes, mainly under arid and semi-arid climatic conditions.

The studied fossils were found in layers of fine-grained silty sand with gravels, where a gradation of material at the upper horizons is observed in coarse-grained sandy silt (Fig. 5). The composition of the sand includes quartz, mica (mainly muscovite), calcite, feldspars, and volcanic altered clusters. Out of the eleven fossil turtles found in Makrygialos and Agiannis, seven, LGPUT MAP-1, LGPUT MAP-3, LGPUT MAP-5, LGPUT MAP-6, LGPUT AG-1, LGPUT AG-2 and LGPUT MAP-32, were found in the sediments of this formation. The specimen LGPUT MAP-2 was found detached from the slope right next to LGPUT MAP-1 that was still attached to it. While the outcrop the specimen LGPUT MAP-18 originated from is known, we do not know the exact spot it was found. The specimens LGPUT MAP-33 and LGPUT MAP-40 were found in the general locality of Makrygialos and Agiannis but the exact spot is unknown.

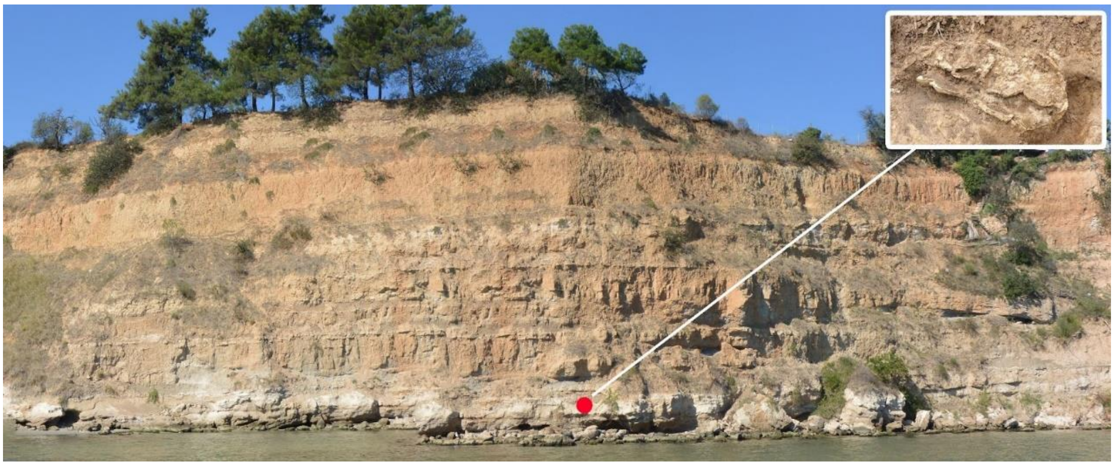

Figure 5: Section of the Makrygialos formation right next to the beach of Makrygialos. The red dot marks the exact spot the specimen LGPUT MAP-3 was located.

1.2.3 Other fossil remains in the Makrygialos Formation

Several other fossil remains have been found in the Makrygialos Formation that are not enough to compose a separate study. In a section along the coast of Makrygialos several bone fragments and teeth of large mammals have been found enclosed in the sediment (Sylvestrou, 2002). A micromammal tooth was also found along with other bone fragments inside a clay layer. Reports of fossil findings have been made in the past but with limited information about the exact location (Benda and Steffens, 1981). Fossils of artiodactyls, carnivorans and a large form of *Hipparion* sp. along with small mammals and representatives of Arvicolidae have been discovered.

Inside the Makrygialos Formation but in different localities, more fossils of mammals have been found. Specifically, in the Asprogiannis locality that belongs stratigraphically in the lower parts of the formation, several *Hipparion*, *Gazella*, *Tragoportax* and possible Rhinocerotidae and Antilopinae specimens have been discovered (Sylvestrou, 2002). In the sand mine Paliabela, NW of Makrygialos, teeth the taxa *Pseudomeriones megistos* Sylvestrou & Kostopoulos 2007, *Prolagus*, *Micromys* cf. *steffensi* Van De Weerd, 1979 and Soricidae have been found.

1.3 Material and Methods

The area of study consists of all the outcrops exposed south of Makrygialos, approximately from the latitude of Pydna settlement, to the north of Agiannis settlement, corresponding to nearly three kilometers of coastline. The fossils were found on the coast, scattered in different collection points. To facilitate the study and reporting of the specimens, the collection points have been grouped into two localities, and marked with the code MAP (MAkrygialos Pieria) for the turtles found closer to the settlement of Makrygialos and AG (AGiannis) for the turtles found closer to the settlement of Agiannis.

A total of eleven fossil turtles have been found in the area of study, seven of which are giant tortoises, two are small-sized tortoises and the other two are small-sized freshwater turtles (Table 1). The five giant tortoises with the specimen codes LGPUT MAP-1, LGPUT MAP-2, LGPUT MAP-3, LGPUT AG-1 and LGPUT AG-2 have been excavated during a period of almost five years. The specimens LGPUT MAP-5 and LGPUT MAP-6 have not yet been removed from the coast of Makrygialos. Of the small-sized turtles, specimens LGPUT MAP-18 and LGPUT MAP-32 are freshwater turtles of the genus *Mauremys*, and LGPUT MAP-33 and LGPUT MAP-40 are tortoises of the species *Chersine hermanni* (Saltsidou et al., 2022). The first five fossil tortoise specimens will be described in this thesis and the discussion will further include all turtle specimens found in the area.

The excavation was particularly difficult because the specimens were located at the base of vertical slopes on the coast, which were very susceptible to landslides due to marine erosion. Also, the locations where the specimens were found were only accessible by foot and for certain hours of the day as the sea level rose during the afternoon hours. Of all the fossils, only LGPUT MAP-1, LGPUT MAP-2, LGPUT MAP-3 LGPUT AG-1, LGPUT AG-2 and the small-sized turtles were excavated. In particular, in May 2015, a preliminary visit was made to the research sites, where a small-sized freshwater turtle, the specimen LGPUT MAP-32, was collected from the coast of Agiannis. In August - September 2016, the team proceeded with the excavation of the specimens LGPUT MAP-2, LGPUT AG-1, LGPUT AG-2, and the preparation of the previous specimens. The specimen LGPUT MAP-2 was found in the coast of Makrygialos just behind the specimen LGPUT MAP-1 that was excavated the previous year. The specimens LGPUT MAP-3 was partially excavated in April of 2019 in an attempt to salvage it from sea erosion. The specimens LGPUT MAP-5 and LGPUT MAP-6 that were found on the coast of Makrygialos have not yet been recovered because they are in a place where they are not at risk from sea erosion.

Moving the specimens was very difficult due to their large size and weight. The specimen LGPUT MAP-2 reached 2134.4 kg in weight, before the preservation, making it one of the heaviest vertebrate fossils excavated in Greece. Specimens LGPUT MAP-1 and LGPUT MAP-2 were very difficult to transport from the land, so they were tied with straps and then a fishing boat pulled them from the sea and transported them to the port of Makrygialos. The transportation of the rest of the specimens, LGPUT MAP-3, LGPUT AG-1 and LGPUT AG-2, was slightly easier but still challenging because they were already fragmented so they were transported in parts from the shore.

After the excavation, the conservation of the fossils began. It initially took place at a facility of the LGPUT (Fig. 6), as a first stage in 2017-2018, where the specimen LGPUT MAP-1 was fully conserved, and LGPUT MAP-2 to a lesser degree. Later, in 2019 the specimens were moved to a facility of the Nouvelle Environmental Park, in Oreokastro, Thessaloniki where the conservation continued. By the end of the summer of 2019 the specimens LGPUT MAP-2 and LGPUT AG-2 were fully preserved. To remove the sediment, hammer and chisel were used at first, and then for details a microhammer. Paraloid dissolved in acetone was used as a stabilizer to protect and solidify the fossils. Because the specimen LGPUT AG-2 was excavated in the form of fragments the specimen that once filled the shell was removed. In order to keep the fragments of the plastron connected and to prepare the specimen for the exhibition, a cast made of plaster and paper towels was created, that is easily removable, and covers the visceral side of the plastron, leaving the bony plates and horny scutes visible for observation. The carapace fragments of the specimen that could be connected were just glued together. The rest of the specimens, several fragments of LGPUT AG-2, the whole LGPUT AG-2 and LGPUT MAP-3 were transported to the Laboratory of Geology and Palaeontology of the Aristotle University of Thessaloniki and were preserved there. The preservation of all the giant tortoises was concluded in January of 2022 in order to prepare them for this thesis.

Figure 6: The conservation of the specimen LGPUT MAP-2 in the facilities of the Aristotle University of Thessaloniki, in September of 2017.

To identify the genus and species of the specimens studied, we compare them with other extinct taxa of giant tortoises from Europe and Asia Minor. They are compared with specimens of the species *Titanochelon bacharidisi* from the eastern side of the Thermaikos gulf, the holotype and paratype from Epanomi, individual EPN I, including specimens LGPUT EPN 100-199, and individual EPN II, including specimens LGPUT EPN 200–287, respectively, the two individuals from Nea Kallikratia, KLK I, including specimens LGPUT KLK 501-529, and KLK II, including specimens LGPUT KLK 500, the material from Nea Michaniona, LGPUT MIC 301-319, and the specimens from Aggelochori, LGPUT AGG 420-422, AMPG 1925-1955, AMPG 1969, and AMPG 1970 (Vlachos et al., 2014; Vlachos, 2015).

The studied specimens are also compared with other species of the genus *Titanochelon* such as specimens NHMW 2009z0103/0001, NHMW 1911/0005/0275, AMNH 1905, AMNH 1772 and MGL 101624 of *Titanochelon schafferi* found on the island of Samos, Greece (Szalai, 1931; Lapparent de Broin, 2002; Vlachos et al., 2019b), specimens MNCN 32773, and MNCN 32771 of *Titanochelon bolivari* found in Spain and Portugal, (Pérez-García and Vlachos, 2014), *Titanochelon perpiniana* from France (Bourgat & Bour, 1983), specimen BGR — KB without number of *Titanochelon kayadibiensis* Turkey, (Karl et al., 2021), *Titanochelon ginsburgi* from France (Lapparent de Broin, 1977), and specimens NWS 13758, and PIMUZ A/III 660 of *Titanochelon vitodurana* from Switzerland, (Biedermann, 1862; Peyer, 1942). Other relevant comparisons made are with specimens from Greece that belong to the genus *Titanochelon* but have not been attributed to a specific species. Those consist of the “Salonique" material from Northern Greece (Arambourg and Piveteau, 1929; Vlachos, 2015), the Pikermi and Liossati material from Attika (Vlachos, 2015; Vlachos et al., 2019a), the Vatera material from the island of Lesvos (Lapparent de Broin, 2002; Vlachos, 2015), and lastly the material from Milia, Grevena (Vlachos, 2015; Vlachos and Tsoukala, 2016) and Kassandra peninsula, Chalkidiki (Vlachos, 2015).

Lastly, we compared our specimens with primitive large-sized tortoises from Europe like the species *Pelorochelon eocaenica* from the Middle Eocene of Austria (Karl, 1996; Pérez-García et al., 2016), *Pelorochelon soriana* from the Middle Eocene of Spain (Pérez-García et al., 2016), *Cheirogaster maurini* from the Late Eocene of France (Lapparent de Broin, 1977), *Taraschelon gigas* from the Early Oligocene of France (Pérez-García, 2016), and *Alatochelon myrtuem* from the Early Pliocene of Spain (Pérez-García et al., 2020).

All the specimens studied in this thesis belong to the collections of the Museum of Geology, Paleontology, Paleoanthropology of the School of Geology of the Aristotle University of Thessaloniki (LGPUT). Most tortoise and turtle specimens are currently included in a temporary public exhibition at the Mammoth Museum of the Nouvelle Environmental Park, in Oreokastro, Thessaloniki, under the supervision of LGPUT.

Table 1: Reptile specimens of Makrygialos

Specimen code	Species	Coordinates
LGPUT MAP-1	*Titanochelon bacharidisi*	Lat. 40.419124° Long. 22.610733°
LGPUT MAP-2	*Titanochelon bacharidisi*	Lat. 40.419124° Long. 22.610733°
LGPUT MAP-3	*Titanochelon bacharidisi*	Lat. 40.418547° Long. 22.610942°
LGPUT MAP-5	*Titanochelon bacharidisi*	Lat. 40.405578° Long. 22.611858°
LGPUT MAP-6	*Titanochelon bacharidisi*	Lat. 40.404521° Long. 22.612648°
LGPUT AG-1	*Titanochelon bacharidisi*	Lat. 40.428344° Long. 22.605801°

LGPUT AG-2	*Titanochelon bacharidisi*	Lat. 40.428836° Long. 22.605792°
LGPUT MAP-18	*Mauremys* sp.	Lat. 40.416033° Long. 22.611431°
LGPUT MAP-32	*Mauremys* sp.	Lat. 40.428963° Long. 22.605746°
LGPUT MAP-33	*Chersine hermanni*	-
LGPUT MAP-40	*Chersine hermanni*	-

We study turtles and tortoises mainly based on the morphology of their shell which is divided in two parts, the carapace, and the plastron (Fig. 7). These two parts are joined laterally in the bridge area, leaving two openings in the anterior and posterior part for the limbs and the neck of the animal. The shell consists of a set of bony plates, which are joined by sutures. Externally, it is covered by a set of horny scutes which consist of keratin and are not fossilized. They are studied in fossil tortoises based on the sulci they leave on the bony plates.

The horny scutes of the carapace consist of a middle row of single plates, usually six, on the central axis. This contiguous row is surrounded by the rest of the horny scutes, which occur in pairs. The bony plates have a similar structure, with a central row of single plates, which are smaller in width than the horny scutes, and are surrounded by paired plates. These are larger in width and shorter in length than the overlying scutes. Peripherally there is a series of plates, horny and bony, the sutures of which do not coincide. In the internal side of the neural plates the vertebrae are attached, while the ribs expand and integrate into the costal plates.

In the plastron all horny scutes are in pairs covering fully covering it. On the contrary, in the bony plates, the presence of a single plate, the entoplastron, is observed between the rest of the paired plates. The entoplastron is placed in the anterior part of the plastron. Posteriorly, the xiphiplastra usually backwards.

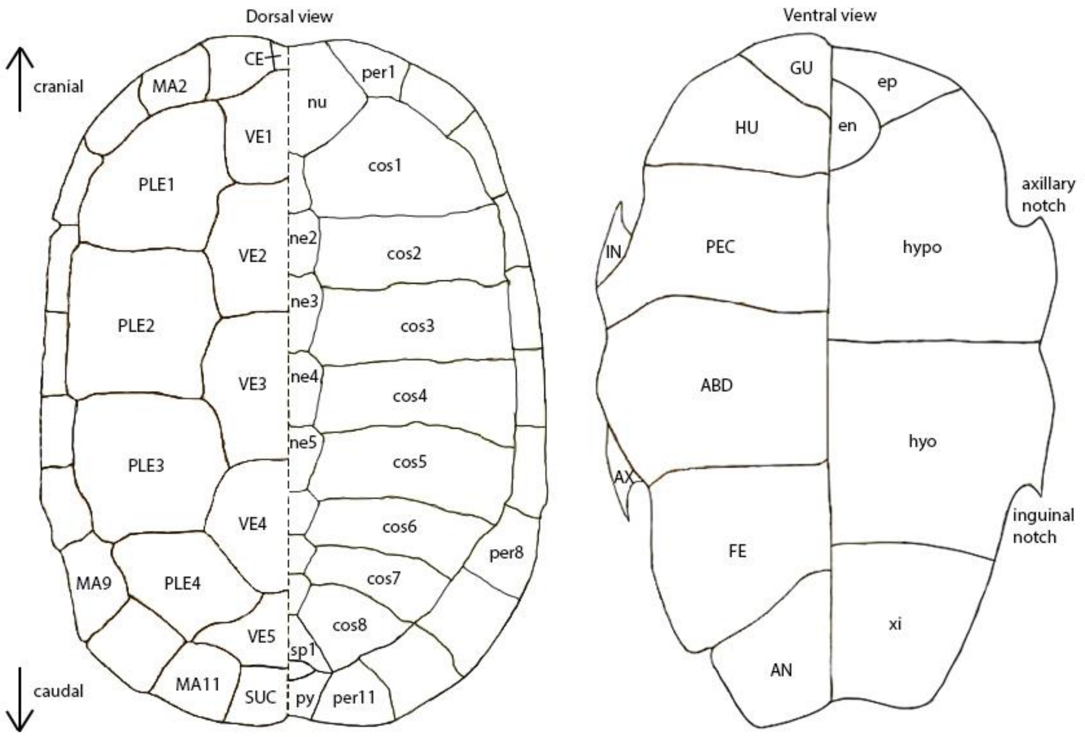

Figure 7: Generalized shape of the carapace (left) and plastron (right) of a turtle. Abbreviations: ABD, abdominal; AN, anal; AX, axillary; CE, cervical; cos, costal; en, entoplastron; ep, epiplastron; FE, femoral; GU, gular; HU, humeral; hyo, hyoplastron; hypo, hypoplastron; IN, inguinal; MA, marginal; ne, neural; nu, nuchal; PEC, pectoral; per, peripheral; PLE, pleural; py, pygal; sp, suprapygal; SUC, supracaudal; VE, vertebral; xi,

Anatomical abbreviations

In the anatomical abbreviations of the tortoises, bony plates are indicated with lowercase letters and horny scutes with uppercase letters. The anatomical abbreviations of the different bones are indicated with lowercase letters. Anatomical abbreviations are as follows: **ABD**, abdominal; **AN**, anal; **as+cal**, astragalocalcaneum; **AX**, axillary; **CE**, cervical; **car**: carpal; **cos**, costal; **en**, entoplastron; **ep**, epiplastron; **FE**, femoral; **fe**, femur; **fi**, fibula; **GU**, gular; **HU**, humeral; **hyo**, hyoplastron; **hypo**, hypoplastron; **IN**, inguinal; **MA**, marginal; **mc**, metacarpal; **mt**, metatarsal; **ne**, neural; **nu**, nuchal; **ost**, osteoderm; **PEC**, pectoral; **per**, peripheral; **PLE**, pleural; **ph**, phalanx; **py**, pygal; **ra**, radius; **sp**, suprapygal; **SUC**, supracaudal; **ul**, ulna; **ung**, ungual; **VE**, vertebral; **xi**, xiphiplastron.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, New York, U.S.A.; **AMPG**, Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, Athens, Greece; **LGPUT**, Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki, Thessaloniki, Greece; **MGL**, Geological Museum of Lausanne, Lausanne, Switzerland; **MN**, European Mammal Neogene biozones; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **NHMW**, Naturhistorisches Museum, Vienna, Austria; **NWS**, Naturmuseum Winterthur, Winterthur, Switzerland; **PIMUZ**, Paläontologische Institut und Museum, Universität Zürich, Zurich, Switzerland; **STUS**, Sala de las Tortugas de la Universidad de Salamanca, Salamanca, Spain; **VM**, Vrisa Museum of Natural History, Lesvos Island.

CHAPTER 2: SYSTEMATIC PALAEONTOLOGY

Order Testudines Batsch, 1788
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
Subfamily Testudininae Batsch, 1788
Tribe Geochelonini Crumly in Swingland and Klemmens, 1989
Genus *Titanochelon* Pérez-García and Vlachos, 2014
Species *Titanochelon bacharidisi* (Vlachos, Tsoukala and Corsini, 2014)

Emended Diagnosis — *Titanochelon bacharidisi* is a member of *Titanochelon* because of the presence of frontals narrower than the prefrontals; a long crista supraoccipitalis; the presence of an elliptical to circular premaxillary pit; two suprapygals; the first surrounding the lenticular second one; the absence of a cervical scute; a convex to flat dorsal lip of the epiplastra; a humero-pectoral sulcus that is perpendicular to the axial plane in the medial region but with a well-developed lateral change of curvature; very short pectoral scutes in the sagittal plane but markedly expanded toward the anterior region, laterally.

Differential Diagnosis — *Titanochelon bacharidisi* is different from the other *Titanochelon* species because of the position of the fossa orbitalis in the midway between the apertura narium externa and the posterior tip of the squamosal; a zygomatic arch that is thick and short; the squamosal processes converging posteriorly toward the midline; the extended ventral emargination, the short gulars contacting the anterior part of the entoplastron, which is covered medially only by humeral scutes and its posterior border coinciding with the humero-pectoral sulcus; the presence of at least one conical, bony, thigh tubercle on each side of the tail. New diagnostic characters, in combination: suprapygal 1 completely embraces suprapygal 2, and contacts the anterolateral sides of the pygal as well (not in *T. bolivari*); the presence of an inguinal scute that is wider than long and contacts the abdominal, marginals 7 and 8, and femoral scutes (not in contact with the femoral scutes in *T. bolivari*).

2.1 The Makrygialos specimens

Material:

Makrygialos, Pieria, Greece (3 individuals):
Individual LGPUT MAP-1, female individual with associated postcranial material. (Figs. 8-9)
Individual LGPUT MAP-2, male individual with associated postcranial material, forelimb, hindlimb, tail vertebrae. (Figs. 10-17)
Individual LGPUT MAP-3, carapace and plastron fragments. (Figs. 18-23)

2.1.1 LGPUT MAP-1

The specimen LGPUT MAP-1 is a partial shell of a tortoise. It preserves most of the right and medial part of the carapace and the plastron (Fig. 8). Although the shell is almost complete no information can be acquired from it in terms of the bony plates and horny scutes morphology (Fig 8A). The plastron is completely flat without the indication of a concavity, so this shell belonged to a female individual (Fig. 8B). Due to the coastal erosion the carapace is very deformed and incomplete, with many holes throughout it. It is filled with lithified sediment. On the side that the carapace and plastron are missing, there are some postcranial elements visible enclosed in the sediment. Only the medial suture that connects the right and left bony plates of the plastron is visible with certainty (Fig. 8B). Based on the preserved material this specimen could probably reach a length of 120 cm.

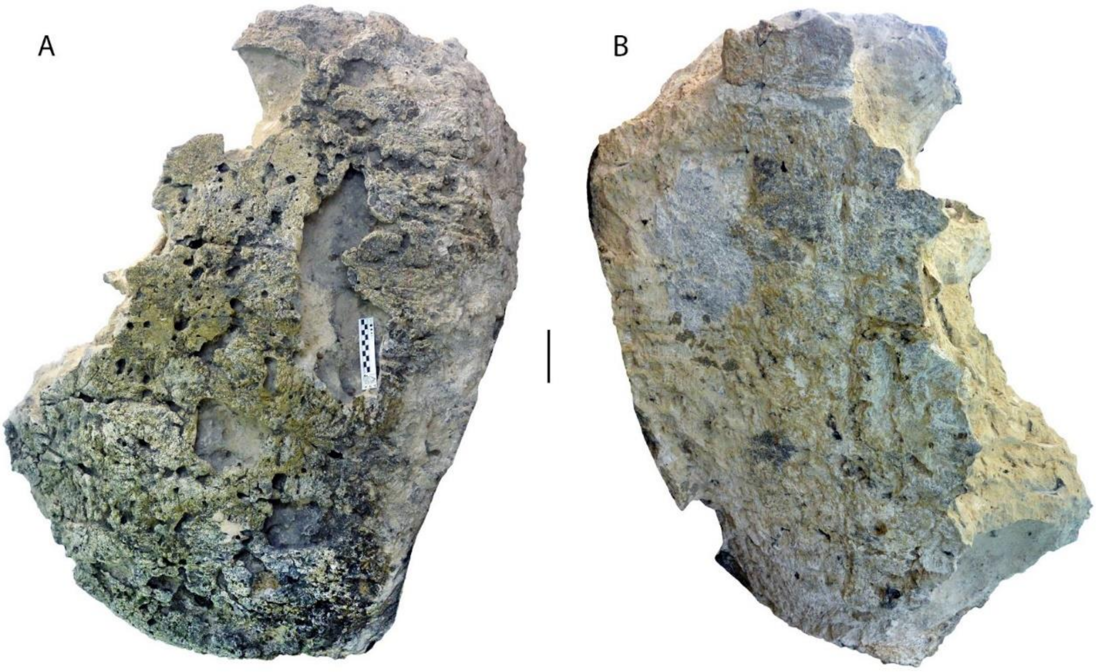

Figure 8: Carapace and plastron of the *Titanochelon bacharidisi* specimen LGPUT MAP-1 from the latest Miocene–Pliocene of Makrygialos, Pieria, Greece. (A) The carapace in dorsal view. (B) The plastron in ventral view. The scale bar equals 10 cm.

Several bones were found enclosed in the sediment inside the shell of the individual. The two that are best preserved and separated from the specimen are a partial femur and another unrecognizable bone fragment (Fig. 9). The femur is long and robust (Fig. 9A). Only the diaphysis is preserved. It is narrow in the middle and wide on the edges. The length of the bone is approximately 23 cm. A small degree of rotation is preserved but the bone is not curved to any direction. The second bone preserved is a fragment of a long bone that has a lateral protrusion that looks like it could be the head of a femur or humerus, but the morphology of the diaphysis prevents us from recognizing it as such (Fig. 9B).

2.1.2 LGPUT MAP-2

The specimen LGPUT MAP-2 is an almost complete shell of a giant tortoise with associated postcranial elements. This individual is much larger than the specimen LGPUT MAP-1 and could probably reach 180 cm in length. It is much better preserved compared to the first specimen but still several holes are noted in the carapace and the plastron. The plastron is almost complete with only the anterior part of the epiplastra and the anterior part of the right hyoplastron missing. The carapace was severely eroded by the sea, and this resulted in the bony plates and horny scutes not being visible. Because of this, the specimen is mounted in such a way that only the plastron is visible (Fig. 10).

Several bones of the appendicular skeleton are preserved in the enclosed sediment within the shell. All of these are found in their recovery position but not articulated, like the continuous series of at least four caudal vertebrae and several vertebrae fragments at the posterior part of the shell, the left forelimb and hindlimb which were later separated during the preservation of the specimen and a partial femur

Figure 9: The two bone fragments from LGPUT MAP-1. (A) The partial femur. (B) The indetermined bone fragment. The scale bar equals 10 cm.

that is still enclosed in the sediment. This indicates that at the time of burial probably all the bones were articulated; this needs to be further corroborated once more bones are prepared from the interior of the sediment. Other smaller bones were found either around the specimen, during the excavation, or enclosed in the sediment, during the conservation, and later individually separated. Those are two caudal vertebrae, several osteoderms and five phalanges. Right below the femur, the vertebra of a monitor lizard has been discovered.

Description

Plastron- Bony plates

The epiplastra are incomplete as their anterior part is not preserved. They are connected posteriorly and medially with the entoplastron and posteriorly and laterally with the hyoplastra. Due to the condition of the plates, we cannot draw any conclusion about their shape and proportions. Because of this it is also not possible to distinguish the existence of an epiplastral lip.

The entoplastron is large, much wider than long, with a rounded and elliptical outline. Its anterior part is much shorter than the posterior. It is connected anteriorly with the epiplastra and posteriorly with the hyoplastra.

The hyoplastra are wider than long. They are connected anteriorly and laterally with epiplastra, anteriorly and medially with the entoplastron and posteriorly with the hypoplastra. The anterior margin is narrower than the posterior. On the anterior and lateral part of the left hyoplastron there is an axillary notch.

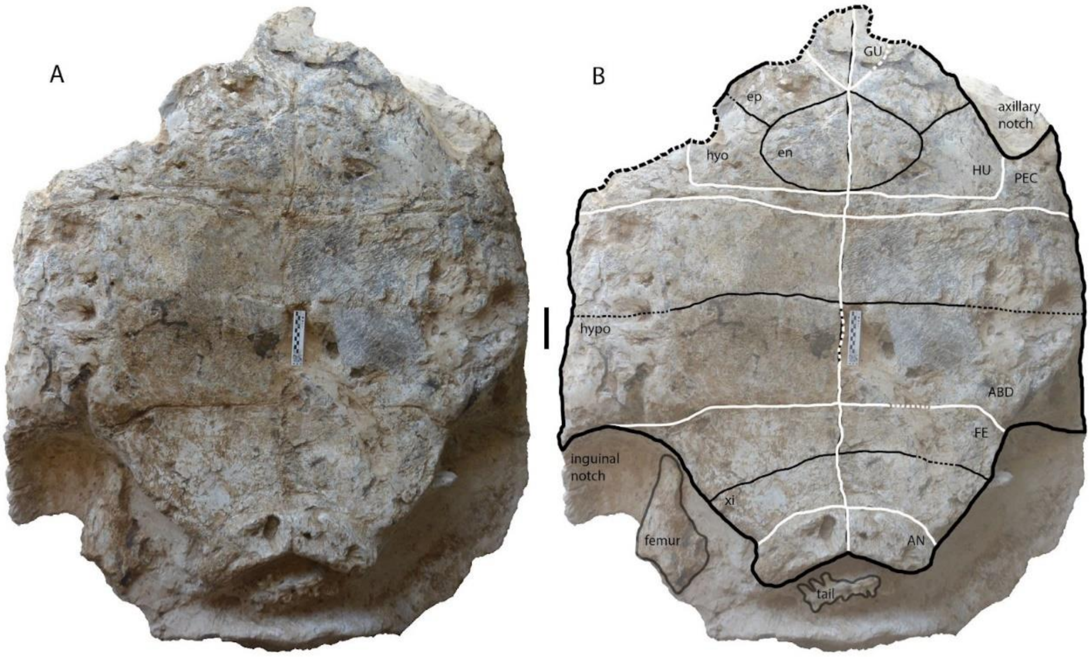

Figure 10: Plastron of the *Titanochelon bacharidisi* specimen LGPUT MAP-2 from the latest Miocene–Pliocene of Makrygialos, Pieria, Greece. (A) The plastron in ventral view. (B) Simplified drawing of the ventral view of the plastron. The scale bar equals 10 cm. Abbreviations: ABD, abdominal; AN, anal; en, entoplastron; ep, epiplastron; FE, femoral; GU, gular; HU, humeral; hyo, hyoplastron; hypo, hypoplastron; PEC, pectoral; xi, xiphiplastron.

The hypoplastra are also wider than long and have almost the same length as the hyoplastra. They are anteriorly connected with the hyoplastra and posteriorly with the xiphiplastra, tightly sutured without evidence of any movable hinge. The anterior margin is twice as wide as the posterior. On the posterior-lateral parts of both hypoplastra there are inguinal notches. A large part of the posterior hypoplastra contributes to the formation of the posterior lobe.

The xiphiplastra are wider than long, representing half of the posterior lobe. They are anteriorly connected with the hypoplastra. Their anterior margin is wider than the posterior. At the posterior-most point, where the two xiphiplastra are connected a short, wide and angular anal notch is formed (ca. 135°). In the posterior and lateral part of the xiphiplastra there is a pronounced narrowing in the femoro-anal sulcus.

Horny scutes

The gulars are incomplete and prevent complete conclusions about their shape and proportions. They are connected posteriorly with the humerals. The gularo-humeral sulci form a right angle. The gulars cover almost 1/3 of the epiplastra and they contact the anterior margin of the entoplastron without overlapping it. It is not possible to confirm the existence of a gular pocket because of the sediment that fills the specimen.

The humerals are wider than long, and their medial length was probably larger than that of the gulars. They are connected anteriorly with the gulars and posteriorly with the pectorals. Their anterior margin is narrower than the posterior. The humerals cover the entire entoplastron, the posterior parts of the epiplastra and the anterior parts of the hyoplastra.

The pectorals are quite short, much shorter than the one-third of the medial length of the hyoplastra and covering only their posterior-most part. They are anteriorly connected with the humerals and posteriorly with the abdominals. Their anterior margin is narrower than the posterior. The humero-pectoral sulcus is mostly straight, with a strongly developed change of curvature upwards and laterally and contacts the posterior margin of the entoplastron without overlapping it.

The abdominals are the largest horny scutes of the plastron and are wider than long. They are connected anteriorly with the pectorals and posteriorly with the femorals. Their anterior margin is wider than the posterior. The pectoro-abdominal sulcus is almost straight throughout its length. The abdomino-femoral sulcus is straight medially but becomes more curved downwards and laterally.

The femorals are connected anteriorly with the abdominals and posteriorly with the anals. They are wider than long, and their anterior margin is wider than the posterior.

The anals are wider than long. They are anteriorly connected with the femorals. Their anterior margin is almost the same width as the posterior. They are much shorter medially compared to the femorals. The femoro-anal sulcus is gently rounded. The part of the xiphiplastra that is covered by the anal scutes is thickened.

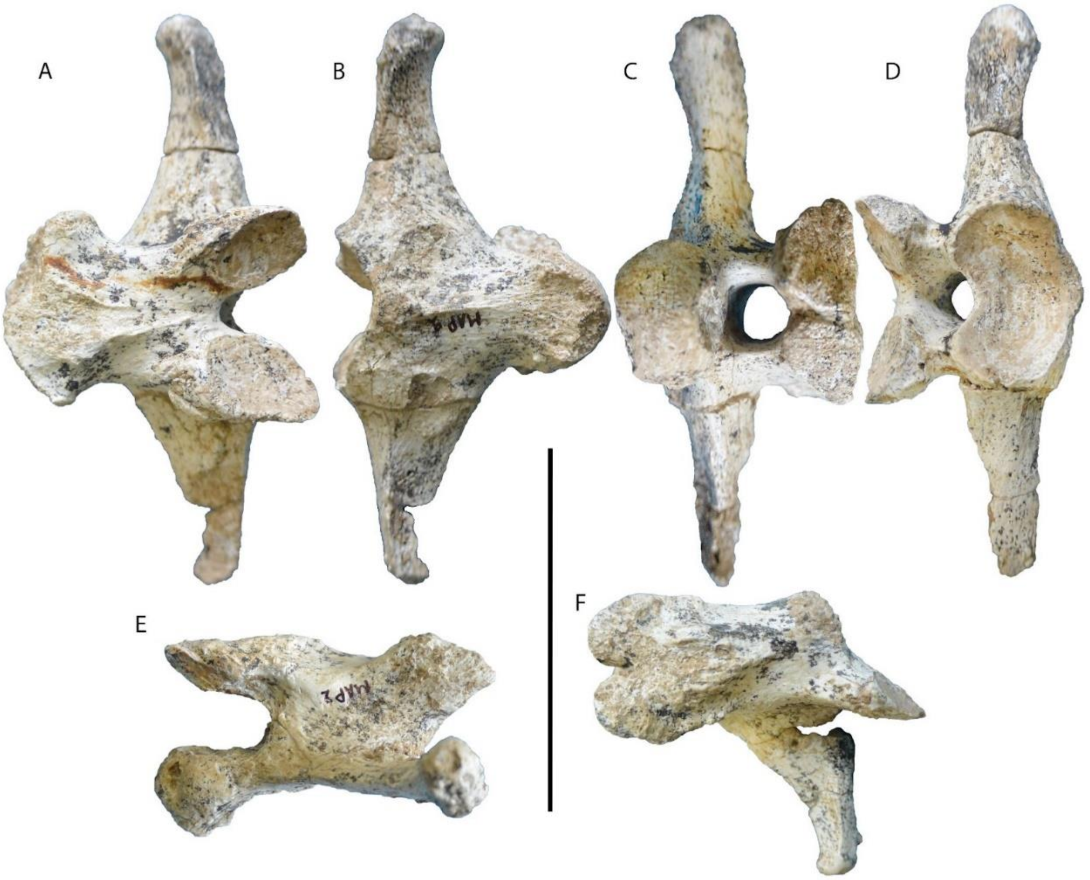

Figure 11: Caudal vertebrae of the specimen LGPUT MAP-2. Complete caudal vertebra in (A) ventral, (B) dorsal, (C) posterior and (D) anterior views. Partial caudal vertebra in (E) lateral and (F) ventral view. The scale bar equals 10 cm.

The anterior lobe was probably slightly longer than the posterior but because it is not well preserved, we cannot be sure. The posterior lobe is slightly wider than the anterior. There is no movable hinge, its existence being a character standard for the *Testudo s.s.* lineage, between the hypoplastra and xiphiplastra.

The plastron is longer than wide and has a strong concavity that affects the posterior part of the entoplastron, the hyoplastra, the hypoplastra and the xiphiplastra, suggesting that it belonged to a male individual. The presence of strong, thick xiphiplastral extremities with rounded tips also corroborates this assessment. The sutures between the bony plates are fully ossified suggesting that LGPUT MAP-2 is and adult individual.

The plastral formula, according to the length of each bony plate and horny scute, is hyoplastra ≈ hypoplastra > xiphiplastra > epiplastra > entoplastron. Abdominals > femorals ≈ humerals > gulars > anals > pectorals.

Caudal vertebrae

Two vertebrae of the specimen are preserved separately (Fig. 11A-F). They are both caudal vertebrae and while one is very well preserved the other misses its left transverse process and superior articular process. The morphology of the vertebrae is simple, they are both procoelous, with the cotyle anteriorly being concave and the condyle posteriorly being convex. The neural arches are fused to the body of the vertebrae. The length of the vertebral body of the complete one (Fig. 11A-D) is almost 8 cm while the same measurement on the partial one (Fig. 11E-F) is almost 9 cm. The length of the transverse processes of the first vertebra is almost 6 cm while the length of the left transverse process that is preserved in the second vertebra is almost 5 cm. On the dorsal side, the neural arch contains an anterior convex articular surface. The posterior part contains a double, slightly concave articular surface. A circular vertebral foramen runs throughout the vertebra. The shape and size of both vertebrae reveals the strong structure of the animal’s tail.

Figure 12: Caudal vertebrae of the specimen LGPUT MAP-2 enclosed in the sediment behind the xiphiplastra. The scale bar equals 10 cm.

Four additional vertebrae and several fragments are preserved enclosed in the sediment right behind the xiphiplastra, in near anatomical recovery position (Fig. 12). They are caudal vertebrae that belong to the tail of the individual. They are all shorter than the previously mentioned caudal vertebrae, measuring, from left to right, 4.5 cm, 4.3 cm, 3 cm, and 3 cm, thus they belong further back to the vertebral column of the tail. They are also procoelous and have the same simple vertebra morphology. Several fragments are scattered around the four vertebrae, also enclosed in the sediment, probably belonging to other caudal vertebrae that were not preserved intact.

Forelimb

The left forelimb was found attached at the posterior of the specimen but was later separated during the conservation. It consists of the radius, the ulna, and several carpal bones, metacarpals, an ungual phalanx, osteoderms and several bone fragments that cannot be recognized with certainty but probably belong to carpal elements and osteoderms. None of these bones are articulated with each other and most of them are poorly preserved (Fig, 13A-D).

The radius is almost fully preserved but the lower epiphysis is not clearly observed because it is covered by sediment. It is long and straight, with a narrow diaphysis and wide epiphyses. The length of the bone is approximately 22 cm. The proximal end of the radius that articulates with the distal end of the humerus is almost two times wider than the rest of the bone and is composed of two concave surfaces that are quite eroded. No other characteristics are visible in the diaphysis because of the poor preservation (Fig. 13C-D).

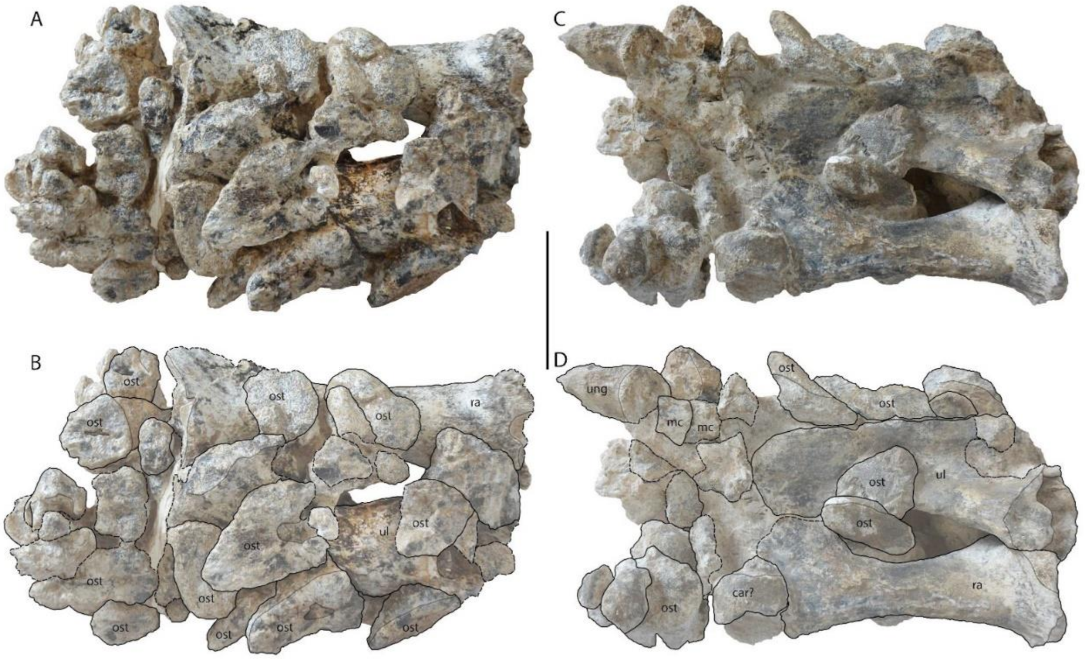

Figure 13: The forelimb of the specimen LGPUT MAP-2. (A) The forelimb in dorsal view. (B) Simplified drawing of the forelimb in dorsal view. (C) The forelimb in ventral view. (D) Simplified drawing of the forelimb in ventral view. The scale bar equals 10 cm. Abbreviations: car, carpal; ost, osteoderm; mc, metacarpal; ra, radius; ul, ulna; ung, ungual.

The ulna is not very well preserved. Only half of the proximal epiphysis is preserved, which is eroded, and the distal epiphysis is missing. The proximal end of the bone is wide and broad. Towards the distal end the bone becomes narrower. The lateral part of the bone has a triangular cross-section. The preserved part of the bone has almost the same length as the radius. The radius and ulna are firmly articulated proximally and distally, leaving in between a tear-shaped fenestra (Fig. 13C-D).

The two metacarpals preserved have a simple discoid morphology being narrower in the center and wider in the edges. The articular surfaces are covered with sediment, so they are not visible (Fig. 13C-D).

The ungual phalanx preserved on the forelimb is long and wide. The articular surface with the phalanx, on the proximal part of the bone and the tip on the distal part are poorly preserved and no characters are visible (Fig. 13C-D).

Several osteoderms are preserved on the forelimb that are quite eroded. Two of them are half-pointed and several others are flattened. They are severely eroded and on several of them holes have been created in the middle. They are preserved in their natural position, on top of the bones of the forelimb (Fig. 13A-D).

Hindlimb

The left hindlimb was also found attached at the posterior of the specimen but was later separated during the conservation. It consists of the distal part of the fibula, the astragalocalcaneum, several metatarsals and phalanges, an ungual phalanx and several bone fragments that cannot be determined with certainty but probably belong to tarsal elements and osteoderms. None of these bones are articulated with each other and most of them are poorly preserved (Fig. 14A-D).

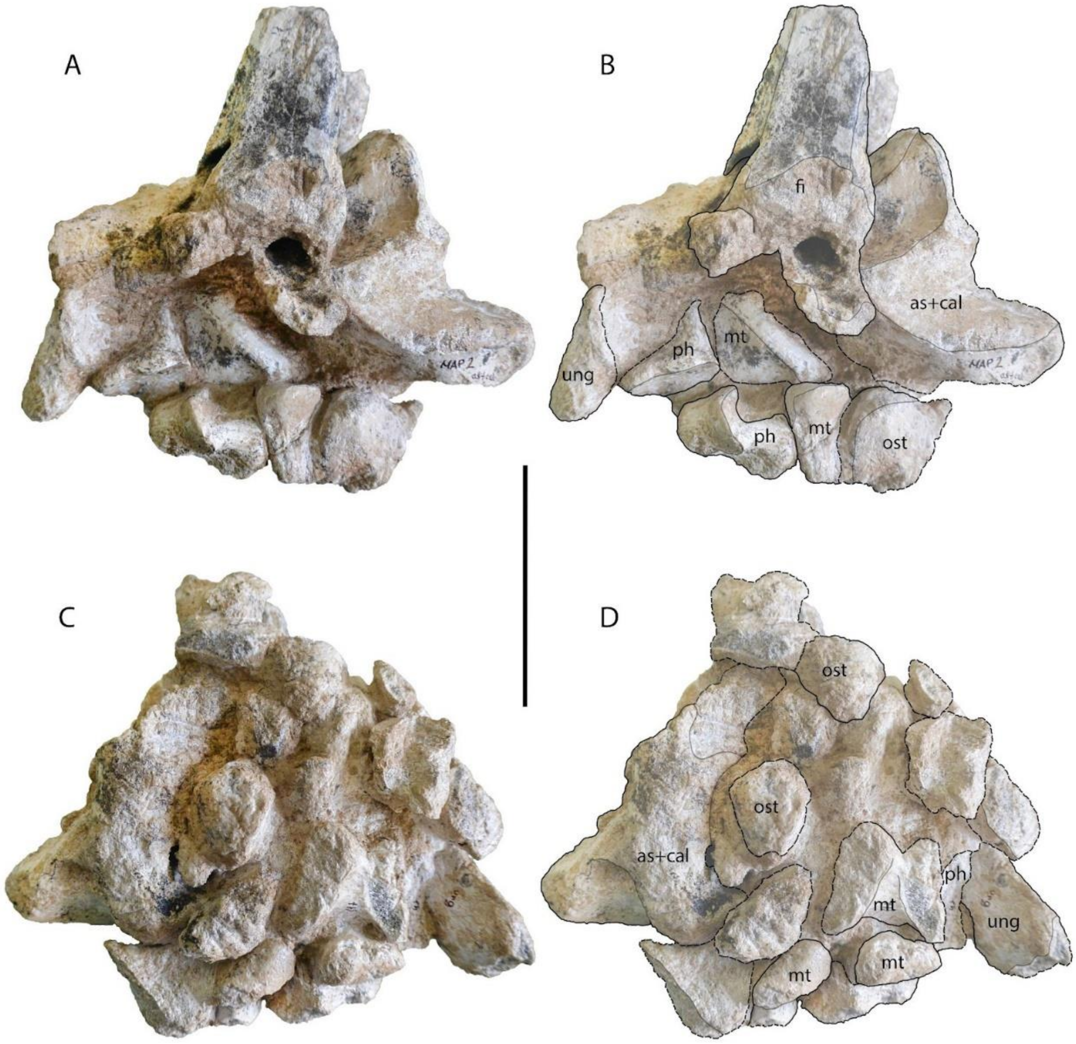

Figure 14: The hindlimb of the specimen LGPUT MAP-2. (A) The hindlimb in ventral view. (B) Simplified drawing of the hindlimb in ventral view. (C) The hindlimb in dorsal view. (D) Simplified drawing of the hindlimb in dorsal view. The scale bar equals 10 cm. Abbreviations: as+cal, astragalocalcaneum; fi, fibula; mt, metatarsal; ost, osteoderm; ph, phalanx; ung, ungual.

The fibula preserves only its distal part. It has a narrow diaphysis and a wider epiphysis. Due to the poor preservation the articular surface for the astragalocalcaneum is not visible (Fig. 14C-D).

The astragalus and calcaneum are fused creating the astragalocalcaneum that is preserved right next to the fibula. The suture of the two bones is not visible on the specimen. Only the dorsal side of the bone is clearly visible with the others being either poorly preserved or covered with sediment and other bone fragments. The bone has a broad in the astragalus part, with a smaller sized extension in the part of the calcaneum. The astragalocalcaneum creates, on the dorsal side, a continuous articular surface that consists of three smaller concave articular surfaces for the articulation of the tibia and the fibula. All three articular surfaces are separated from each other with small crests (Fig. 14A-B).

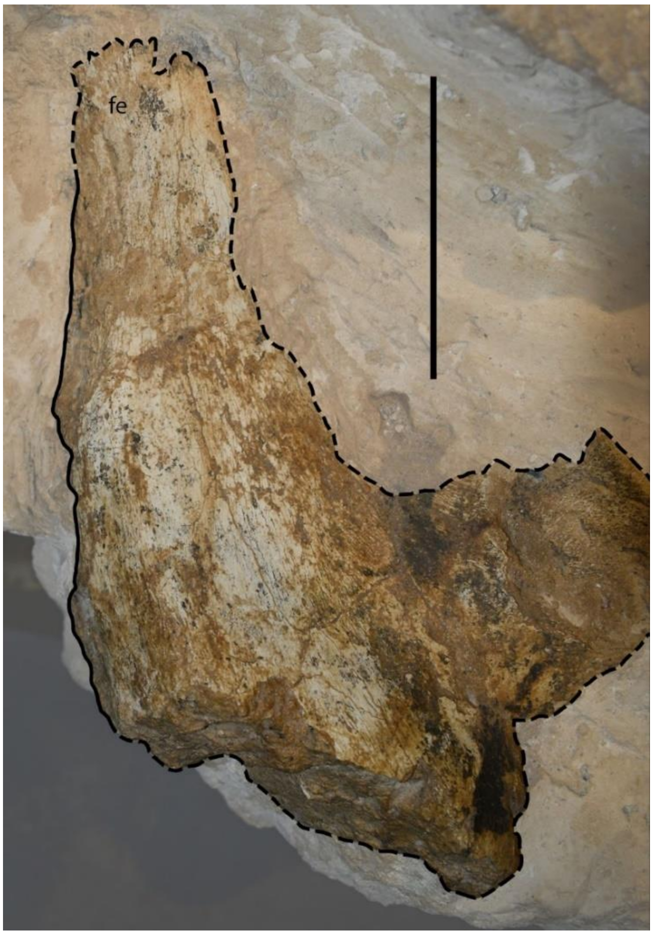

Figure 15: The femur of the specimen LGPUT MAP-2, preserved enclosed in the sediment right next to the posterior lobe. The scale bar equals 10 cm. Abbreviations: fe, femur.

Three metatarsals are preserved in this bone concentration. They are short, with the larger one having a maximum length of approximately 5.5 cm, with a narrow diaphysis and wider epiphyses. The proximal part is a concave articular surface of elliptical shape where the distal tarsal is articulated. The distal part is also an articular surface but this one is convex with a transverse depression where the proximal part of the first phalanx is articulated. The inner side has a shorter length than the outer side, giving an asymmetrical appearance to the bone.

Two phalanges are clearly visible on the posterior limb. Their morphology is simple, being narrow in the center of the bone and wide at the edges. The proximal articular surface has an elliptical shape and is concave. This surface, where the metatarsal bone is articulated, is divided in two smaller parts by a faint crest. The distal articular surface, where the ungual is connected, is convex. The inner side has a slightly shorter length than the outer side, giving an asymmetrical appearance to the bone.

One wide, posterior ungual phalanx is preserved but due to the poor preservation no characteristics from the tip or the articular surface are visible. It is slightly wider than the one preserved on the forelimb.

Three flattened osteoderms are preserved but are very eroded. They are preserved in their natural position, on top of the bones of the hindlimb.

Femur

The right femur is robust and is preserved on the posterior part of the specimen, right next to the plastron (Fig. 15). Only the proximal part is preserved and a part of the diaphysis. The femoral head, as well as the entire proximal epiphysis are severely eroded. The diaphysis, which is also in poor condition, is narrower in the distal part and becomes wider towards the proximal part. Only a small degree of rotation is observed in the diaphysis. The part of the femur preserved has a length of approximately 32 cm. This femur, if complete, could probably be almost twice the size of that of the specimen LGPUT MAP-1.

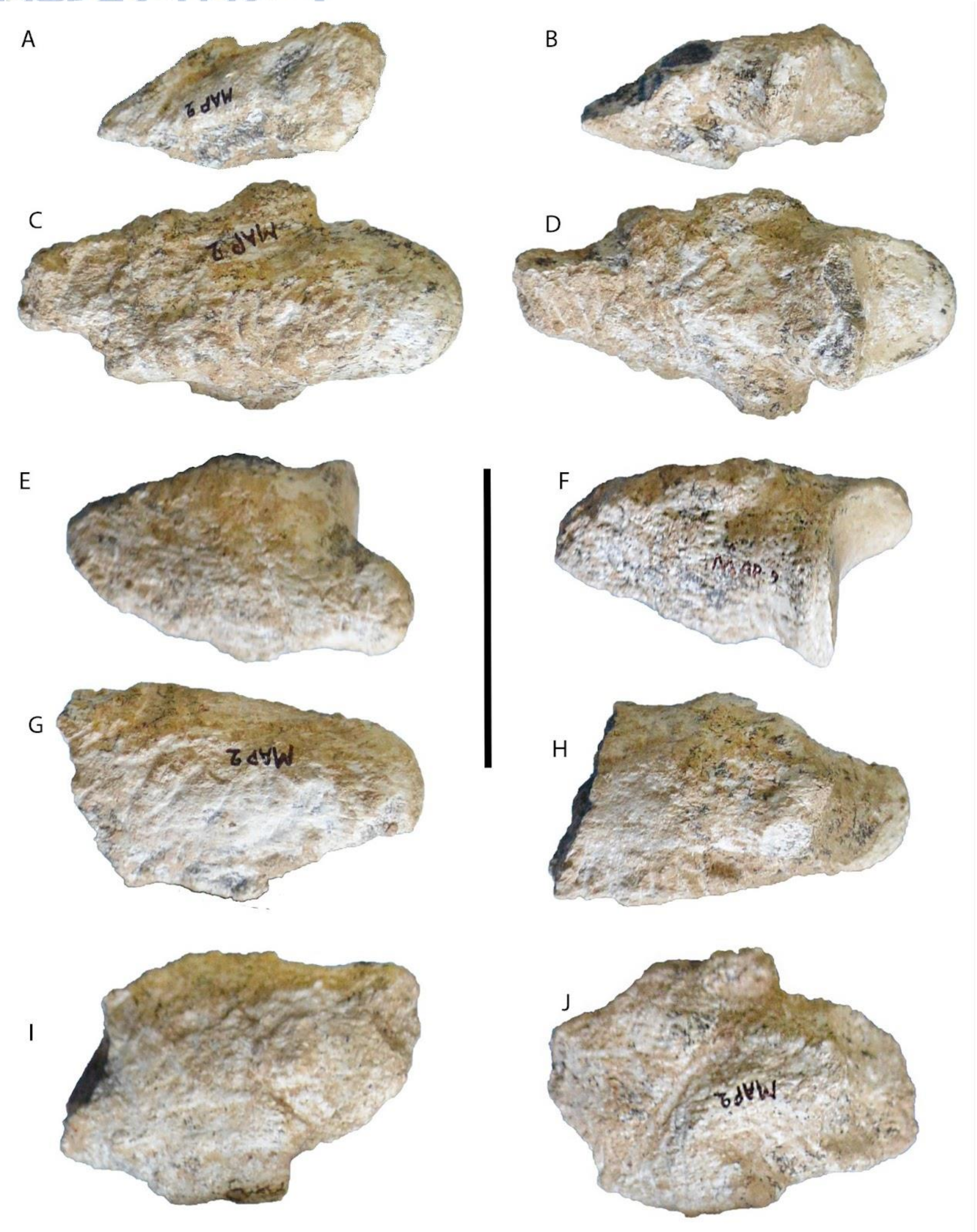

Figure 16: The ungual phalanges of the specimen LGPUT MAP-2. (A-F) The phalanges of the forelimb. (G-J) The phalanges of the hindlimb. The scale bar equals 5 cm.

Phalanges

Five different phalanges are preserved from LGPUT MAP-2 with all of them being ungual phalanges, also named claws (Fig. 16A-J). All of them are elongated, with a concave or pointed proximal and a convex distal end, where the articular surface is. Three of them probably belong to the forelimb because they are narrower (Fig. 16A-F), and the two wider ones belong to the hindlimb (Fig. 16G-J). The smaller one of those belongs most probably to the fifth finger (Fig. 16A-B).

Osteoderms

Several osteoderms of different shapes and sizes are preserved from LGPUT MAP-2 (Fig. 17A-O). They were found around the specimen during the excavation or enclosed in the sediment inside the specimen during the preservation and were later separated. They are twelve in total with one pointed (Fig. 17L-O), two half-pointed (Fig 17A-B) and nine flattened (Fig. 17C-K), with three of them being smaller sized and rounded to oval (Fig. 17C-E). The pointed osteoderm, also named thigh spur or thigh tubercule, is placed behind the femur and when on the animal it is usually accompanied by other smaller rounded osteoderms. The half-pointed and rounded osteoderms may belong either to the forelimb or the hindlimb. The biggest, flat, rounded osteoderm probably covered the outer or inner side of the radius and the ulna. More osteoderms are preserved in their natural position on the forelimb and hindlimb.

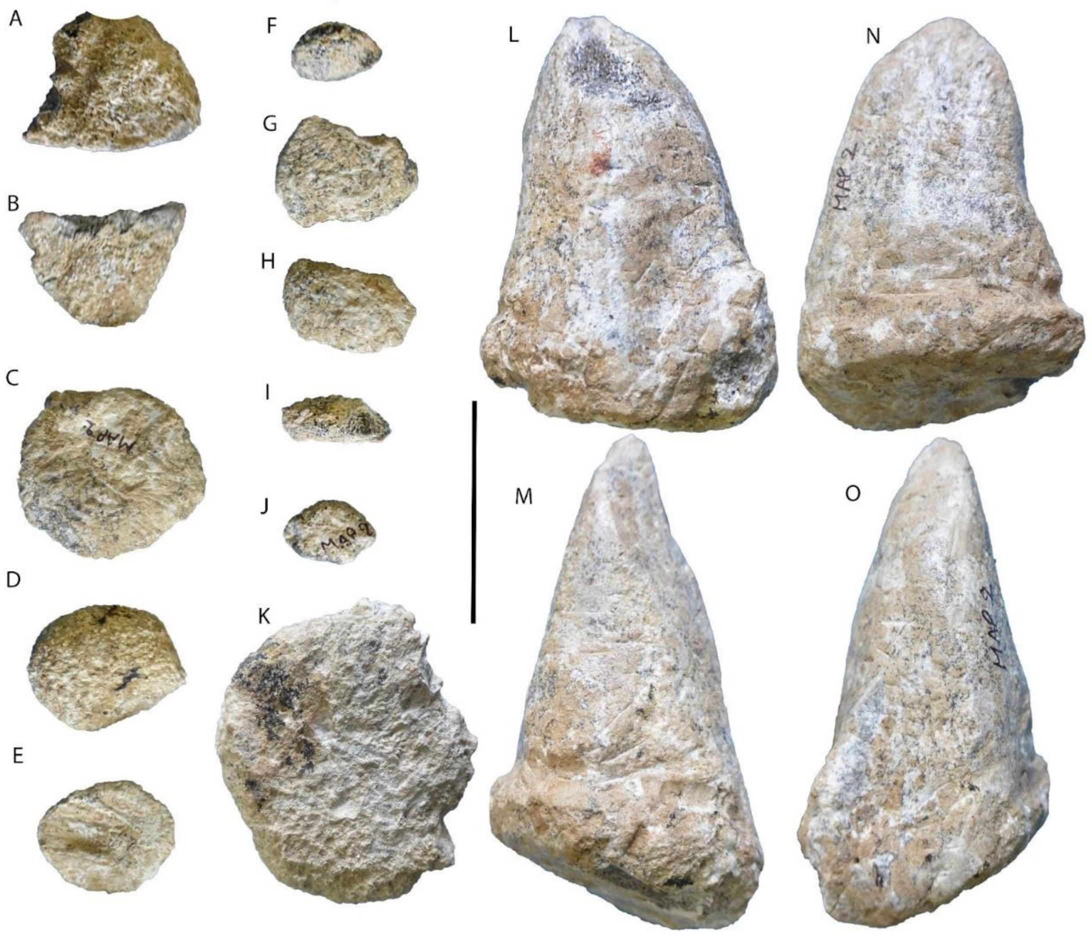

Figure 17: The osteoderms of the specimen LGPUT MAP-2. (A-B) The half pointed osteoderms. (C-K) The rounded to oval, flattened osteoderms. (L-O) The thigh tubercle. The scale bar equals 5 cm.

2.1.3 LGPUT MAP-3

The specimen LGPUT MAP-3 consists of several fragments of the carapace and plastron of a giant tortoise. It is poorly preserved because it was severely eroded but preserves information that the rest of our specimens, even the best-preserved ones, did not provide. Only parts of it were excavated in an attempt to save the specimen from ongoing sea erosion. Only a few of those are able to provide any information about the specimen. The fragments preserved belong both to the carapace and plastron with no appendicular elements discovered so far. Still, some of the identified specimens are quite informative.

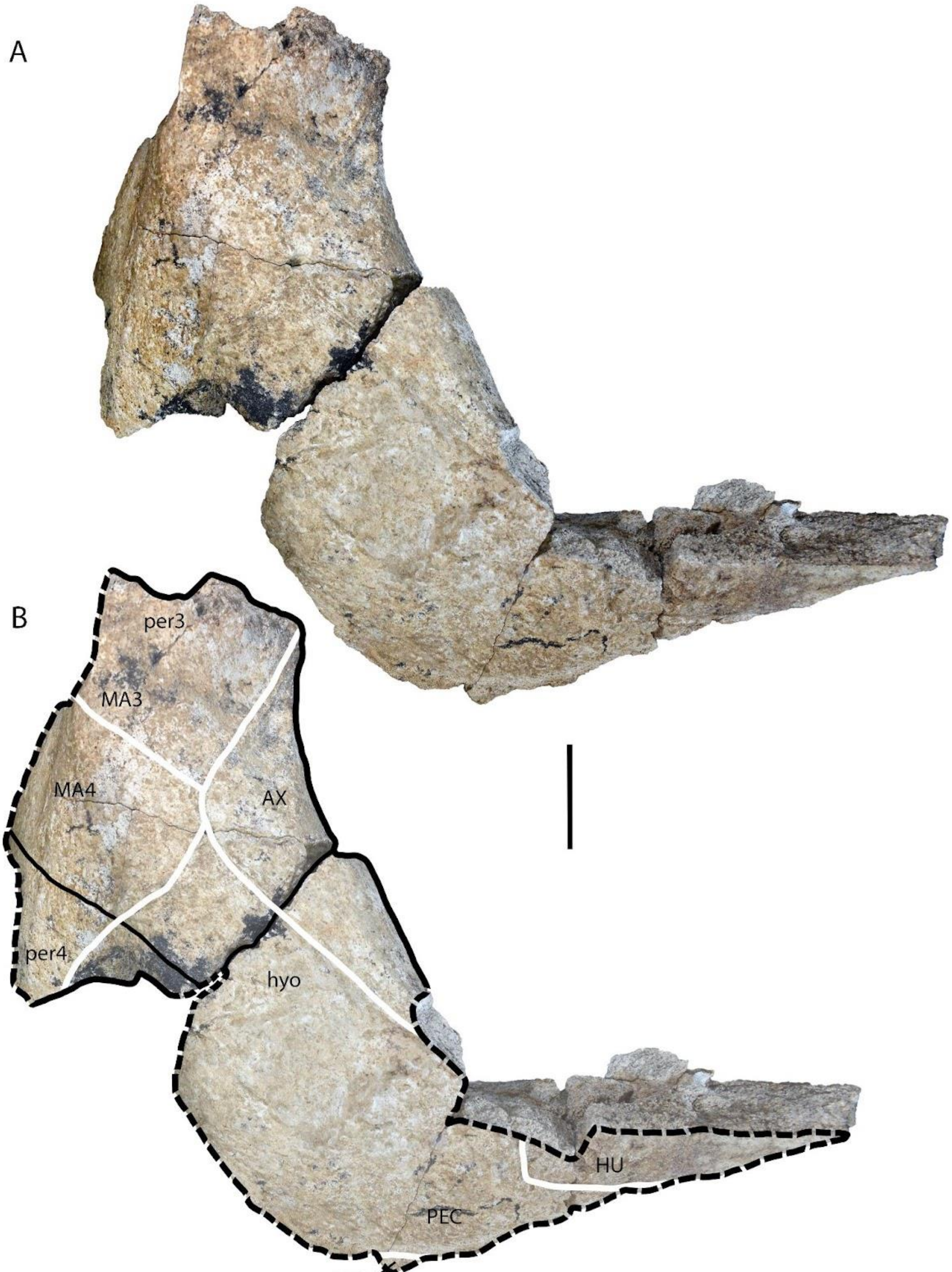

Figure 18: The anterior part of the bridge with a small part of the anterior plastron and a complete axillary scute of the *Titanochelon bacharidisi* specimen LGPUT MAP-3. (A) The bridge and plastron in ventral view. (B) Simplified drawing of the ventral view of the bridge and plastron. The scale bar equals 5 cm. Abbreviations: ABD, abdominal; AX, axillary; HU, humeral; hyo, hyoplastron; MA, marginal; PEC, pectoral; per, peripheral.

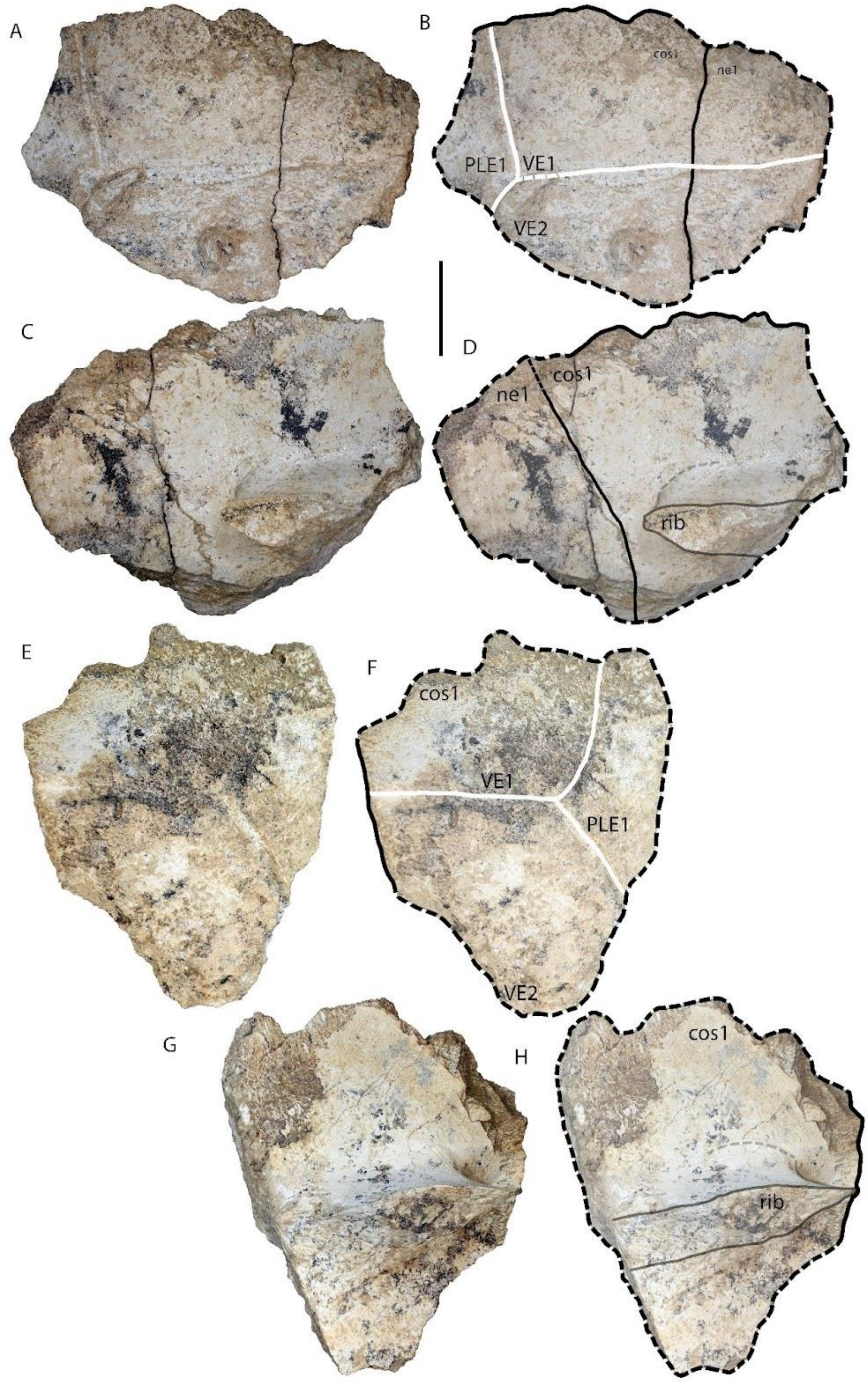

Figure 19: The two costals 1 and neural 1 of the specimen LGPUT MAP-3. (A) The left costal 1 in dorsal view. (B) Simplified drawing of the left costal 1, connected to neural 1 in dorsal view. (C) The left costal 1 and neural 1 in ventral view. (D) Simplified drawing of the left costal 1 in ventral view. (E) The right costal 1 in dorsal view. (F) Simplified drawing of the right costal 1 in dorsal view. (G) The right costal 1 in ventral view. (H) Simplified drawing of the right costal 1 in ventral view. The scale bar equals 5 cm. Abbreviations: cos, costal; ne, neural; PLE, pleural; VE, vertebral.

Description

A large fragment of the anterior part of the right bridge is preserved (Fig. 18A-B). The fragment preserved belongs to the part where the carapace connects to the plastron anteriorly. From the bony plates of the carapacial part peripherals 2 and 3 are preserved, and from the horny scutes marginals 3 and 4. From the bony plates of the plastral part of the fragment, the anterior-most and lateral part of the hyoplastron is preserved, and from the horny scutes almost the whole axillary, a small part of the lateral part of the humeral, the lateral part of the pectoral, and a very small part of the anterior abdominal are preserved. They are not fully preserved so their shapes and proportions are not observable. The axillary scute, which is the only one almost fully preserved, connects with marginals 3 and 4 and the pectoral, and has a triangular shape. The part of the humero-pectoral sulcus preserved has the same morphology as LGPUT MAP-2 where it is straight medially with a strongly developed change of curvature upwards laterally.

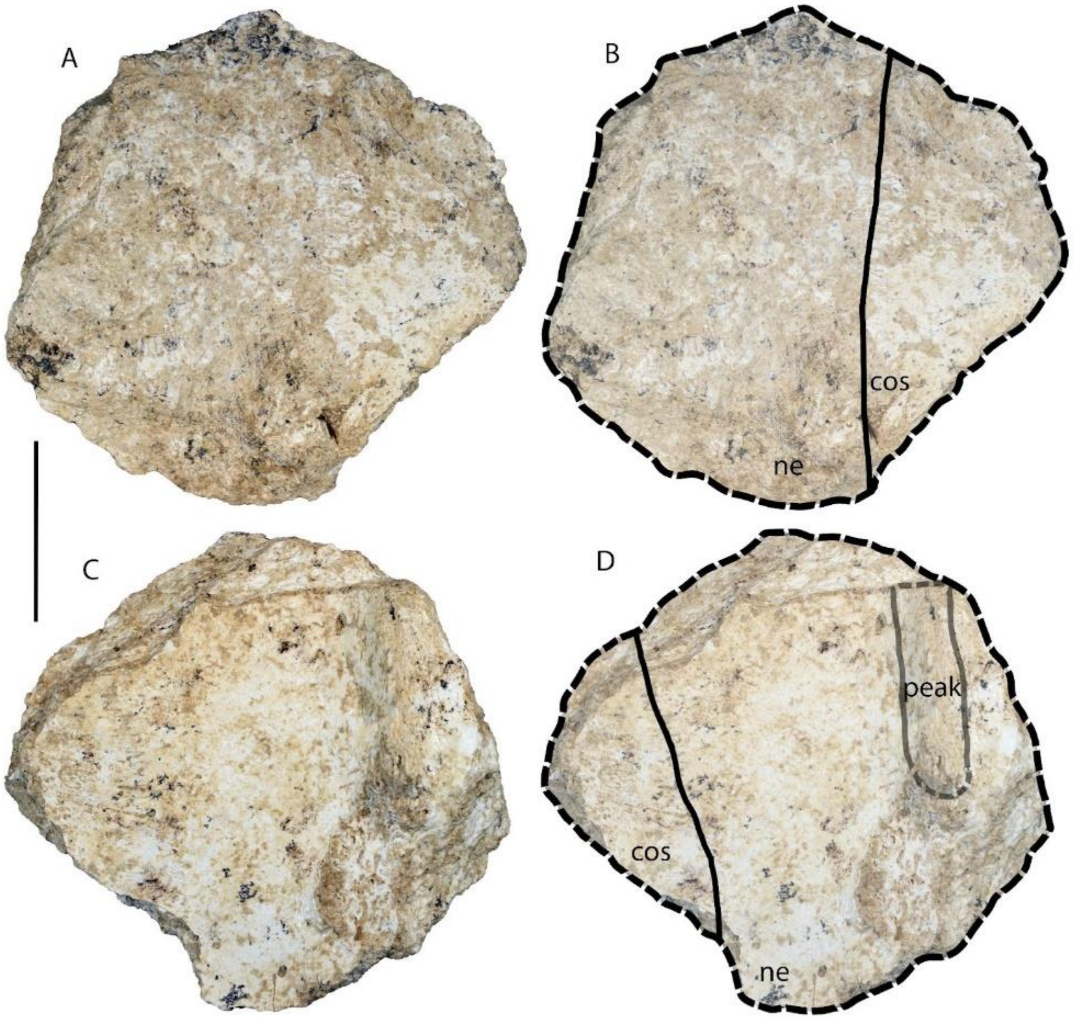

Figure 20: A neural connected with a costal of LGPUT MAP-3. (A) The neural and costal in dorsal view. (B) Simplified drawing of the neural and costal in dorsal view. (C) The neural and costal in ventral view with the peak visible. (D) Simplified drawing of the neural and costal in ventral view. The scale bar equals 5 cm. Abbreviations: cos, costal; ne, neural.

From the carapace two fragments of costals 1 are preserved with one being in contact with neural 1 (Fig. 19A-H). In both fragments vertebrals 1 and 2 and pleural 1 are visible (Fig. 19A-B & E-F). In the visceral sides of both plates, part of the first rib is preserved, which has a significantly larger articular facet (the part that connects with the vertebra) than the rest of the ribs (Fig. 19C-D & G-H). Neural 1 is partially preserved only on the left side and is connected laterally to the left costal. It is crossed by the sulcus between vertebral 1 and vertebral 2 and as the first plate of the neural line, if fully preserved, it would have a rectangular shape. If costals 1 were fully preserved, they would be the longest costals of the carapace. On the visceral side of the right costal the suture between this plate and neural 1 is visible. Another fragment of a neural is preserved with a smaller part of a costal being connected with it (Fig. 20A-D). We recognize that this is a neural because in the visceral side the peak where the vertebra connects to the carapace is preserved (Fig 20C-D).

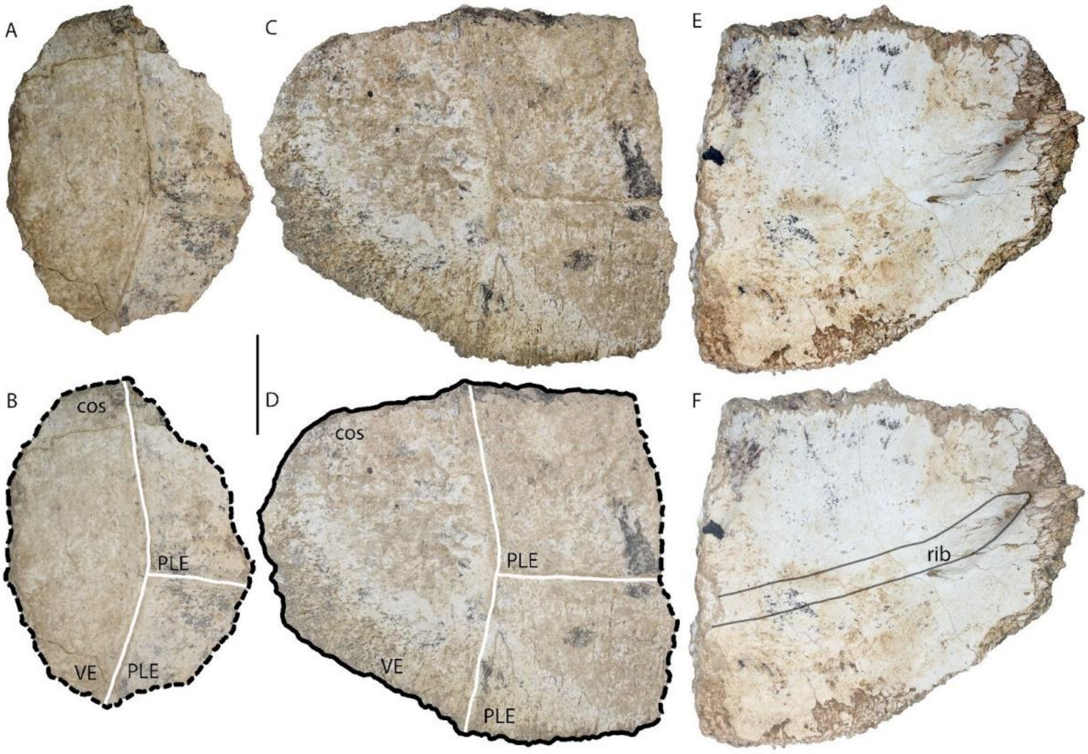

Figure 21: The two costals of the specimen LGPUT MAP-3. (A) A costal in dorsal view crossed by the sulci of the vertebral and the two pleurals. (B) Simplified drawing of the costal in dorsal view. (C) A costal in dorsal view crossed by the sulci of the vertebral and the two pleurals. (D) Simplified drawing of the costal in dorsal view. (E) The costal in ventral view with the rib visible. (F) Simplified drawing of the costal in ventral view. The scale bar equals 5 cm. Abbreviations: cos, costal; PLE, pleural; VE, vertebral.

There are other fragments preserved from the carapace that can be recognized only to a general degree. Three other costal fragments are preserved (Figs. 21A-F, 22A-D). In two of them the rib is visible in the visceral side (Figs. 21E-F, 22C-D). Two fragments are crossed by the sulci of a vertebral and two pleurals (Fig. 21A-D) and the other one only by a sulcus between a vertebral and pleural (Fig. 22A-B). One fragment is medially short and becomes longer laterally (Fig. 21C-D). This fragment probably belongs to costal 2, 4, or 6 as the shape resembles the typical morphology of the costals of Testudinidae where they correspond to the alternating pattern of the neurals. Lastly, a fragment from the bridge area is preserved (Fig. 22E-F). On this fragment two peripherals, two marginals and most probably part of the abdominal, as it is the largest horny scute of the plastron and covers the largest part of the bridge on the side of the plastron, are visible.

From the plastron part of the left side of the anterior lobe is preserved (Fig. 23A-B). From the bony plates a big part of the entoplastron, the posterior-most part of the left epiplastron and the anterior-most part of the left hyoplastron are preserved. No sulcus between any other horny scutes is preserved but this part of the plastron is technically covered by the humerals.

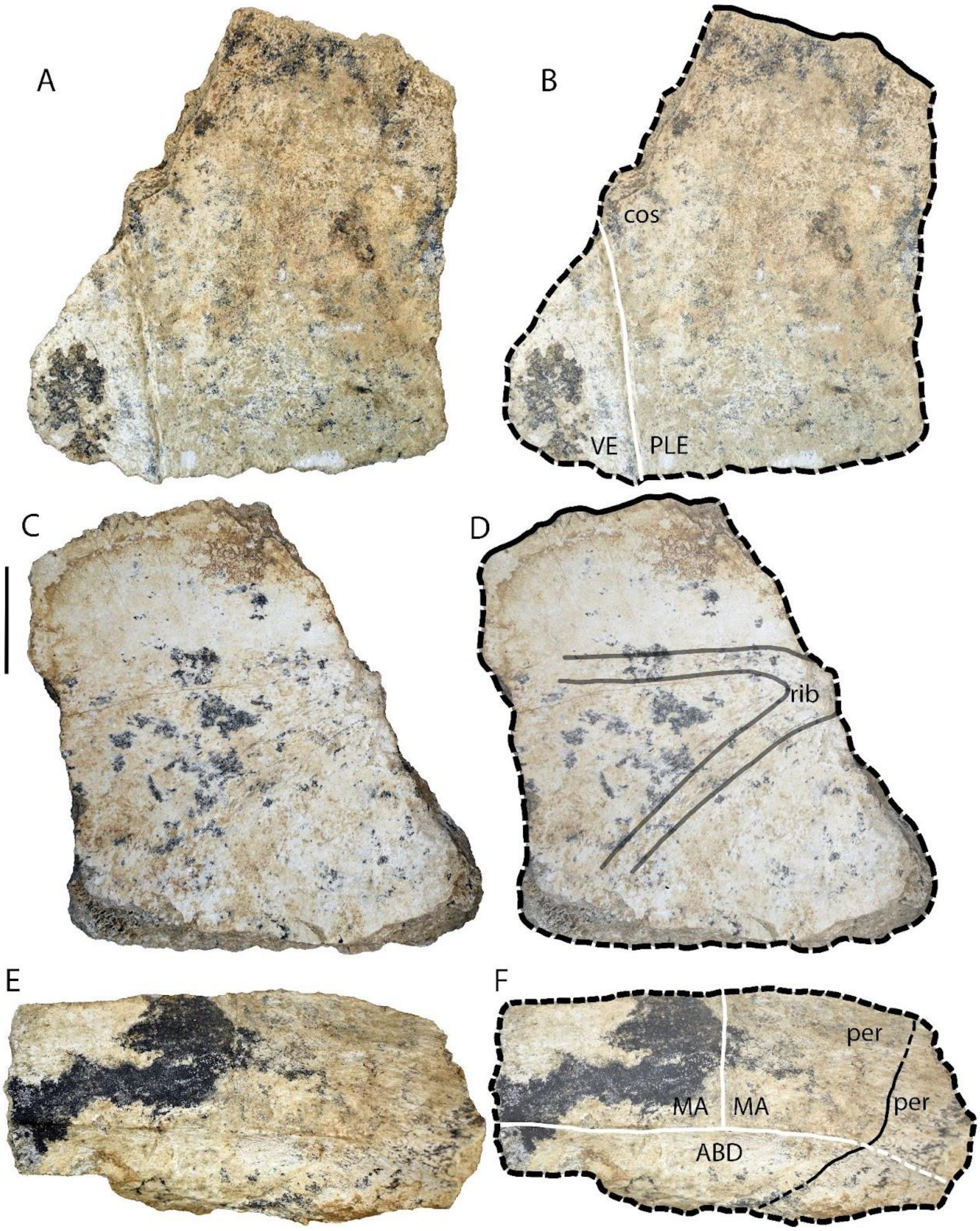

Figure 22: The costal and the part of the bridge of the specimen LGPUT MAP-3. (A) A costal in dorsal view crossed by the sulcus between the vertebral and pleural. (B) Simplified drawing of the costal in dorsal view. (C) The costal in ventral view with the rib visible. (D) Simplified drawing of the costal in ventral view. (E) Part of the bridge area crossed by the sulci of the marginals and the abdominal. (F) Simplified drawing of the part of the bridge area. The scale bar equals 5 cm. Abbreviations: ABD, abdominal; cos, costal; MA, marginal; per, peripheral; PLE, pleural; VE, vertebral.

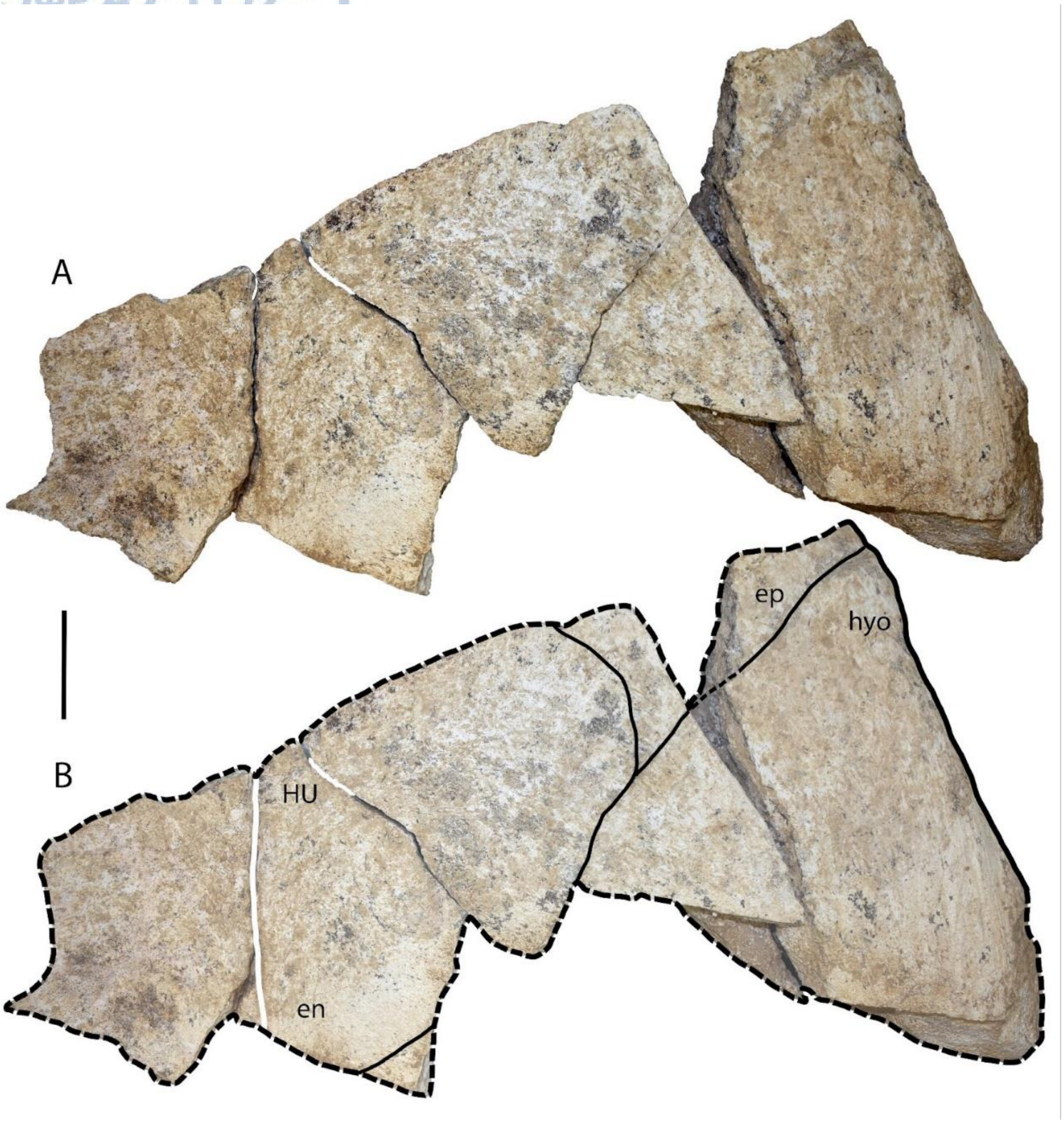

Figure 23: Part of the plastron of the specimen LGPUT MAP-3. (A) The plastron in ventral view with parts of the entoplastron, epiplastron and hyoplastron preserved. (B) Simplified drawing of the plastron in ventral view. The scale bar equals 5 cm. Abbreviations: en, entoplastron; ep, epiplastron; HU, humeral; hyo, hyoplastron.

2.2 The Agiannis specimens

Material:

Agiannis, Pieria, Greece (2 individuals):
Individual LGPUT AG-1, male individual, carapace and plastron fragments. (Figs. 24-26)
Individual LGPUT AG-2, male individual, partial carapace, and plastron with associated fragments. (Figs. 27-33)

2.2.1 LGPUT AG-1

The specimen LGPUT AG-1 consists of fragments from the carapace and plastron of a giant tortoise. The largest fragment and most important preserved from this specimen are the left medial and posterior-most part of the xiphiplastra with a small part from the hypoplastron attached to it. From the horny scutes, the femorals that cover the xiphiplastra and the anals are preserved. Just from the size of the posterior part of the xiphiplastra we can assume that this individual would be way larger than the individual MAP-1 and it could potentially be larger than MAP-2. Furthermore, several fragments of neural plates preserved are worth mentioning, including an almost complete octagonal neural plate.

Description

Carapace

Six fragments that we can attribute to neural plates are preserved from this specimen (Figs. 24-25A-L). We recognize them as neurals firstly because of their shape and secondly because most of them preserve, in their visceral side, the peak where the vertebra connects to the plate. The most important one is not a fragment but an almost complete octagonal neural (Fig. 24). In the ventral side of the plate the peak where the vertebra connects to it is visible. It is not crossed by any horny scutes. The anterior and posterior margins have almost the same width and the lateral margins are almost parallel to each other. This morphology is usually observed in the fourth plate of the neural series, so we recognize this plate as a neural 4. There is another fragment that most probably belongs to an octagonal neural (Fig. 25A-B), so with neural 2 being the only other octagonal neural, we recognize it as such. There is also a fragment that probably belongs to a hexagonal one (Fig. 25C-D). The other three probably belong to quadrangular or even hexagonal neurals, so neural 1, 3, and 5 to 8 (Fig. 25E-L). One of them is crossed by a sulcus of two horny scutes so it could be neural 1, 2, 5 or 8 (Fig. 25E-F).

Plastron

The hypoplastron contacts the xiphiplastron posteriorly but the part that is preserved is so small that no other information can be acquired from it (Fig. 26A-B). From the part of the xiphiplastra that is preserved we can understand that they are wider than long but no other conclusion about the size and proportions can be drawn. At the posterior-most point, where the two xiphiplastra are connected a short, wide and slightly angular anal notch is formed (ca. 150°). The angle between the xiphiplastra is not that sharp making the posterior margin of the plastron look like it creates a concave line. In the posterior and lateral part of the xiphiplastra there is a pronounced narrowing in the femoro-anal sulcus.

The posterior part of femorals that are preserved cover the hypoplastron and the xiphiplastra. They are connected with the anals posteriorly. Due to the poor preservation, we cannot draw any more conclusion about the proportions and shape of these scutes. The anals are short and wide. They cover the posterior part of the xiphiplastra, and they are connected anteriorly with the femorals. The sulcus between the femorals and the anals creates a line that is almost perpendicular to the axial plane and slightly concave. At the point where this sulcus meets the margin of the plastron a transversal narrowing is created.

The part of the plastron preserved is too small to allow us to observe any degree of curvature. The part of the xiphiplastra covered by the anals, however, are thickened. This character is an indication that the specimen LGPUT AG-1 represents a male individual.

Other fragments of the carapace and plastron are also preserved but only a few provide any kind of information (Fig. 27A-J). However, those fragments cannot be recognized because they are only crossed by a suture of horny scutes, and their shape is not indicative of what they could be.

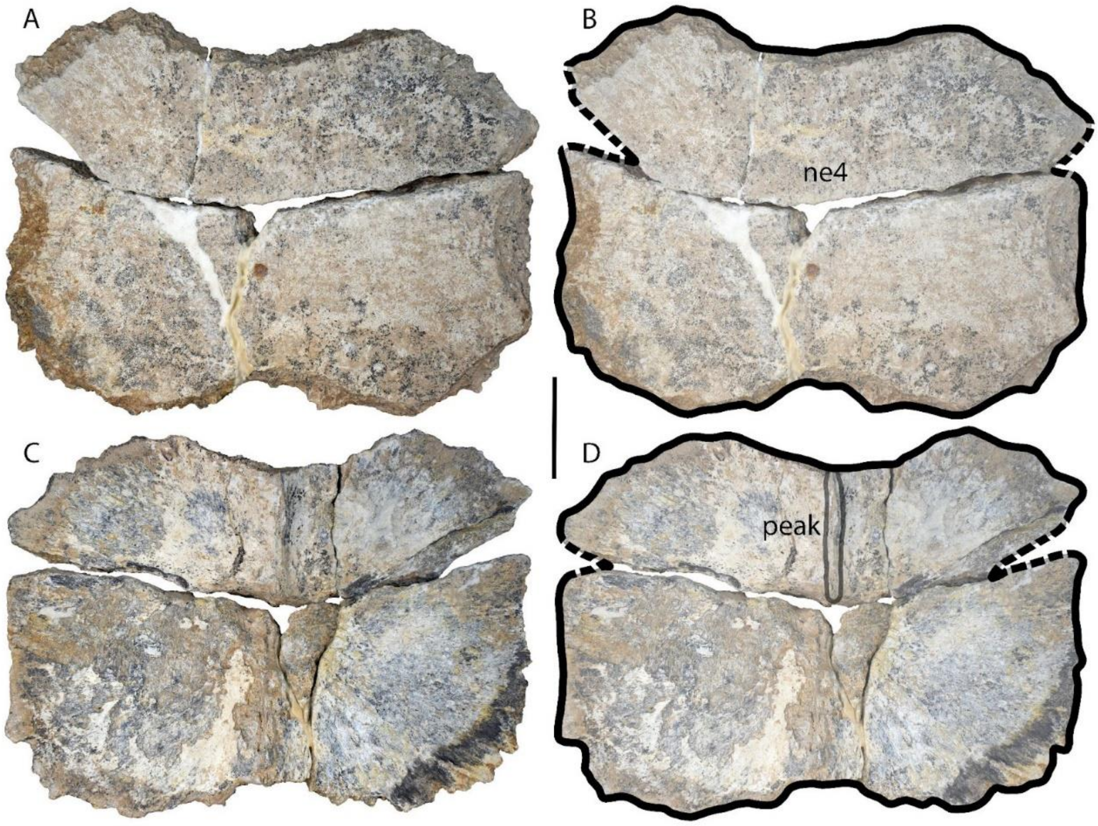

Figure 24: The octagonal neural of the specimen LGPUT AG-1. (A) The neural in dorsal view. (B) Simplified drawing of the neural in dorsal view. (C) The neural in ventral view with the peak that connects to the vertebra preserved. (D) Simplified drawing of the neural in ventral view. The scale bar equals 5 cm. Abbreviations: ne, neural.

2.2.2 LGPUT AG-2

The specimen LGPUT AG-2 is a partial shell of a giant tortoise (Fig. 28-30). It is smaller than LGPUT MAP-1 and LGPUT MAP-2 but probably surpassed 120 cm in length. The parts of the shell that are preserved are the posterior part of the carapace (Figs. 28-29), including the posterior-most part of the bridge (Fig. 30C-D) and the medial and posterior part of the plastron (Fig. 29A-B). The bony plates preserved on the carapace are the posterior part of peripheral 6, peripherals 7 to 11, costals 5 to 8 without their medial parts, the posterior part of suprapygal 1, suprapygal 2 and the pygal. The horny scutes preserved are the posterior part of marginal 7, marginals 8 to 11, pleurals 3 and 4 without their medial part, the posterior-most left parts of vertebral 4 and vertebral 5. The bony plates preserved on the plastron are the posterior part the left hyoplastron and the posterior medial part of the right hyoplastron, the whole left hypoplastron and the medial part of the right hypoplastron and the xiphiplastra. The horny scutes preserved are the left abdominal, without the anterior-most part, the medial part of the right abdominal, the femorals, the anals and a small sized scute right next to the femorals that is called inguinal. Except for the bigger fragments of the shell, other smaller fragments of the carapace and plastron are also preserved including fragments of neural plates.

<u>Description</u>

Carapace- Bony plates

Costal 5 is probably wider than long (Fig. 28). Due to the condition of the plate, we cannot draw any more conclusion about their shape and proportions. It is connected posteriorly with costal 6 and laterally with peripheral 7. Costal 6 is wider than long. It is connected with costal 5 anteriorly, costal 7 posteriorly and peripheral 8 and 9 laterally. Costal 7 is wider than long. It is connected anteriorly with costal 6, posteriorly with costal 8 and laterally with peripherals 9 and 10. Costal 8 is probably wider than long. Because only the anterior part of the plate is preserved, we cannot draw any more conclusions about its proportions. It is connected anteriorly with coastal 7, posteriorly with suprapygal 2 and laterally with peripherals 10 and 11. Because of the poor preservation of the carapace we cannot observe with certainty the typical alternating pattern of the costals, a characteristic of testudinids.

Peripheral 6 is connected posteriorly with peripheral 7. Due to the condition of the plate, we cannot draw any conclusion about their shape and proportions. Peripheral 7 is wider than long. We cannot compare the proportions of the anterior and posterior margins because the anterior and medial part of the plate are missing. It is anteriorly connected with peripheral 6, posteriorly with peripheral 8 and medially with costal 5. Peripheral 8 is wider than long. The anterior margin has the same width as the posterior. It is connected anteriorly with peripheral 7, posteriorly with peripheral 9 and medially with costal 6. Peripheral 9 is wider than long. The anterior margin is wider than the posterior. It is connected anteriorly with peripheral 8, posteriorly with peripheral 10 and medially with costals 6 and 7. Peripheral 10 is slightly wider than long. The anterior margin is as wide as the posterior. It is connected anteriorly with peripheral 9, posteriorly with peripheral 11 and medially with costals 7 and 8. Peripheral 11 is longer than wide. The anterior margin is as wide as the posterior. It is connected anteriorly with peripheral 10, posteriorly with the pygal and medially with costal 8 and suprapygal 2.

From suprapygal 1, only the posterior part is preserved (Fig. 29). It is connected posteriorly with the suprapygal 2 and with the lateral anterior sides of the pygal, with their suture creating a concave line, and laterally with costals 8. As such, suprapygal 1 fully embraces suprapygal 2, which is much narrower than suprapygal 1. Suprapygal 2 is wider than long and has a lenticular shape. It is connected anteriorly with suprapygal 1 and posteriorly with the pygal. It is crossed by the sulcus between vertebral 5 and the supracaudal that create a wavy line.

The pygal is longer than wide and has an almost trapezoid shape (Fig. 29). The anterior margin, which is convex, is wider than the posterior. It is connected anteriorly with suprapygal 2, anteriorly and laterally with the suprapygal 1, and laterally with peripherals 11.

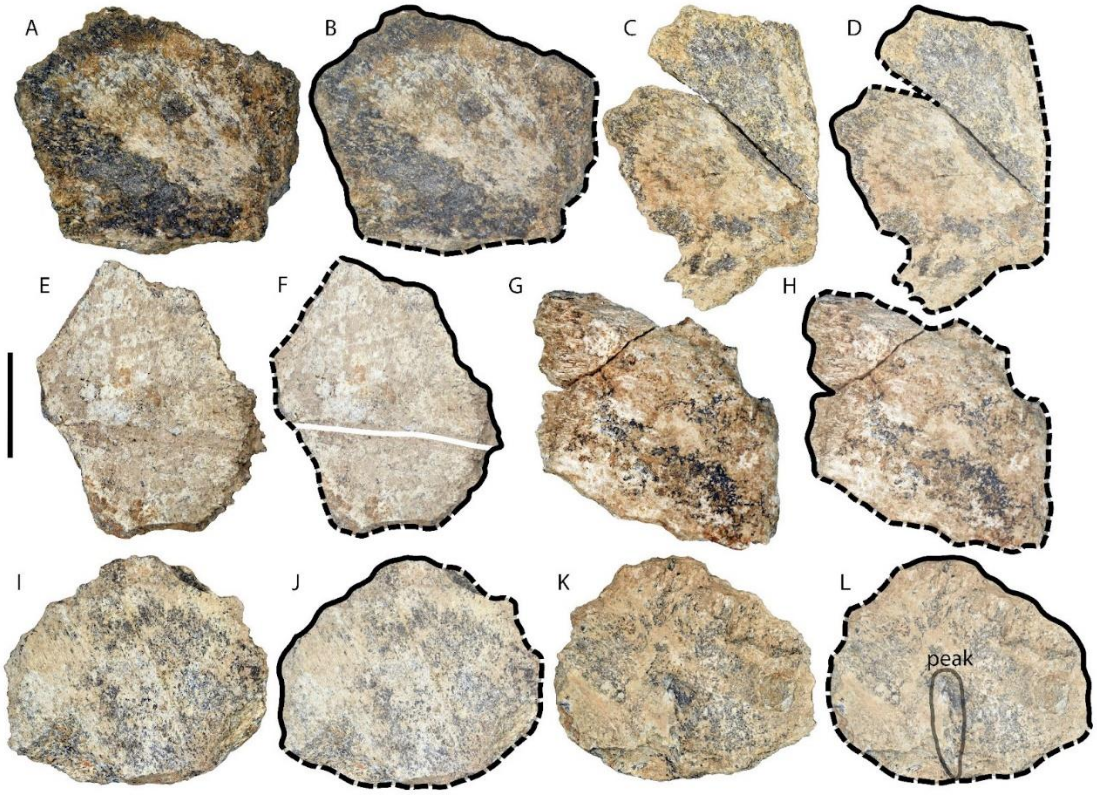

Figure 25: Neurals of the specimen LGPUT AG-1. (A) The possible octagonal neural in dorsal view. (B) Simplified drawing of the neural in dorsal view. (C) The possible octagonal or hexagonal neural in dorsal view. (D) Simplified drawing of the neural in dorsal view. (E) The neural crossed by a sulcus in dorsal view. (F) Simplified drawing of the neural in dorsal view. (G) The possible quadrangular neural in dorsal view. (H) Simplified drawing of the neural in dorsal view. (I) The possible quadrangular of hexagonal neural in dorsal view. (J) Simplified drawing of the neural in dorsal view. (K) The previously mentioned neural in ventral view with the peak that connects to the vertebra visible. (L) Simplified drawing of the neural in dorsal view. The scale bar equals 5 cm.

Horny scutes

From vertebral 4, only the lateral posterior parts are preserved and thus it is not possible to draw any conclusion about its size and proportions. It connects posteriorly to vertebral 5 and laterally to pleural 4. From vertebral 5, the medial part is missing. The scute is wider than long with the anterior margin narrower than the posterior. It is connected anteriorly with vertebral 4, posteriorly with the supracaudal and peripherals 11, and laterally with pleural 4.

Figure 26: Part of the posterior lobe of the plastron, mainly the xiphiplastron, of the specimen LGPUT AG-1. (A) The plastron in ventral view. (B) Simplified drawing of the plastron in dorsal view. The scale bar equals 5 cm. Abbreviations: AN, anal; FE, femoral; hypo, hypoplastron; xi, xiphiplastron.

From pleural 3 only the posterior part is preserved. The scute is most probably wider than long but we cannot draw any more conclusion about its proportions due to its poor preservation. It is connected posteriorly with pleural 4 and laterally with marginal 8. Pleural 4 is wider than long. It is connected anteriorly with pleural 3, posteriorly with vertebral, laterally with marginals 8, 9, 10 and 11 and medially with vertebral 4.

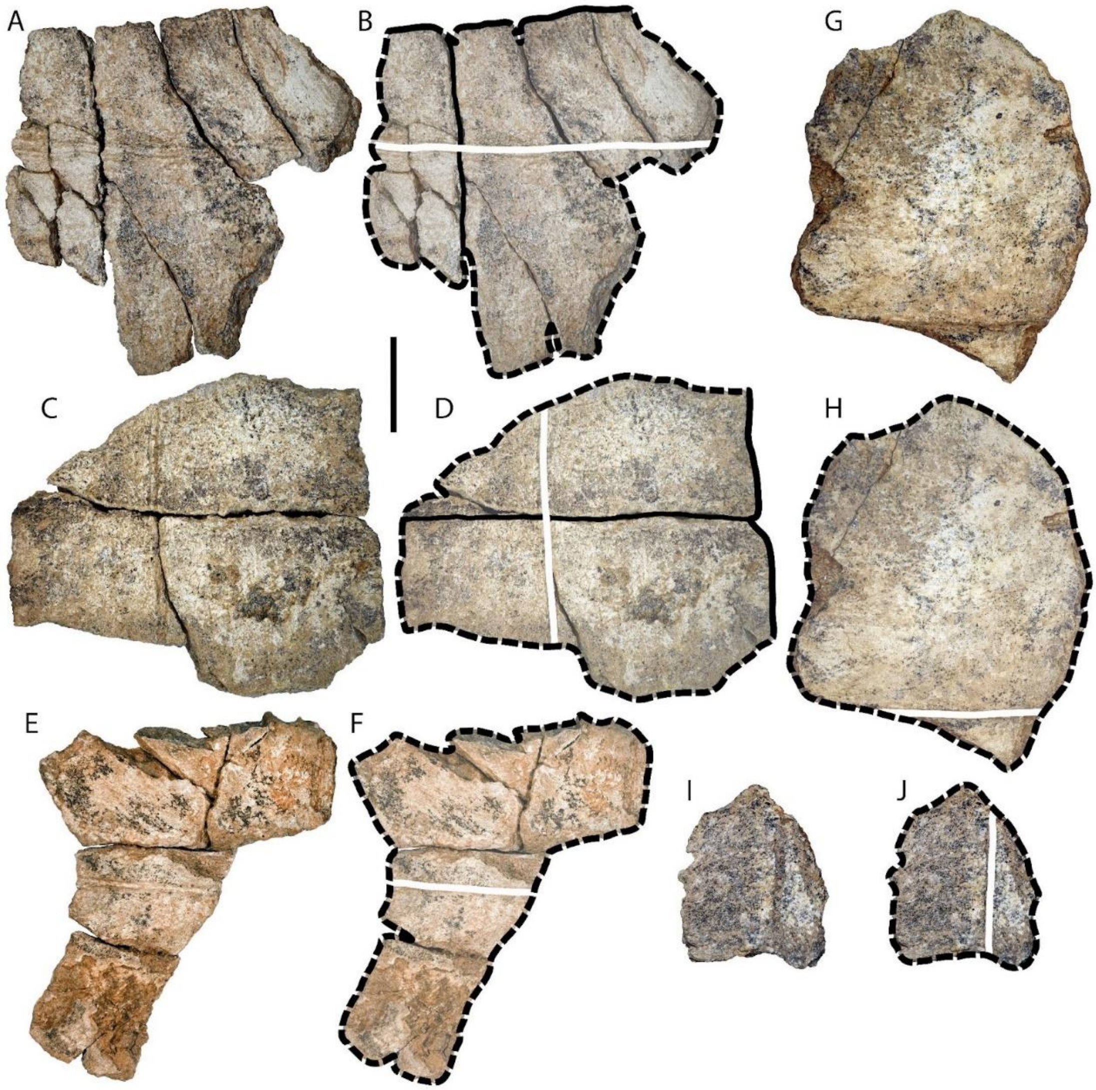

Figure 27: (A-J) Carapace and plastron indetermined fragments of the specimens LGPUT AG-1 with their respective simplified drawings. The scale bar equals 5 cm.

Marginal 7 is connected posteriorly with marginal 8. Due to the condition of the scute, we cannot draw any conclusions about its shape and proportions. Marginal 8 is wider than long with the anterior margin having almost the same width as the posterior. It is connected anteriorly with marginal 7, posteriorly with marginal 9 and medially with pleurals 3 and 4. Marginal 9 is wider than long with the anterior margin having the same width as the posterior. It is connected anteriorly with marginal 8, posteriorly with

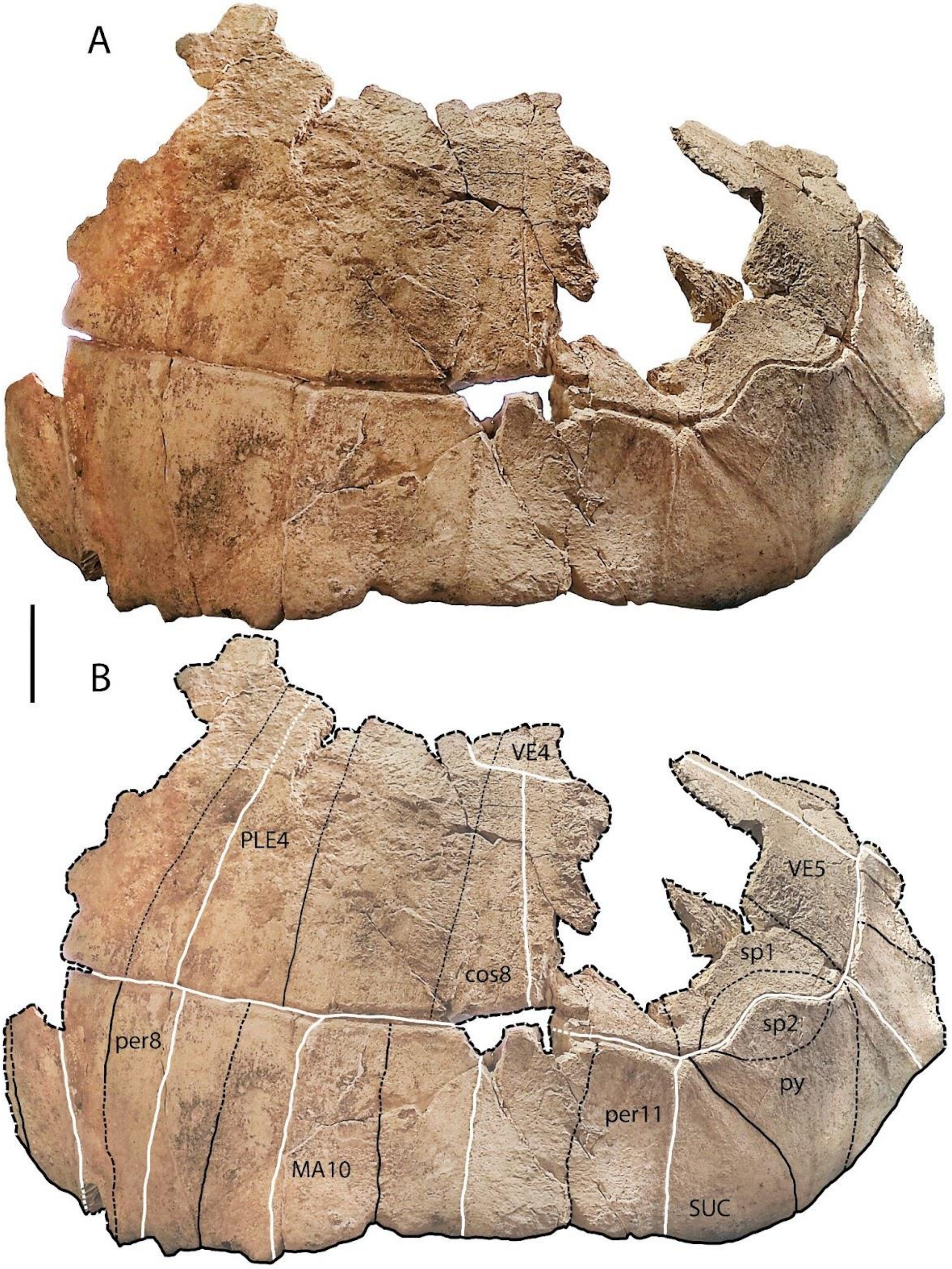

Figure 28: The lateral and posterior part of the carapace of the specimen LGPUT AG-2. (A) The carapace in dorsal view. (B) Simplified drawing of the carapace in dorsal view. The scale bar equals 10 cm. Abbreviations: cos, costal; MA, marginal; per, peripheral; PLE, pleural; py, pygal; sp, suprapygal; SUC, supracaudal; VE, vertebral.

marginal 10 and medially with pleural 4. Marginal 10 is wider than long with the anterior margin being wider than the posterior. It is connected anteriorly with marginal 9, posteriorly with marginal 11 and medially with pleural 4. Marginal 11 is as wide as long with the anterior margin being slightly wider than the posterior. It is connected anteriorly with marginal 10, posteriorly with the supracaudal and medially with pleural 4 and vertebral 5.

The supracaudal is wider than long. The anterior margin is wider than the posterior. It is connected anteriorly with vertebral 5 and laterally with marginals 11. The anterior margin that crosses suprapygal 2 creates a wavy line.

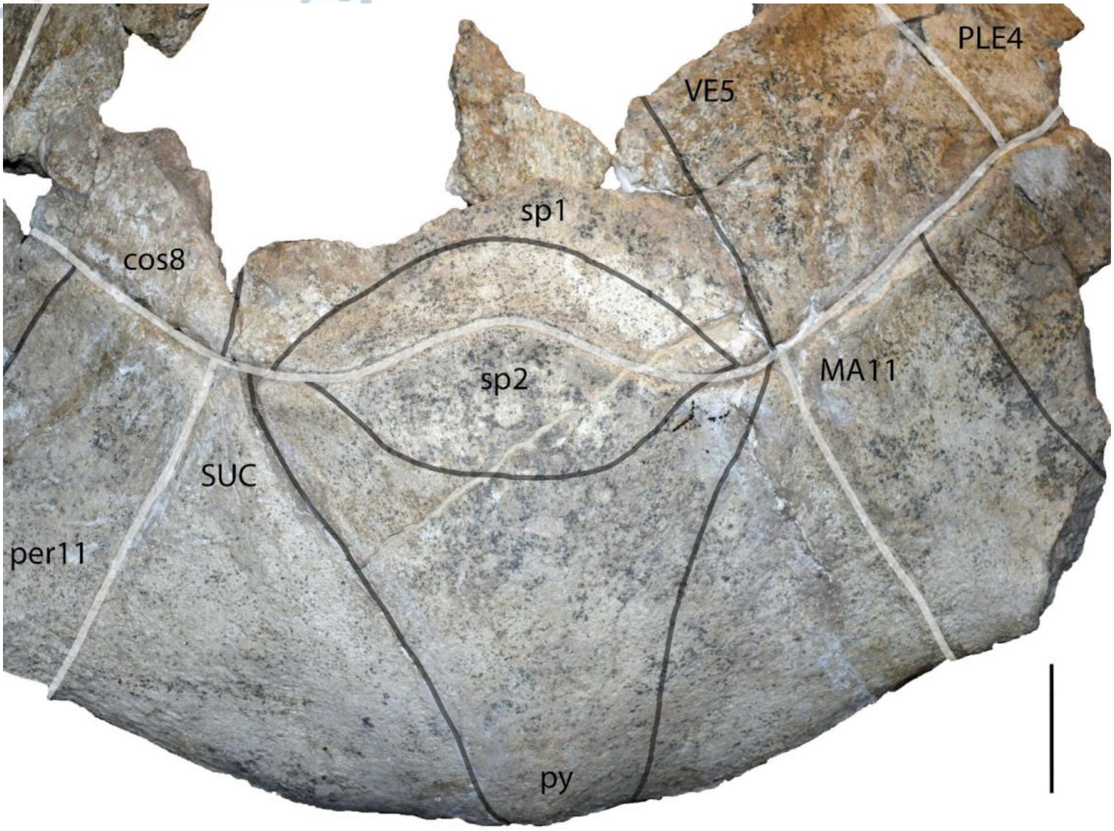

Figure 29: The posterior part of the carapace of the specimen LGPUT AG-2 with the bony plates and horny scutes illustrated. The scale bar equals 10 cm. Abbreviations: cos, costal; MA, marginal; per, peripheral; PLE, pleural; py, pygal; sp, suprapygal; SUC, supracaudal; VE, vertebral.

Plastron- Bony plates

The hyoplastra preserve only their posterior-most and mostly left part and are connected posteriorly with the hypoplastra (Fig. 30). Due to the condition of the plates, we cannot draw any conclusion about their shape and proportions.

The hypoplastra are slightly wider than long. The anterior margin is wider than the posterior. They are anteriorly connected with the hyoplastra, posteriorly with the xiphiplastra and laterally, at the posterior of the preserved bridge area, with peripheral 8. At the lateral part of the hypoplastra where the posterior part of the bridge is preserved an inguinal notch is created. A small part of the posterior hypoplastra contributes to the formation of the posterior lobe.

The xiphiplastra are wider than long, representing half of the posterior lobe. They are anteriorly connected with the hypoplastra. Their anterior margin is wider than the posterior. At the posterior-most point where the two xiphiplastra are connected a short, wide and angular anal notch is formed (ca. 135^{o}). In the posterior and lateral part of the xiphiplastra there is a pronounced narrowing in the femoro-anal sulcus but bellow that, the lateral parts of the plates are almost parallel.

The posterior-most part of the bridge, the part that connects the carapace with the plastron, is preserved on LGPUT AG-2. It is created by the hypoplastra that contacts peripheral 8.

Horny scutes

The abdominals are connected posteriorly with the femorals and the inguinal. Due to the condition of the plates, we cannot draw any conclusion about their shape and proportions.

The femorals are connected anteriorly with the abdominals, posteriorly with the anals and laterally with the inguinal. They are wider than long, and their anterior margin is wider than the posterior. The abdomino-femoral sulcus is medially straight but laterally concave.

The anals are wider than long. They are anteriorly connected with the femorals. Their anterior margin is almost the same width as the posterior and is tilted downwards. The part of the xiphiplastra that is covered by the anal scutes is slightly thickened.

The inguinal scute is wider than long (Fig. 31). It is placed laterally of the femorals and covers the posterior-most part of the bridge where the inguinal notch is. The anterior margin is wider than the posterior. It is connected anteriorly with the abdominal and laterally with marginals 7 and 8 and the femorals.

We cannot compare the anterior and posterior lobes because the anterior lobe is not preserved. There is no movable hinge, standard for the *Testudo* s.s. lineage, between the hypoplastra and xiphiplastra.

The plastron of LGPUT AG-2 is completely flat, without any curvature in any part of the hyoplastra and hypoplastra, where it would normally be observed, and has thin xiphiplastral extremities suggesting that it belonged to a female individual. The sutures between the bony plates are fully ossified suggesting that LGPUT AG-2 is an adult individual.

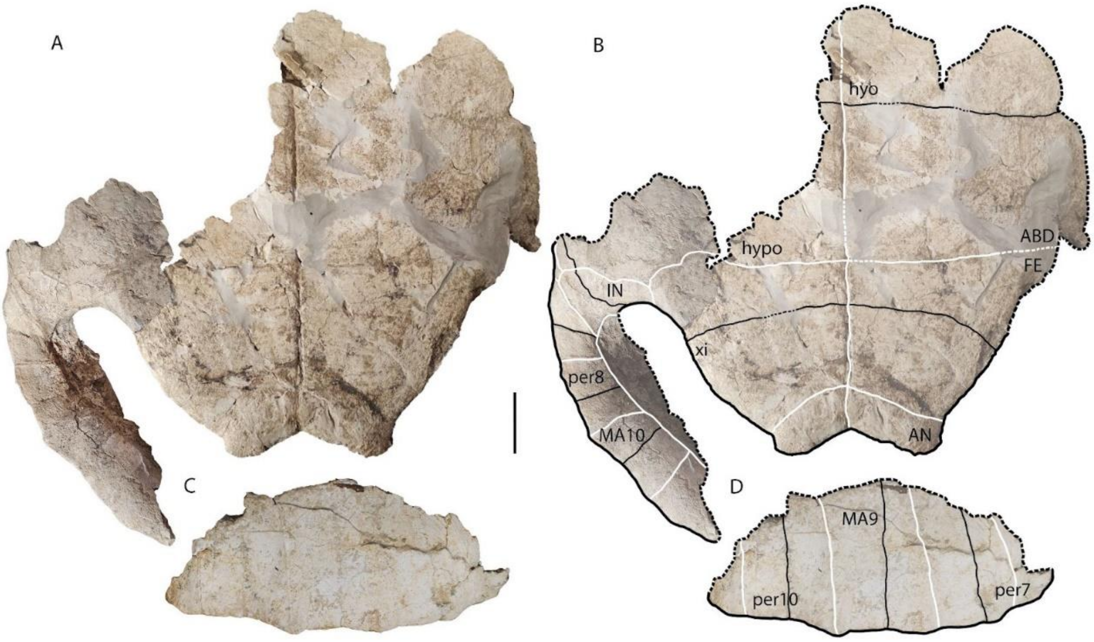

Figure 30: The plastron and the part of the carapace attached to it of the specimen LGPUT AG-2. (A) The plastron in ventral view. (B) Simplified drawing of the plastron in ventral view. (C) The part of the lateral carapace attached to the plastron in dorsal view. (D) Simplified drawing of the carapace in dorsal view. The scale bar equals 10 cm. Abbreviations: ABD, abdominal; AN, anal; FE, femoral; hyo, hyoplastron; hypo, hypoplastron; IN, inguinal; MA, marginal; per, peripheral; xi, xiphiplastron.

Fragments

Several fragments of the carapace and plastron of the specimen LGPUT AG-2 were also found but only a few were able to provide information. Two other fragments found belong to two bony plates with a suture in the middle, each (Fig. 32). The first one could belong to two costal plates because it is very thin and has curvature. The second fragment is substantially thicker at the posterior part and thinner at the anterior, with a smaller degree of curvature so it could belong to the margin of the carapace, probably to a peripheral plate that connects with a costal.

Vertebrae

Three vertebrae were preserved from this specimen, all of them being in poor condition (Fig. 32). The first two are thoracic vertebrae with the second one (Fig. 33D-F) being smaller sized than the first (Fig. 33A-C), therefore belonging further back to the vertebral column. The third vertebra is a caudal vertebra (Fig. 33G). All of them have a simple morphology.

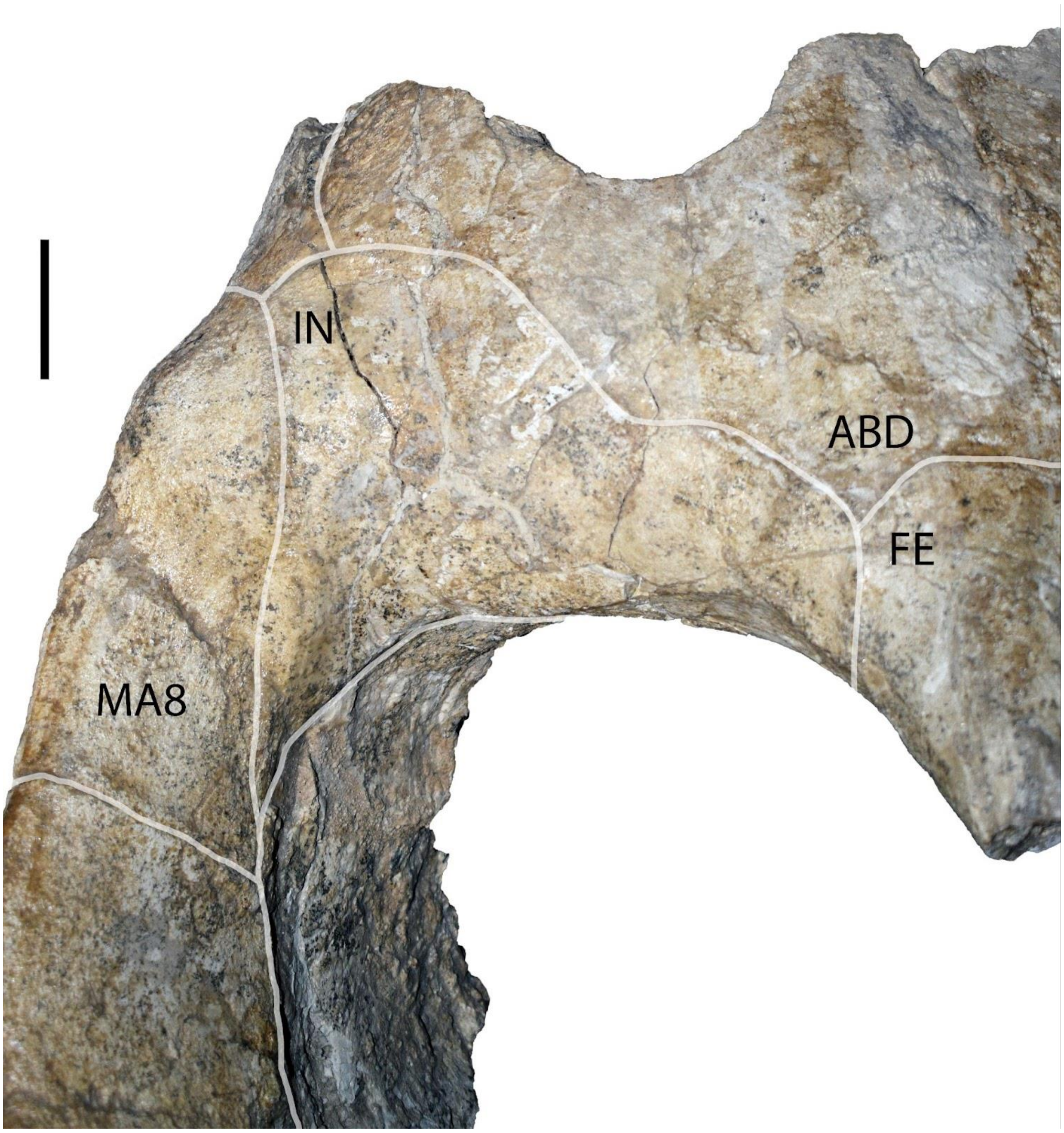

Figure 31: The posterior part of the bridge where the inguinal scute of the specimen LGPUT AG-2 is preserved, with the horny scutes illustrated, in ventral view. The scale bar equals 5 cm. Abbreviations: ABD, abdominal; FE, femoral; IN, inguinal; MA, marginal.

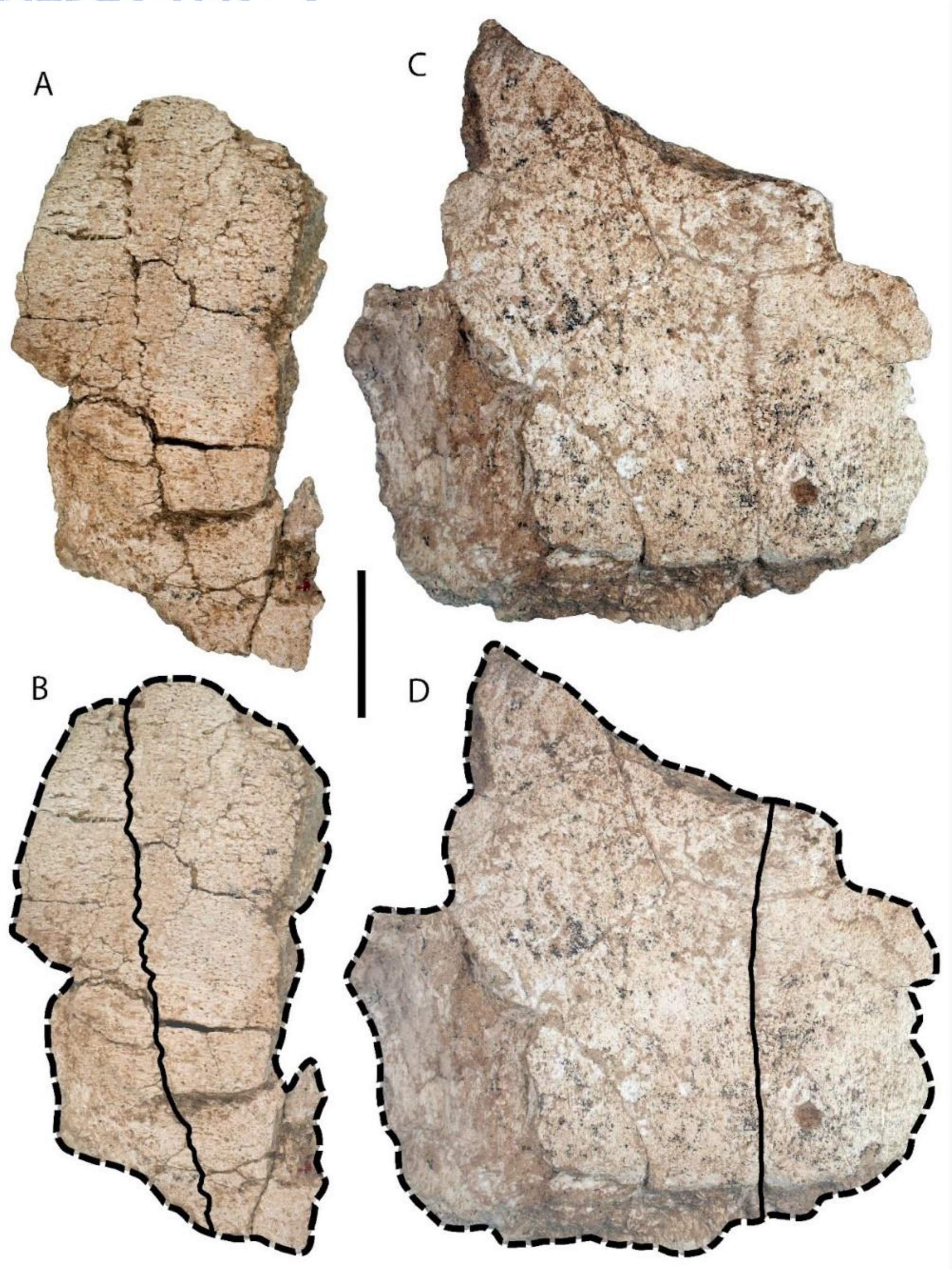

Figure 32: The two undetermined fragments of the specimen LGPUT AG-2 crossed by sutures, with their respective illustration. The scale bar equals 5 cm.

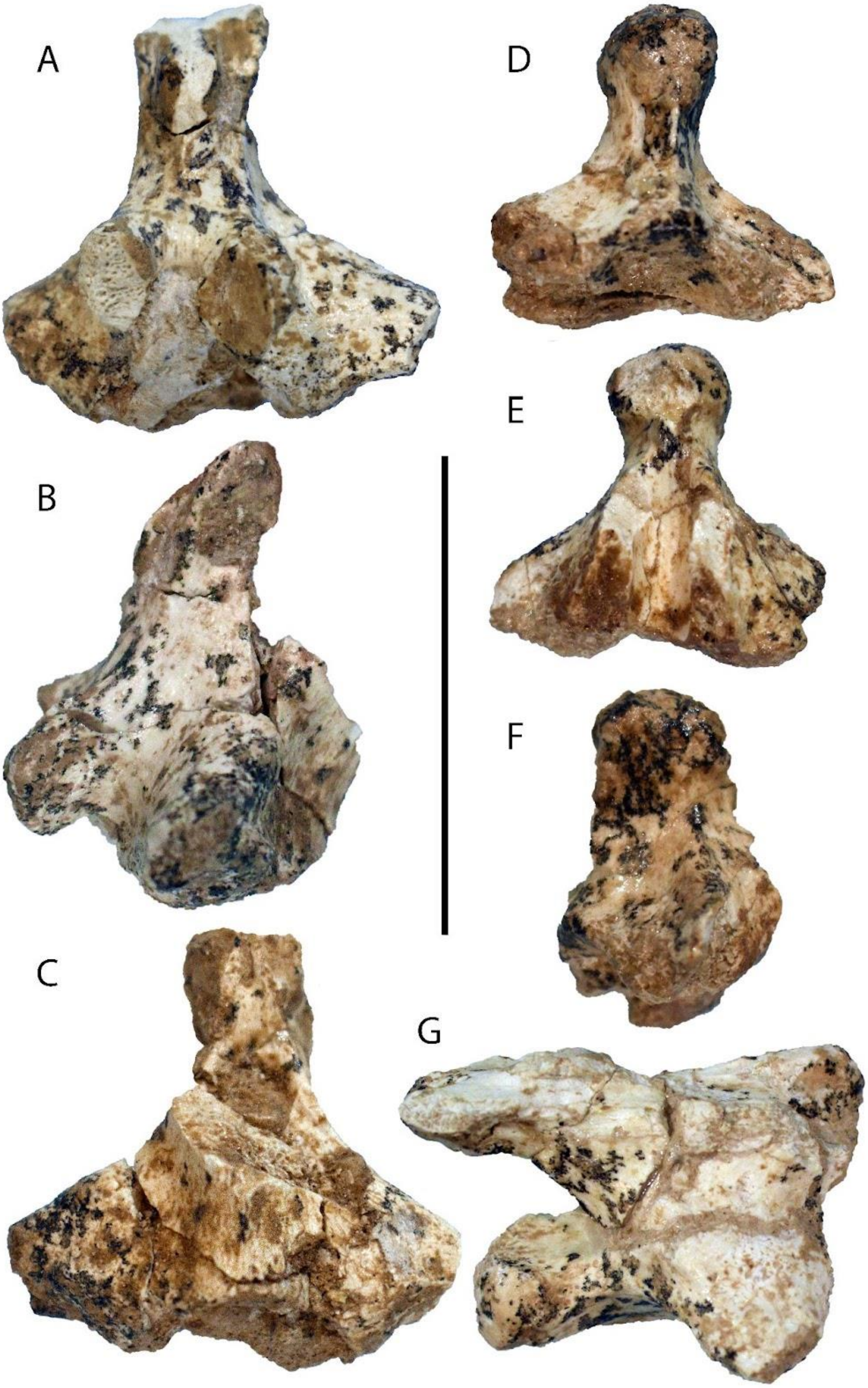

Figure 33: The vertebrae of the specimen LGPUT AG-2. One of the thoracic vertebrae in (A) ventral and (B) lateral view. Another thoracis vertebra in dorsal view. The smallest thoracic vertebra preserved in (D) dorsal, (E) ventral and (F) lateral views. (G) Caudal vertebra in lateral view. The scale bar equals 5 cm.

CHAPTER 3: COMMENTS AND COMPARISONS

The specimens may have been found in different collection points along the coasts of Makrygialos and Agiannis but most of them were positioned in the same formation. Two out of the five individuals studied herein were found separated from the outcrop, exposed by natural processes on the coast. We attribute all the specimens to the same species, *Titanochelon bacharidisi*, because we encounter many similarities with the specimens found on the opposite side of the Thermaikos gulf. The age of the fossils on both sides of the gulf is similar and the locations of discovery are in geographic proximity. The morphology of the carapace and plastron of all the specimens, where it is possible to be observed and compared, is almost identical.

The material from Makrygialos and Agiannis preserves several diagnostic characters of the genus *Titanochelon*. Those characters are the longer than wide pygal, the presence of a supracaudal scute, i.e. the fused marginals 12, the absence of plastral hinges, the wide plastral lobes, the anterior plastral lobe being longer than the posterior, the humero-pectoral sulcus being perpendicular to the axial plane in the medial region, but having a well-developed lateral change of curvature, the very short pectoral scutes in the sagittal plane but markedly expanded towards the anterior region, laterally, the presence of inguinal scutes, the males having a well-developed ventral thickening in the area covered by the anal scutes, and the fused astragalus and calcaneum (Pérez-García and Vlachos, 2014).

Several characters help us attribute these specimens to the species *Titanochelon bacharidisi*. The posterior rim of the carapace does not have indentations in the supracaudal and marginal 11 sulcus area, the gulars are short and contact the anterior part of the entoplastron, the entoplastron is covered only by the humeral scute medially, the posterior border of the entoplastron coincides with the humero-pectoral sulcus and the xiphiplastral notch is obtuse and reduced.

In order to reinforce this statement, we will compare the specimens found in Makrygialos and Agiannis with other confirmed *Titanochelon bacharidisi* specimens from Greece as well as with other species of the genus *Titanochelon* from Greece, Europe, and Turkey. Furthermore, comparison will be made with material of giant tortoises from Greece that has been attributed to the genus *Titanochelon* but not to a specific species. Lastly, we will compare our specimens with more primitive forms of giant tortoises that were found in Europe.

3.1 Comparisons with more primitive forms

Giant tortoises have existed in Europe since the beginning of the Eocene. There were many large sized species of tortoises that roamed Europe before *Titanochelon* that are worth mentioning. Although *Titanochelon* is a genus that represents the giant tortoises of the Neogene, it is interesting to compare our specimens with more primitive forms.

3.1.1 Comparison with *Pelorochelon eocaenica*

The species *Pelorochelon eocaenica*, is found in the middle Eocene of Germany and Austria. It was formerly known as *Testudo eocaenica* Hummel, 1935. Later the species *Cheirogaster steinbacheri* found in the middle Miocene of Salzburg, Austria (Karl, 1996) also known as *Manouria (Hadrianus)* cf. *eocaenica* (Hummel, 1935) and *Titanochelon steinbacheri* (Pérez-García and Vlachos, 2014) was reassigned as *Pelorochelon* cf. *eocaenica* (Pérez-García et al., 2015). The former holotype of "*Cheirogaster steinbscheri*" from Salzburg is different from our specimens in several characters with the most important one being the size, where *Pelorochelon* cf. *eocaenica* barely reaches 70 cm in length. On the carapace the pygal is almost as wide as long and narrower than suprapygal 2, while in the specimen AG-2 it is longer than wide and wider than suprapygal 2; the sulcus between vertebral 5 and the supracaudal is straight, while in LGPUT AG-2 it is wavy. The plastron is severely eroded but several differences are still visible. The posterior lobe is long and narrow, with the lateral margins being almost parallel and there is no transversal narrowing in the xiphiplastra.

3.1.2 Comparison with *Pelorochelon soriana*

The species *Pelorochelon soriana* is found in the middle Eocene of Mazateron locality of the Soria Province, Spain (Pérez-García et al., 2015). The material attributed to this species was initially described as *Hadrianus* sp. by Jiménez Fuentes et al. (1988). Its holotype, STUS 14223, is an almost complete shell that is very deformed but there are several other specimens that help create a more complete picture of the carapace and plastron morphology of the species. In the carapace some important differences from our specimens are the presence of 12 pairs of marginals, and the sulci between vertebral 5 and marginals 12 that create an almost straight line. The plastron of the species *Pelorochelon soriana* is clearly different from that of our specimens in the subrhombic entoplastron; the gulars that in some specimens do not contact the entoplastron; the anterior angle between the axial plane and the gularo-hymeral sulcus that is greater than 65º; the humero-pectoral sulcus that also does not contact the entoplastron; the pectorals that are relatively longer both medially and laterally; the abdomino-femoral sulcus which is medially convex with a change of curvature laterally; the transversal narrowing of the xiphiplastra which is quite faint; and the anal notch that is deeper and smaller angle.

3.1.3 Comparison with *Cheirogaster maurini*

Another important species that must be mentioned is *Cheirogaster maurini* from the Priabonian of Falaise de Baby (Gironde), France, which is the type species of the genus *Cheirogaster,* and the only species remaining in this genus in general (Pérez-García and Vlachos, 2014). Many differences can be spotted between the holotype of the species and our specimens with the first and most important one being the total size of the shell, which is almost 40 cm in the French tortoise (Lapparent de Broin, 1977). Although the carapace is deformed, we can still observe that suprapygal 2 is wider than the pygal. In the plastron the gulars cover the anterior part of the entoplastron, the humero-pectoral sulcus is placed posteriorly of the entoplastron without contacting it, the same sulcus is convex, the abdomino-femoral sulcus is concave, the femoro-anal sulcus is wavy leaning downward, there is no transversal narrowing in the xiphiplastra because the whole posterior part becomes narrower below the femoro-anal sulcus, and, lastly, the anterior margins of the posterior lobe are parallel to each other. An important similarity between the individual from France and AG-2 is the presence of inguinal scutes which, however, do not contact the femorals in *Ch. maurini*.

3.1.4 Comparison with *Taraschelon gigas*

The species *Taraschelon gigas* from the Early Oligocene of Bournoncle- Saint-Pierre, France is also nominally and taxonomically problematic. It was firstly named "*Testudo*" *gigas* Bravard, 1844 but was later reassigned to the genus *Cheirogaster* as did most of the large sized tortoises from Europe (Lapparent de Broin, 1977). It was finally attributed to the genus *Taraschelon* by Pérez-García (2016). Many differences can be spotted between the holotype of the species and our specimens with the first one being the total size of the shell, which is almost 80 cm in the French tortoise. Other differences observed in the carapace are the presence of well-developed protrusions on the medial side of the last pair of the peripherals, the absence of overlap between the suture of the costals and peripherals and the sulcus of the pleurals and the marginals, the shell is relatively tall, the posterior carapace rim is flared outwards. On the plastron the visible differences are the anterior lobe is very narrow compared to the rest of the plastron, the anal notch is very well-developed creating an almost right angle, the gulars cover the anterior part of the entoplastron, the humero-pectoral sulcus is placed posteriorly of the entoplastron without contacting it, the humero-pectoral sulcus is convex, and the pectoral scutes are pretty long in all of their width and become shorter only in the most medial part of the plastron.

3.1.5 Comparison with *Alatochelon myrteum*

The species *Alatochelon myrtuem* from the Lower Pliocene of Puerto de la Cadena, Spain is more recent than the species mentioned before and has African affinities as proposed by Pérez-García et al. (2020). It existed in the early Ruscinian, right after the disappearance of *Titanochelon bolivari*, but that does not exclude the possibility that the two species coexisted. From the holotype, specimen T-3-BC-MU, only the anterior parts of the carapace and the plastron are preserved so the comparisons with our specimens are limited to those areas. In difference from our specimens in *Alatochelon myrtuem* are the gular scutes cover the anterior part of the entoplastron, the humero-pectoral sulcus is positioned posteriorly of the entoplastron without contacting it, the same sulcus is medially concave and laterally leans upwards, the pectoro-abdominal sulcus is concave.

3.2 Comparisons with other *Titanochelon bacharidisi* specimens

Comparing our specimens with those found on the opposite side of the Thermaikos gulf we encounter mostly similarities. The holotype of the species *Titanochelon bacharidisi*, female individual EPN I, the paratype, male individual EPN II, both found in Epanomi, as well as the individuals KLK I and KLK II, found in Nea Kallikratia, are the most important individuals that our specimens should be compared with. Furthermore, comparisons will be made with the specimens found in Aggelochori, and in Nea Michaniona.

3.2.1 Comparison between MAP-2 and EPN I

Figure 34: The holotype of the species *Titanochelon bacharidisi*, EPN I individual. Photo: E. Vlachos.

The holotype of the species *Titanochelon bacharidisi* belongs to a female individual, EPN I (Fig. 34), that preserves the plastron with the lateral parts of the carapace attached and several postcranial elements similar to those of the individual MAP-2. However, a comparison between the two giant tortoises would not be as valid because our specimen LGPUT MAP-2 is a male individual and most of the differences found could be attributed to sexual dimorphism.

Despite the sexual dimorphism there is an important comparison that we must make between the individuals MAP-2 and EPN I. This comparison concerns an important bone that belongs to the hindlimb but was not found articulated on our specimen, the thigh spur or thigh tubercle. This is usually located posteriorly of the femur and is used as a defense mechanism by extant tortoises like *Centrochelys sulcata.* In the fossil record of giant tortoises, it is only found in specimens of the species *Titanochelon bacharidisi* and it is one of its diagnostic characteristics (Vlachos et al., 2014; Vlachos, 2015). The osteoderm from Makrygialos is slightly different in shape from that of Epanomi, LGPUT EPN 184 (Fig. 35), because while the first is conical, relatively long, straight with a slight bend and with wide but flat posterior part the second is also conical but short, bends to the side a bit more than the first and the posterior part is rounded. Of course, the size difference of the two thigh tubercles is probably related to the total size difference of the two individuals and the shape differences could be related to sexual dimorphism.

Figure 35: The thigh tubercle of individual EPN I, specimen LGPUT EPN 184. The scale bar equals 5 cm. Photo: E. Vlachos.

3.2.2 Comparison between AG-2 and EPN I

The holotype (Fig. 34) consists of the left and right peripheral plates of the carapace, LGPUT EPN 100, the plastron, LGPUT EPN 101, the skull and mandible, LGPUT EPN 103, and several postcranial elements, LGPUT EPN 104-199 (Vlachos et al., 2014; Vlachos, 2015). The similarities observed between the holotype and our specimens are numerous but can only be observed in the plastra and the posterior part of the carapace. However, the mounting strategy of the holotype allows us to observe only the visceral side of the plastron, so this comparison can be challenging. Specimen LGPUT AG-2, as it is the only female individual from our collection with most of the plastron preserved, is the best specimen to do this comparison with.

EPN I and AG-2 are very similar in size and proportions. The anterior and posterior plastral lobes of both specimens are short when compared to the total length of the plastron, and the proportions and shapes of the bony plates of the two specimens are similar. Two differences that can be easily spotted are the degree of the transversal narrowing of the xiphiplastra, where they are crossed by the femoro-anal sulcus, which is stronger in the specimen LGPUT AG-2 than in LGPUT EPN 101, the anal notch which is slightly deeper in LGPUT AG-2 and creates an angle with a slightly smaller degree than in the Epanomi specimen, where there is almost no angle created.

3.2.3 Comparison between MAP-2 and EPN II

The paratype of the species *Titanochelon bacharidisi* belongs to a male individual and consists of a partial plastron, LGPUT EPN 285, several fragments of the carapace, LGPUT EPN 283, 286, 287 with the most important the posterior part that includes the suprapygals, the pygal and the supracaudal, LGPUT EPN 284 (Fig. 36), and several postcranial elements, LGPUT EPN 200–282 (Vlahos et al.,2014; Vlachos, 2015). The similarities and differences between the individual EPN II and our male individual MAP-2 are more easily spotted in this case because we are able to study the dorsal side of the plastron. An important difference that can be spotted is the size difference of the two individuals; the plastron of EPN II is almost 114 cm while that of MAP-2 is almost 150 cm. The entoplastra of both specimens are wider than long but in EPN II it is relatively larger in size with more distinct corners. The proportions and positions of all the other bony plates and horny scutes are almost identical in the two tortoises, especially the curvature of the humero-pectoral sulcus. The xiphiplastron of LGPUT MAP-2 is extremely similar with that of EPN II, with the same degree of transverse narrowing and angle created in the anal notch.

The forelimb and hindlimb of EPN II are also preserved and despite the obvious difference in the size of the bones the morphology is quite similar with those of MAP-2. The radius and ulna of the right forelimb, LGPUT EPN 201 and LGPUT EPN 202 respectively, are fully preserved in the Epanomi individual and they are very similar in shape and proportions with those of the left forelimb from the Makrygialos specimen. The same applies to the osteoderms and the ungual phalanx from Makrygialos when compared with LGPUT EPN 216 and LGPUT EPN 231-273, 275 respectively.

The bones of the left hindlimb are also very similar with those of EPN II despite the size difference. The distal part of the fibula, that is one of the only two long bones of the posterior limb that are preserved on our specimen, is very similar to LGPUT EPN 276. One significant difference that can be observed in the hindlimb is that the astragalocalcaneum in EPN II preserves the suture between the two bones, whereas in the Makrygialos tortoise this suture is not preserved. This could indicate that the individual from Makrygialos is older in age than the paratype from Epanomi.

Figure 36: The posterior part of the carapace of individual EPN II, specimens LGPUT EPN 284. The scale bar equals 10 cm. Photo: E. Vlachos.

3.2.4 Comparison between AG-1, AG-2 and EPN II

The comparison of the two partial specimens from Agiannis with the paratype is also important, as one of them, AG-1, is male and the other one (AG-2) has part of the carapace preserved. The posterior part of the xiphiplastra of LGPUT AG-1 presents some differences when compared to the plastron, LGPUT EPN 285, of EPN II. The area covered by the anals in AG-1 is relatively shorter than that of EPN II and the degree of the transversal narrowing is stronger in the first individual. The angle of the anal notch of the Agiannis specimen is not that well defined as that of EPN II, and it resembles a concave line. Those differences are similar with those found between the other male individual from our study area, LGPUT MAP-2, and the plastron of the individual EPN I, LGPUT EPN 101. We could attribute those differences to intraspecific variation.

The individual EPN II is the only specimen from the eastern side of Thermaikos gulf that preserves part of the carapace with recognizable elements, LGPUT EPN 284. It preserves the posterior portion where peripherals 10 and 11, suprapygals 1 and 2, the pygal, marginal 11 and the supracaudal are visible. This whole region is very similar in both LGPUT AG-2 and LGPUT EPN 284, with the only differences being that in the former suprapygal 1 is slightly larger in size and the pygal is slightly narrower. In both specimens, marginals 12 are fused creating a supracaudal and the sulcus between that scute and vertebral 5 creates a wavy line that crosses suprapygal 2. The morphology of the bony plates and horny scutes of the carapace does not seem to be affected by sexual.

3.2.5 Comparisons with KLK II

The individual KLK II consists of just the plastron without the lateral parts, LGPUT KLK 500 (Fig. 37). It is very similar to the specimen LGPUT MAP-2 in the morphology of the plastron, the shape and proportion of the bony plates and horny scutes. One important difference that can be spotted is the shape of the entoplastron which is rhombus shaped in KLK II and as wide as long but more elliptical in MAP-2.

Figure 37: The anterior lobe of the plastron of individual KLK II, from Kallikratia, specimen LGPUT KLK 500. Photo: E. Vlachos.

The morphology of the plastron of the individual KLK II, LGPUT KLK 500, is also very similar with that of both Agiannis specimens. A difference that can be observed between LGPUT KLK 500 and LGPUT AG-1 is the femoro-anal sulcus which is medially straight but laterally leans downwards in the first specimen but almost straight throughout its width in the latter.

3.2.6 Comparisons with EPN III and KLK I

The individual EPN III corresponds to a femur, LGPUT EPN 99, that was found separately from the other individuals (Vlachos et al., 2014; Vlachos, 2015). It unfortunately cannot be compared with the femur of MAP-2 due to the poor preservation of the second.

The material preserved from the second individual from Nea Kallikratia, KLK I, specimens LGPUT KLK 501-529, is very limited. The xiphiplastra preserved, LGPUT KLK 502, are similar to those of our specimens, with a distinct transversal narrowing and a wide anal notch. The metatarsals and phalanges of the posterior limb, LGPUT KLK 512-522, are also comparable in morphology to those of LGPUT MAP-2. This individual from Nea Kallikratia also preserves an articulated thigh tubercle, LGPUT KLK 523, like that of EPN I exhibiting the same differences with the osteoderm of LGPUT MAP-2.

3.2.7 Comparison with the Nea Michaniona material

There is additional material that belongs to *Titanochelon bacharidisi* that has been found in Nea Michaniona, LGPUT MIC 301-319, and consists mainly of fragments from the plastron and a few postcranial elements (Vlachos, 2015). Not many characters can be compared due to the preservation of the material. One important similarity is the presence of a thigh tubercle, LGPUT MIC 312, which, although a small part from the posterior of it is missing, is more similar to that of LGPUT MAP-2 than the ones preserved from the individuals EPN I and KLK I.

3.2.8 Comparison with the Aggelochori material

The material from the locality Aggelochori, also known as Megalo Emvolon, is poor and is divided into two collections, LGPUT AGG 420-422 and AMPG 1925-1955, 1969, 1970 (Vlachos, 2015). Only a few plastral fragments are preserved from the shell and several postcranial elements. In the part of the anterior lobe preserved, in the specimen AMPG 1925, the gular does not overlap the entoplastron, a morphology similar with the specimen LGPUT MAP-2. From the posterior part of the preserved anal, AMPG 1926, we can observe that the anal notch is only slightly deeper than those of Makrygialos and Agiannis. The postcranial elements preserved from Aggelochori are almost identical with those from Makrygialos.

Concluding, the material from both localities shows only minor differences allowing their attribution to the same species. Further preparation of the already existing specimens and excavation of new ones, especially the discovery of a skull, in the area of study would be enable more detailed comparisons.

3.3 Comparisons with other *Titanochelon* species

Some very relevant comparisons have been made to highlight and enrich the differences between the specimens from Makrygialos and Agiannis, and the other species of the genus *Titanochelon* that has been found in Greece, *Titanochelon schafferi* from the island of Samos and the type species of the genus, *Titanochelon bolivari* from Spain and Portugal. Lastly, it is important to compare our specimens with other European and Asian giant tortoises that either belong in the genus *Titanochelon*, like *Titanochelon perpiniana* from Perpignan, France, *Titanochelon ginsburgi* from Artenay, France, *Titanochelon vitodurana* from Switzerland and *Titanochelon kayadibiensis* from western Turkey, or not, like *Alatochelon myrteum* south-eastern Spain.

Figure 38: The anterior lobe of the plastron of the specimen AMNH 1905 of the species *Titanochelon schafferi*. Photo: E. Vlachos.

3.3.1 Comparison with *Titanochelon schafferi*

The species *Titanochelon schafferi* is found in the Late Miocene of the island of Samos (Szalai, 1931; Lapparent de Broin, 2002) and presents several differences with our individuals. The most important specimen found in Samos is a skull of a giant turtle, specimen NHMW 2009z0103/0001, but unfortunately, we do not have one in our material that we can compare with. From the fragments of the plastra found in Samos, AMNH 1905, 1772 (Figs. 38-39), and MGL 101624, we can observe several important differences from our specimens (Vlachos et al., 2019b). The gularo-humeral sulcus of *Titanochelon schafferi*, visible in the specimen AMNH 1905 (Fig. 38), does not contact the anterior part of the entoplastron and the humero-pectoral sulcus does not contact the posterior part of it, whereas in known specimens of *Titanochelon bacharidisi*, and in LGPUT MAP-2, where those characters are preserved, those sulci contact the margins of the entoplastron. The transversal narrowing in the Samos species, specimen AMNH 1772 (Fig. 39), is quite faint compared to the Agiannis and Makrygialos specimens and the anal notch is slightly deeper with more pointy xiphiplastral extremities. Another character that differentiates *Titanochelon schafferi* from *Titanochelon bacharidisi* is the shape of the distal femur (Vlachos et al., 2014), but we cannot make this comparison with our material because while in the individual MAP-2 the femur is partially preserved, the distal part is missing.

Figure 39: The plastron of the specimen AMNH 1772 of the species *Titanochelon schafferi*. The scale bar equals to 10 cm. Photo: E. Vlachos.

3.3.2 Comparison with *Titanochelon bolivari*

The species *Titanochelon bolivari* is the type species of the genus *Titanochelon* and is found in several locations of Spain and Portugal. There are several specimens found around those two countries with a chronological distribution from Aragonian to Early Vallesian (Langhian to Early Tortonian) (Pérez-García and Vlachos, 2014). It differs from our specimen and therefore from *Titanochelon bacharidisi* in the following characters: the gulars cover the anterior part of the entoplastron, the entoplastron is narrow when compared to the total width of the plastral lobe, the posterior margin of the entoplastron is located anterior to the humero-pectoral sulcus but sometimes it is in contact with it, and lastly the inguinal scutes do not contact the femorals.

Of great importance are the specimens found in the type locality of the genus *Titanochelon*, Alcalá de Henares, Spain. Several specimens of *Titanochelon bolivari* were found there with the most important being the lectotype, carapace specimen MNCN 32773, and the plastron MNCN 32771 (Pérez-García and Vlachos, 2014). Several differences in the plastra can be observed in comparison with the individuals from Makrygialos and Agiannis that are spotted mainly in the plastra. Except for the main differences that distinguish those two species that are mentioned above, the xiphiplastra are relatively wider with a fainter transversal narrowing and the anal notch created between them is shallow, creating only a concave line. Those differences are enough to claim that the individual from Spain and our specimens belong to different species. Similar differences can be observed between our specimens and other specimens of *Titanochelon bolivari* from Spain and Portugal. Another character that is not preserved in the specimen of *Titanochelon bolivari* mentioned above but is visible in other individuals is the shape of the femoro-anal sulcus, which is perpendicular to the axial plane medially but creates a wavy line and leans downwards and laterally. Lastly, an important similarity between several specimens of *T. bolivari*, MNCN 32766, STUS 5137, STUS 8373, and LGPUT AG-2 is the presence of a single pair inguinal scutes, that in the case of the Iberian species, do not contact the femorals (Pérez-García and Vlachos, 2014).

3.3.3 Comparison with *Titanochelon perpiniana*

The giant tortoise species found in the Late Pliocene of Perpignan, France, is of great importance because it is considered a sister group to *Titanochelon bacharidisi* (Vlachos, 2015) and is represented by an almost complete skeleton of a female individual (Fig. 40; Bourgat & Bour, 1983). It is different from our specimens in the gulars that do not reach the entoplastron, the relatively larger entoplastron compared to the anterior lobe and the faint transversal narrowing in the xiphiplastra, where the femoro-anal sulcus meets the margin of the plastron. The anterior and posterior lobes are narrow in comparison with the whole plastron. The carapace of the French specimen although preserved its surface if very eroded so the morphology is not visible. Therefore, we can claim that this tortoise and our specimens belong to different species.

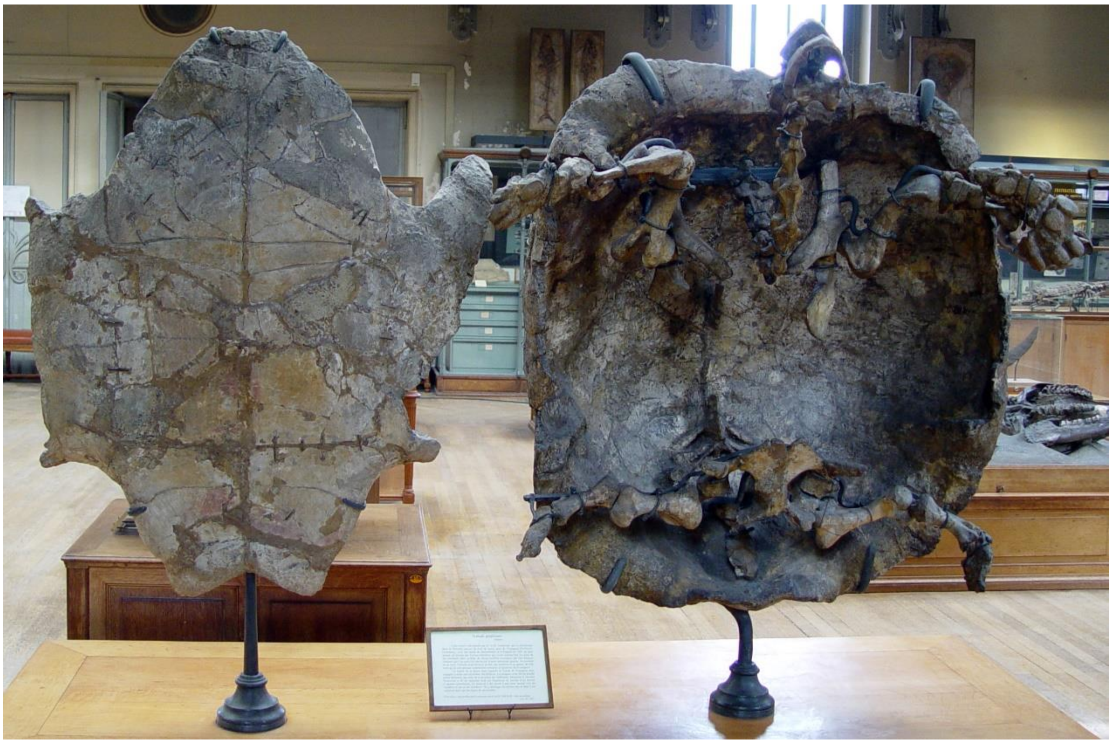

Figure 40: The holotype of the species *Titanochelon perpiniana* in the Muséum National d’Histoire Naturelle, Paris, France. Photo: E. Vlachos.

3.3.4 Comparison with *Titanochelon kayadibiensis*

Titanochelon kayadibiensis is known from the Miocene of western Turkey (Karl et al., 2021). The specimen BGR — KB, without number, exhibits many differences from our specimens. The entoplastron is narrower and rounder compared with the one on MAP-2 which is quite wide and elliptical. The gulars do not contact the entoplastron and the humero-pectoral sulcus does not contact its posterior margin. The posterior lobe is almost quadrangular as the anal notch is almost nonexistent and it creates a very obtuse angle. The anals have a triangular shape as they meet the margin of the carapace at the posterior-most part of the xiphiplastra and not the lateral and there is no transversal narrowing created. These differences are enough to separate the two species.

3.3.5 Comparison with *Titanochelon ginsburgi*

The species *Titanochelon ginsburgi*, previously known as *Testudo ginsburgi* (Lapparent de Broin, 1977) is represented by the holotype (MNHN AR 538), from the Middle Miocene (MN4) of Artenay, France. There are several differences between the plastron of the French specimen and the ones from Makrygialos and Agiannis. The gulars cover the anterior part of the entoplastron, the entoplastron is hexagonal, the pectorals are relatively longer, the femoro-anal sulcus is perpendicular to the axial plane medially but creates a wavy line and leans downwards laterally and the transversal narrowing in the xiphiplastra is very faint. The plastron in *Titanochelon ginsburgi* is also relatively narrower than that of our specimens. Those differences prove that the MAP and AG specimens do not belong to the species *Titanochelon ginsburgi.*

3.3.6 Comparison with *Titanochelon vitodurana*

The species *Titanochelon vitodurana* is represented by two specimens from the Middle Miocene (MN6) of Switzerland, the holotype from Winterthur (NWS 13758, Biedermann, 1862) and another specimen from Veiltheim (PIMUZ A/III 660, Peyer, 1942). Apart from the size difference (*Titanochelon vitodurana* barely reaches 100 cm in length) this species is different from *Titanochelon bacharidisi* and our specimens in several characters. In the holotype the gulars cover the anterior part of the entoplastron, the entoplastron is hexagonal with sharp corners, the pectoro-abdominal sulcus is medially straight and perpendicular to the axial plane but leans downwards and creates a wavy line laterally, the transversal narrowing in the xiphiplastra is faint and the anal notch is wide and does not create an angle but a concave line. The specimen from Veiltheim is slightly different from the holotype because it has a stronger transversal narrowing at the xiphiplastra, but it is also different from our specimens in the relatively longer part of the xiphiplastra that is covered by the anals. This difference between the two specimens of the species *Titanochelon vitodurana* could be attributed to sexual dimorphism. An important similarity between the individual from Veiltheim and AG-2 is the presence of inguinal scutes. New material that was attributed to the species *Titanochelon vitodurana* was later found in the Swabian marls of Southern Germany (Karl, 2013) but it is very scarce and not enough to compare it with our specimens and its taxonomic attribution should be taken with caution.

3.4 Comparisons with *Titanochelon* sp. from Greece

Other relevant comparisons that can be made are with other specimens found in Greece that belong to the same genus but have not been attributed to a species. This material is from Pikermi, the island of Lesvos and Thessaloniki.

3.4.1 Comparison with the “Salonique” material

The specimens from the locality “Salonique” published by Arambourg and Piveteau (1929) could be either from Axios valley or Megalo Emvolon. Their age is probably Late Miocene to Pliocene, so similar to that of the *Titanochelon bacharidisi* material. They are mentioned as *Titanochelon* cf. *bacharidisi* by Vlachos (2015). This material consists of a skull and some postcranial material, but there are no fragments of the carapace or plastron. The appendicular elements that are comparable to our material are a right and left radius, three right and one left ulna, an ungual phalanx and several osteoderms, including a thigh tubercule. All the above postcranial materials are morphologically very similar to the bones preserved from the hindlimb and forelimb of LGPUT MAP-2. The thigh tubercule preserved is one of the characteristics that distinguish *Titanochelon bacharidisi* from the other *Titanochelon* species found in Greece. Thus, the attribution of the “Salonique” material to *Titanochelon bacharidisi* seems plausible.

3.4.2 Comparison with the Pikermi material

From the Pikermian giant tortoises several fragments of the carapace and plastron, AMPG 1880-1884, and several postcranial elements are preserved, AMPG 1871-1879 (Vlachos, 2015; Vlachos et al., 2019a). Specimen AMPG 1880 is a complete left epiplastron which preserves the gularo-pectoral sulcus and the suture between the epiplastron and the entoplastron. It is clearly different from our specimen because the gular covers a small part in the anterior of the entoplastron. Another difference is the shape of the radius and ulna, AMPG 1872 and AMPG 1871 respectively, which are more robust, and the radius also has a larger and wider distal part, whereas those of LGPUT MAP-2 are thinner and leaner. Despite these important differences it is necessary to obtain more information about the Pikermian tortoises possibly from new specimens, in order to confirm them.

3.4.3 Comparison with the Lesvos material

The material discovered in the Vatera locality of the island of Lesvos consists of several postcranial elements that belong to a giant tortoise. It was initially attributed to the species “*Cheirogaster*” aff. *schafferi* by Lapparent de Broin (2002) but was later referred to as *Titanochelon* sp. by Vlachos (2015) because the material is not enough in order to classify it to the level of species. The bones preserved are a diaphysis of a left femur, VM PO 186 F, a left partial distal tibia, VM PO 184 F, three ungual phalanges, VM PO 067 F, VM PO 176 F, VM PO 188 F, a carpal element, a possible metatarsal and several osteoderms, flat, half pointed, pointed and a possible crucal one. This material unfortunately is not enough to make the comparison with our specimens. The osteoderms and ungual phalanges are of similar shape but that is not enough to claim that the Lesvos material belongs to the same species as the material from Makrygialos and Agiannis. More specimens of giant tortoises from this locality must be found in order to have a more complete picture of the Lesvos taxon.

3.4.4 Comparison with other material from Greece

Many isolated specimens of giant tortoises have been found in various localities of Greece. They are mostly carapace, plastron and bone fragments and osteoderms. They are attributed to the genus *Titanochelon* but do not contribute anything else in terms of taxonomy. However, they help us understand the spatial and temporal distribution of the genus in Greece.

A fragment of the coracoid, LGPUT MIL 1511, and an osteoderm fragment, LGPUT MIL 1834, of a giant tortoise were found in the Late Pliocene site of Milia, Grevena, but they are not enough to make a comparison with our specimens (Vlachos, 2015; Vlachos and Tsoukala, 2016). It is, however, an indication that giant tortoises also existed in the central part of N. Greece.

At the Kassandra peninsula of Chalkidiki, at the Late Miocene localities of Kryopigi and Fourka, several fragments of giant tortoises were found. In Kryopigi, a partial tibia, LGPUT KRY 4206, and two half-pointed osteoderms, LGPUT KRY 4481, 4430 were found and in Fourka only a fragment of the lip of the anterior plastral lobe, LGPUT FRK 26 (Vlachos, 2015). Those specimens are not enough to make any comparison with our specimens. The preserved material is scarce but confirms the presence of giant tortoises in Chalkidiki in the Miocene.

3.5 Taxonomic remarks

All the above comparisons help us place the studied specimens from Makrygialos and Agiannis in the species *Titanochelon bacharidisi*. The similarities with the individuals found at the eastern side of Thermaikos gulf, in size and morphology, and the differences with all the other species from Greece and Europe are strong.

The specimens from Makrygialos provide three new characters that were not previously known in the individuals from the eastern side of the Thermaikos gulf. The first one is the suprapygal 1 that completely embraces suprapygal 2 and contacts the anterolateral sides of the pygal. The other two characters are the presence of the axillary and inguinal horny scutes. The presence of an inguinal that contacts the femoral scute is important because it is also a distinctive feature from *T. bolivari*, where the inguinals do not contact the femorals. A possible explanation of why these scutes are not found in the Epanomi and Nea Kallikratia specimens could be because they do not preserve the lateral parts of their plastra. Had the individual EPN I not been mounted the way it did we would probably be able to examine if these scutes exist. Nevertheless, these characters give us new details about the shell morphology of the species.

CHAPTER 4: DISCUSSION

The discovery of giant tortoises of the species *Titanochelon bacharidisi* in both the eastern and western sides of the Thermaikos gulf confirms older hypotheses about the state of the area in the past. A similar picture to that of the Makrygialos Formation is observed in the area of western Chalkidiki in the sediments described as the Gonia Formation (Syrides, 1990). Really important is the presence of volcanic material in this formation similar to that found in the Makrygialos Formation (Syrides, 1990; Sylvestrou, 2002; Paschalidou, 2020). Same as in Makrygialos, the area of western Chalkidiki was fed by large paleocurrents coming from the volcanic centers of Almopia. The age of the Gonia Formation, based on a micromammal fauna identified in the lower layers at the Nea Silata site is dated to the Miocene-Pliocene boundary (Syrides, 1990; Vasileiadou et al., 2003). Similar volcanic material has been found in deposits in the Alatini and Nea Elvetia areas of Thessaloniki, and in Aggelochori/ Megalo Emvolon area (Syrides, 1990).

The fossils of *Titanochelon bacharidisi* found in both sides of the gulf, with Makrygialos and Agiannis almost exactly opposite of the coasts of Epanomi, Nea Michaniona, Aggelochori/ Megalo Emvolon and Nea Kallikratia, corroborate the hypothesis that during the Pliocene the area was a single plain inhabited by tortoises of various sizes that spanned from today's northern coast of Thermaikos gulf till today's foothills of Mount Olympus (Saltsidou, 2020; Paschalidou, 2020).

All the above evidence are supported by the fact that the Gonia Formation, in the eastern part of the wider Axios-Thermaikos basin, and the Makrygialos Formation, in the western part, show similar depositional conditions at the end of the Miocene and the beginning of the Pliocene. The main difference is observed only in the development of at least three limestone horizons that are wide spread in the wider area of western Chalkidiki and create characteristic terraces in the morphology of the area (Syrides, 1990); these are missing from the area of Makrygialos except as calcite horizons of small thickness but of considerable extent. In other words, it seems that in addition to the main river systems, periodic shallow lakes with intense evaporation operate in western Chalkidiki, but in the wider area of Makrygialos they are of shorter duration.

Until 2017 it was believed that the youngest occurrence of the genus *Titanochelon* was that of the locality of Vatera of the island of Lesvos, Greece, with an estimated age of 2.4 Ma (Lapparent de Broin, 2002). The youngest occurrence of a giant tortoise in the Iberian Peninsula was found in the site of Las Higueruelas of Ciudad Real, Spain, with an estimated age of 3.3 Ma (Jiménez Fuentes, 1994). However, new study by Pérez-García et al. (2017) reveals that the last known member of the *Titanochelon* lineage was located at the paleontological site of Fonelas P-1 in the Guadix Basin of Granada, Spain. The site is believed to be a hyaenid den and the estimated age is 2 million years. A femur of a giant tortoise was found which was classified as *Titanochelon* sp. This new discovery shows that the genus survived at least 1.3 million years more than speculated before in the Iberian Peninsula and almost 400,000 in the continental Europe and Asia Minor according to the available evidence (Pérez-García et al., 2017).

By looking at the extant species of large sized tortoises we can understand and possibly recreate the climate and environment that the extinct forms inhabited. Only two extant species of tortoises could be considered giants, with their shell exceeding 1 m in length, and both of them are insular forms: *Chelonoidis nigra* (Quoy and Gaimard, 1824) is found in the Galapagos Islands of the Pacific Ocean, and *Aldabrachelys gigantea* (Schweigger, 1812), that exclusively inhabits the Aldabra Atoll of Indian Ocean. There are several continental forms that can be considered large-sized with a shell length almost exceeding 70 cm that also inhabit intertropical and warm regions: *Chelonoidis denticulata* (Linnaeus, 1766) also known as the Brazilian giant tortoise from the Amazon basin, *Chelonoidis carbonaria* (Spix, 1824) also from the northern South America, *Centrochelys sulcata* that is found in the southern edge of the Sahara Desert in Africa and Saudi Arabia and Yemen, and *Stigmochelys pardalis* (Bell, 1828) that can be found in the savannas of eastern and southern Africa, from Sudan to the South Africa and Namibia.

Considering all the above it is clear that the large size in testudinids is closely related to warm climate conditions (Pérez-García et al., 2017). It is believed that the presence of large-sized tortoises suggests a subtropical climate, or at least a climate with mild winters, frost free with temperatures well above freezing (Hibbard, 1960; Holman 1971, 1976). Therefore, during the time that those giant tortoises roamed Europe and Asia Minor the climate in those areas was subtropical. Their extinction is believed to have been caused by the climate events that took place during Lower Pleistocene. As noted by Pérez-García et al. (2017) the presence of these temperature-sensitive animals in southern Spain during the Lower Pleistocene confirms previous claims that the climate was warmer in the area, with abundant water resources, as opposed to the rest of Europe where the conditions were cooler and drier.

Not many fossil sites of Greece have that many different taxa of turtles. This kind of diversity is observed only in the Upper Pliocene locality of Milia, in Grevena, including three taxa: *Testudo brevitesta* Vlachos and Tsoukala, 2016, *Mauremys* sp., and *Titanochelon* sp. (Vlachos, 2015; 2022, Vlachos and Tsoukala, 2016). In Makrygialos and Agiannis, three different taxa of turtles have also been found, *Chersine hermanni*, *Mauremys* sp. and the herein studied *Titanochelon bacharidisi* specimens (Saltsidou et al., 2022). This makes Makrygialos and Agiannis (considering them as a single locality because of their geographic proximity) one of the most diverse and rich sites in fossil turtles in Greece with at least three taxa and, in total, eleven specimens found so far along the coastline.

Compared to our area of study, the fossil localities at the eastern side of the Thermaikos gulf are not that diverse and the turtle fauna is slightly different. Except for the *Titanochelon bacharidisi* specimens, and the small-sized freshwater turtles, recognized as *Mauremys* sp. the small-sized tortoises are different. In the fossil sites of Aggelochori, or Megalo Envolon, “Salonique”, and Allatini and Pylea of Thessaloniki, the tortoises found, belong to the species *Testudo graeca* (Vlachos, 2015; Vlachos et al., 2015). This species is limited, both extant and as a fossil, at the eastern side of Axios river, so it is not strange that it is not found in the west side of Thermaikos gulf (Vlachos, 2015; Saltsidou et al., 2022). The exact same thing occurs with the species *Testudo marginata*, but in this case the taxon is limited to the west side of Axios river. (Vlachos, 2015) The hypothesis that can be made from this is that the river probably existed during the Miocene-Pliocene and acted as a natural border for the spread of these tortoises, as it does today. The same thing, apparently, did not apply to the giant tortoises as their fossils are found in both sides of the river.

Important similarities can be observed between the genus *Titanochelon* and the extant African lineages of *Centrochelys* and *Stigmochelys*. It was initially proposed by Lapparent de Broin (2000) and later by Pérez-García et al. (2020) that at least two dispersal events of African species took place in Europe. The first dispersal event took place probably before or at the beginning of the Neogene period and was most possibly related with the ‘*Gomphotherium* land bridge’ that connected Eurasia to Afro-Arabia and led to the dispersal of many other clades and especially mammals. This event led to the appearance of the *Titanochelon* clade in Europe (Pérez-García et al., 2020). The second dispersal event took place probably at the Pliocene-Miocene boundary, during the Messinian Salinity crisis which also led to the dispersal of many clades of mammals and some reptiles. This event, allegedly, led to the dispersal of *Alatochelon* in Europe.

The possible African affinities of the genus *Titanochelon* have been discussed for over two decades (Lapparent de Broin, 2000, 2002). It is proposed that the extant genus *Centrochelys* is a sister taxon to the extinct genus *Titanochelon* because of the many morphological similarities they exhibit. Those characteristics are the low shell, the absence of a cervical scute and the similar humerus. Of course, there are many more differences between the two taxa. What is even more interesting is the possibly close relationship between *Titanochelon bacharidisi* and the extant species *Centrochelys sulcata* (Miller, 1779)*,* the spurred tortoise from Africa (Vlachos et al., 2014)*.* Their main similarity is the presence of two to three thigh tubercles on the posterior side of their thigh. *Titanochelon bacharidisi* is the only species of *Titanochelon* so far with these types of tubercles preserved, although no more than one has been preserved in each specimen they have been found on. So far though, the two species are separated in phylogenetic analyses (Vlachos, 2015; Vlachos & Rabi, 2018). They were initially found in two individuals, in EPN I separated and in KLK I in situ. Now a third specimen, LGPUT MAP-2 studied herein, of the species is discovered that preserves the same character, at the western side of Thermaikos Gulf.

CONCLUSIONS

The giant tortoises from Makrygialos and Agiannis, described and discussed in this thesis, belong to the species *Titanochelon bacharidisi*. Along with the already known diagnostic characters, two new characters were proposed to be included in the emended diagnoses of the species. These are the suprapygal 1 that completely embraces suprapygal 2, and contacts the anterolateral sides of the pygal, and the presence of an inguinal scute that is wider than long and contacts the abdominal, marginals 7 and 8, and femoral scutes. Another new character of this species, but not a diagnostic one, was also added to the description and that is the presence of an axillary scute that contacts marginals 3 and 4 and the hyoplastron.

The material from our area of study and specifically the Agiannis specimens LGPUT AG-1 and LGPUT AG-2 provide new information about the morphology of the bony plates and horny scutes of the carapace of *Titanochelon bacharidisi* that was not available from the individuals of Epanomi and Kallikratia. This new information helps us create a more complete picture of the species.

The thigh tubercle preserved from the specimen LGPUT MAP-2 is only preserved in two other individuals of *Titanochelon bacharidisi*, in EPN I separated and in KLK I in situ. This bone supports the African affinities hypothesis of the species *Titanochelon bacharidisi* and the possible close relationship with the species *Centrochelys sulcata* that has been suggested in the past.

The specimens from Makrygialos and Agiannis belong to the same species that was described in the eastern part of the Thermaikos Gulf. This discovery along with the correlation of the Gonia Formation from the eastern side and the Makrygialos Formation of the western side of the Thermaikos Gulf corroborates the hypothesis that during the late Miocene to Pliocene, the gulf was a great plane that was inhabited by turtles and tortoises of different sizes, that spanned from today's northern coast of Thermaikos gulf till today's foothills of Mount Olympus.

The specimen LGPUT MAP-2 is the largest fossil tortoise found in Greece, with a shell length of almost 180 cm.

With eleven turtle individuals found in total, four small-sized, two of which are freshwater turtles and the other two tortoises, and seven giants, and at least three different species of turtles, *Titanochelon bacharidisi*, *Chersine hermanni* and *Mauremys* sp., the general locality of Makrygialos and Agiannis is the richest and most diverse in Greece in terms of turtle fossils.

The material described in this thesis is, along with the material from Epanomi, one of the most complete, to date, in Greece and one of the most complete ones in Europe, in terms of giant tortoises, with five individuals described from each locality. When the two specimens from Makrygialos that have not been excavated yet, LGPUT MAP-5 and LGPUT MAP-6, be prepared and studied, the general locality of Makrygialos and Agiannis will have the richest material in Greece and Europe.

ABSTRACT

In this thesis, new material of giant tortoises from the localities of Makrygialos (MAP) and Agiannis (AG) is described, which has been excavated from 2015 to 2017 and prepared till 2022. The study of this material confirmed the presence of the species *Titanochelon bacharidisi* in the western side of the Thermaikos Gulf right across its type locality, Epanomi. The age of the fossils, as determined by the age of the Makrygialos formation, inside of which, three of the five specimens were discovered, is Late Miocene to Pliocene. This discovery strengthens the hypothesis that, during the Miocene to Pliocene, the Thermaikos gulf was a wide plane that extended from Thessaloniki till today's foothills of Mount Olympus.

Five different individuals are described, two male, two female and one of indetermined sex, that provide new information about the species. Two new characters are added in the emended diagnosis of the species, the first being the suprapygal 1 that completely embraces suprapygal 2, and contacts the anterolateral sides of the pygal, and the second the presence of an inguinal scute that is wider than long and contacts the abdominal, marginals 7 and 8, and femoral scutes. Another new character, that is not diagnostic, is added in the general description of the species and that is the presence of an axillary scute that contacts marginals 3 and 4 and the hyoplastron. Furthermore, the newly described specimens provide additional information about the morphology of the carapace that was known from the specimens of the eastern side of the gulf.

The material described herein is one of the most complete material in Greece and Europe as only in the eastern side of the Thermaikos gulf, more than five specimens of giant tortoises have been discovered. The material from Makrygialos and Agiannis, including the small-sized turtles, is one of the most complete ones in Greece and Europe both in terms of number of species, and specimens. This study lays the groundwork for future research into the morphology, evolution and origin of these animals.

ΠΕΡΙΛΗΨΗ

Στην παρούσα διπλωματική εργασία περιγράφεται νέο υλικό γιγαντιαίων χελωνών από τις θέσεις Μακρύγιαλος (MAP) και Αγιάννης (AG), Πιερία το οποίο έχει ανασκαφεί από το 2015 έως το 2017 και έχει συντηρηθεί έως το 2022. Η μελέτη αυτού του υλικού επιβεβαίωσε την παρουσία του είδους *Titanochelon bacharidisi* στη δυτική πλευρά του Θερμαϊκού κόλπου ακριβώς απέναντι από την τυπική θέση, Επανομή. Η ηλικία των απολιθωμάτων, όπως καθορίζεται από την ηλικία του σχηματισμού του Μακρυγιάλου, μέσα στον οποίο ανακαλύφθηκαν τρία από τα πέντε δείγματα, κυμαίνεται από το ανώτερο Μειόκαινο έως το Πλειόκαινο. Η ανακάλυψη αυτή ενισχύει την υπόθεση ότι, κατά το Άνω Μειόκαινο έως το Πλειόκαινο, ο Θερμαϊκός κόλπος ήταν μια μεγάλη πεδιάδα που εκτεινόταν από τη Θεσσαλονίκη μέχρι τους σημερινούς πρόποδες του Ολύμπου.

Περιγράφονται πέντε διαφορετικά άτομα, δύο αρσενικά, δύο θηλυκά και ένα ακαθόριστου φύλου, που παρέχουν νέες πληροφορίες για το είδος. Δύο νέοι χαρακτήρες προστίθενται στην διάγνωση του είδους: ο πρώτος είναι η οστέινη πλάκα suprapygal 1 που αγκαλιάζει πλήρως τη suprapygal 2 και έρχεται σε επαφή με τις εμπρόσθιες και πλάγιες πλευρές της pygal, και ο δεύτερος είναι η παρουσία κεράτινης πλάκας inguinal που είναι πιο φαρδιά από ότι επιμήκης και εφάπτεται την κεράτινη πλάκα femoral, τις peripheral 7 και 8, και τη femoral. Ένας ακόμη νέος μη διαγνωστικός χαρακτήρας, προστίθεται στη γενική περιγραφή του είδους και αυτός είναι η παρουσία μιας axillary κεράτινης πλάκας που έρχεται σε επαφή με τις peripheral 3 και 4 και το hyoplastron. Επιπλέον, τα νέα δείγματα παρέχουν επιπρόσθετες πληροφορίες για τη μορφολογία του κελύφους γνωστό ως σήμερα από δείγματα της ανατολικής πλευράς του Θερμαϊκού κόλπου.

Το υλικό που περιγράφεται στην παρούσα εργασία είναι από τα πληρέστερα στην Ελλάδα και την Ευρώπη καθώς μόνο στην ανατολική πλευρά του Θερμαϊκού κόλπου έχουν ανακαλυφθεί περισσότερα από πέντε δείγματα γιγαντιαίων χελωνών. Το υλικό από τον Μακρύγιαλο και τον Αγιάννη, συμπεριλαμβανομένων των μικρού μεγέθους χελωνών, είναι ένα από τα πληρέστερα στην Ελλάδα και την Ευρώπη τόσο σε αριθμό ειδών, όσο και σε αριθμό δειγμάτων. Η μελέτη θέτει τις βάσεις για μελλοντική έρευνα σχετικά με τη μορφολογία, την εξέλιξη και την προέλευση αυτών των ζώων.

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