AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Food for thought: sub-fossil and fossil chelonian remains from Franchthi Cave and Megalopolis confirm a glacial refuge for Emys orbicularis in Peloponnesus (S. Greece)

This is the author's manuscript

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/1589861 since 2017-05-17T12:04:55Z

Published version:

DOI:http://dx.doi.org/10.1016/j.quascirev.2016.08.027

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

24 January 2025

This Accepted Author Manuscript (AAM) is copyrighted and published by Elsevier. It is posted here by agreement between Elsevier and the University of Turin. Changes resulting from the publishing process - such as editing, corrections, structural formatting, and other quality control mechanisms - may not be reflected in this version of the text. The definitive version of the text was subsequently published in QUATERNARY SCIENCE REVIEWS, 150, 2016, http://dx.doi.org/10.1016/j.quascirev.2016.08.027.

You may download, copy and otherwise use the AAM for non-commercial purposes provided that your license is limited by the following restrictions:

(1) You may use this AAM for non-commercial purposes only under the terms of the CC-BY-NC-ND license.

(2) The integrity of the work and identification of the author, copyright owner, and publisher must be preserved in any copy.

(3) You must attribute this AAM in the following format: Creative Commons BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/deed.en), http://dx.doi.org/10.1016/j.quascirev.2016.08.027

When citing, please refer to the published version.

Link to this full text:
http://hdl.handle.net/2318/1589861

This full text was downloaded from iris - AperTO: https://iris.unito.it/

iris - AperTO

University of Turin's Institutional Research Information System and Open Access Institutional Repository

Food for thought: sub-fossil and fossil chelonian remains from Franchthi Cave and Megalopolis confirm a Glacial refuge for *Emys orbicularis* in Peloponnesus (S. Greece)

Evangelos Vlachos[a,b*] and Massimo Delfino[c,d]

[a] CONICET – Museo Paleontologico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut, Argentina.

[b] School of Geology, Aristotle University of Thessaloniki, University Campus, 54124 Thessaloniki, Greece.

[c] Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, 10125 Torino, Italy.

[d] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, (UAB), Edifici Z, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

* corresponding author: evlacho@mef.org.ar; evlacho@gmail.com

ABSTRACT

Peloponnesus peninsula (S. Greece) shows a remarkable extant chelonian fauna that has received considerable attention from a molecular and morphological point of view. Here we present new evidence from the fossil and sub-fossil record of two important sites in the area, Franchthi Cave and Megalopolis. The archaeological material from Franchthi Cave (Upper Paleolithic – Neolithic / latest Pleistocene –

early Holocene) represents food remains from small game prey of the humans that inhabited the cave. The palaeontological material from Megalopolis (Late Pleistocene) comes from old and new excavations. The studied specimens, combined with information from molecular, climatic and zoological works, provide for the first time direct evidence for the presence of the European pond turtle, *Emys orbicularis*, in the glacial refuge of South Greece that was hypothesized on the basis of the results of molecular investigations. We also describe other chelonian taxa present in the localities, the Hermann's tortoise *Testudo hermanni* and the Balkan stripe-necked terrapin *Mauremys rivulata*, and review previously published chelonian material from Peloponnesus.

Keywords: zooarchaeology; human exploitation; climate change; European pond turtle; tortoise; Testudines.

HIGHLIGHTS

- Study of chelonian food remains of humans from Franchthi Cave (Peloponnesus, S. Greece)
- New chelonian material from the Late Pleistocene site of Megalopolis (Peloponnesus, S. Greece)
- Review of the entire chelonian material from Peloponnesus (S. Greece).
- Confirmation of genetic evidence for a glacial refuge for the European pond turtle, *Emys orbicularis*.
- A framework for the analysis of other sites with human interaction with chelonian taxa.

INTRODUCTION

The Peloponnesus is the largest peninsula of Greece, constituting the southernmost continental part of the South Balkans (Fig. 1A). Its diverse geographical and geological setting, reflecting a complex history, is home to a quite interesting chelonian fauna that has received considerable recent attention, from both molecular and morphological perspectives. Bour (1996) for example, has identified a dwarf population of the marginated tortoise, *Testudo marginata*, near Taygetos mountain in the south Peloponnesus, which he named as a new species, *Testudo weissengeri* although molecular evidence presented by Fritz et al. (2005b) did not support this distinction. Interestingly, Fritz et al. (2006) also reported some distinct haplotypes of *Testudo hermanni* from more or less the same area of Taygetos mountain. In addition to the testudinid taxa, two freshwater turtle taxa are found in Peloponnesus as well. *Mauremys rivulata* (Balkan stripe-necked terrapin) is the representative of the family Geoemydidae (see Fritz et al., 2008), whereas *Emys orbicularis hellenica* (European pond turtle) is the representative of the family Emydidae (see Fritz et al., 2009). The European pond turtle, is of particular interest in our paper, and the records from Peloponnesus are among the southernmost in Europe (see Fritz et al., 2015).

In this paper we present important new *E. orbicularis* fossil and sub-fossil records from Peloponnesus, which include the only confirmed records of this taxon in Greece prior to the Holocene (see Vlachos, 2015). The material presented herein comes from two of the most important Pleistocene localities on the peninsula, Franchthi Cave and Megalopolis (Fig. 1B). Franchthi Cave preserves a remarkable record of human subsistence evolution over thousands of years from the Late Pleistocene through the early Holocene (Stiner & Munro, 2011:618). Thousands of osteological specimens from diverse taxa were collected during excavation of the cave (Jacobsen, 1981). The meticulous study of this material has provided insights into the changing hunting strategies of the humans that inhabited the cave (Stiner & Munro, 2011; references therein for further information regarding the cave). Turtles and tortoises were occasionally exploited throughout the sequence and were especially important during the Final Paleolithic period when humans began to diversify their diets and rely more heavily on lower-ranked small game prey. Stiner & Munro (2011) undertook a quantitative analysis of diachronic change across the long sequence of the cave, and focused specifically on the timing of the appearance and changing abundance of chelonian taxa in relation to other prey species. In contrast, here we analyze the turtle material from a morphological (with anatomical drawings of the most diagnostic specimen), taxonomic, and biogeographic point of view. Our work presents new information on the morphology and taxonomy of this material, as well as a first estimation of the minimum number of individuals.

The site of Megalopolis is well known for the recovery of significant remains of the straight-tusked elephant (see Tsoukala et al., 2011 and references therein). The site has also yielded turtle remains that were previously described by Melentis (1966). We reinterpret the original material in light of the discovery of new specimens by recent expeditions in the area (see Material & Methods). In addition to *E. orbicularis*, we provide information on other chelonian taxa present in these localities (i.e., the testudinid *Testudo hermanni* and the geoemydid *Mauremys rivulata)*. Finally, we integrate other published records from Peloponnesus to provide a detailed revision of the fossil record of this peninsula spanning the Late Pleistocene and early Holocene.

The material presented here also has important implications for the phylogeography of *E. orbicularis* in Europe during the Late Pleistocene and early

Holocene. Fritz et al. (2007, 2009) showed that *Emys* was confined to refugia in Anatolia and the south-eastern Balkans during the Glacial period. The mitochondrial phylogeography they present (Fritz et al., 2007, 2009) indicates that *Emys* expanded north and colonized the rest of Europe during the warmer parts of the Holocene. Also, absolute dates from sub-fossil remains enabled Sommer et al. (2007, 2009) to reconstruct the expansion of *Emys* from glacial refugia. The *E. o. hellenica* populations from Peloponnesus represent endemic haplotypes (Vamberger et al. 2015 and references therein) suggesting a distinct refuge in the area (Fritz et al., 2007). Similar refuges have been hypothesized in other parts of Europe below 40°N latitude, as for example in Spain (Lenk et al., 1999), with adequate fossil and sub-fossil record of *Emys orbicularis* (e.g. Blain et al., 2013; Jiménez-Fuentes, 1986; Pérez-García et al., 2015 and references therein).

Although the skeletal material from Franchthi is not directly dated using absolute methods, radiocarbon dating of volcanic ash and charcoal from associated layers allows a detailed chronological reconstruction of the distribution of material within the cave's stratigraphy (see Material & Methods). The information presented herein allows us to investigate the climatic response of *E. orbicularis* to changing conditions across the Late Pleistocene to early Holocene transition in the South Balkans. We also discuss the implications of the confirmed presence of *M. rivulata* in the Pleistocene and Neogene times in Greece on recent results from genetic studies (Vamberger et al. 2014).

Institutional Abbreviations: AMPG, Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, Greece; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; UU MEG, Institute of Earth Sciences, Utrecht University (The Netherlands), Megalopolis collection.

Anatomical Abbreviations: Bony plates are indicated with small letters, horny scutes with capitals. ABD, abdominal; AN, anal; car, carapace; CE, cervical; cos, costal; ent, entoplastron; ep, epiplastron; FE, femoral; fr, fragment; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral; hum, humerus; juv, juvenile; MA, marginal; neu, neural; nuc, nuchal; PEC, pectoral; per, peripheral; pla, plastron; PLE, pleural; py, pygal; SUC, supracaudal; sp, supragygal; VE, vertebral; xi, xiphiplastron.

MATERIAL & METHODS

Franchthi Cave: The skeletal material from Franchthi Cave derives from anthropogenic deposits in the cave, which is developed in a Lower Cretaceous limestone formation. The excavation in Trench H1-B was carried out in a series of archaeological units that followed the anthropogenic stratigraphy within larger lithostratigraphic layers (layers P-Z; Units 106-215+; Farrand, 2000; Stiner & Munro, 2011). The earliest dates in the cave derive from K-Ar dates on windblown volcanic ash, originating in Naples, Italy. Radiocarbon dates on charcoal provide dates from a number of other units from different trenches in the cave. A summary of these dates and the archaeological occupation phases for Trench H1-B published in Stiner & Munro (2011:620) provides the chronology used here. For this study, the Pleistocene/Holocene boundary is important, and likely corresponds roughly to the division between Stratum U (Units 151/152-154; 11,700 – 12,500 radiocarbon years

BP) and Stratum V (Units 148-151, undated) in H1B. In addition to the remains of turtles and tortoises described here, thousands of specimens of ungulates, carnivorans, small mammals, birds, fishes, and other reptiles representing the diet of the past human occupants were recovered (Stiner & Munro, 2011). The material is stored in the collections of the D’ Ephorate of Prehistoric Archaeology, Nafplion (S. Greece). Because of the large size of the assemblage, each specimen was not given its own specimen number, but is referenced according to its excavation unit number provided during excavation. Here we present an overview of the material from Trench H1-B for each taxon, and where necessary we mention individual specimens and the corresponding archaeological unit (e.g. 155). Table 2 in Stiner and Munro (2011) indicates the corresponding lithostratigraphic layer for each excavation unit.

Megalopolis: The material originates from sections exposed by ongoing use of the Megalopolis basin for the production of electricity. The material described by Melentis (1966) could not be located in the AMPG collections, and thus the re-interpretations presented here are based on the original drawings of Melentis. The new, so far unpublished, material is currently stored in the collections of the Institute of Earth Sciences at Utrecht University (The Netherlands).

Shell nomenclature follows Zangerl (1969), whereas taxonomy follows Joyce et al. (2004), Parham et al. (2006) and van Dijk et al. (2012). The Number of Identified Specimens (NISP) refers to specimens that could be identified to taxonomic category (*Testudo*/*Emys*) and to an anatomical portion of a skeletal element (a bony plate or appendicular element). Given the disarticulated and fragmented nature of the material and the wide distribution of specimens across a variety of stratigraphic units in Franchthi Cave, the Minimum Number of Individuals was calculated separately for each Unit. MNI was calculated only when specimens could be confidently identified and not for indeterminable carapace and plastron remains. In the few cases where the MNI was greater than 1, the count was based on diagnostic neural plates of the carapace.

The specific identification of both *Emys orbicularis* and *Mauremys rivulata* are based on the current distribution of these species and not only on the morphology of their remains. So far no reliable morphological characters have been proposed to discriminate between skeletal remains of *E. orbicularis* and *Emys trinacris* (a Sicilian endemism; see Fritz et al., 2005a; Vamberger et al. 2015), and to identify the several *Mauremys* species inhabiting Europe and the Mediterranean area.

THE CHELONIANS FROM FRANCHTHI CAVE

Testudines Batsch, 1788
Cryptodira Cope, 1868
Emydidae Bell, 1825
Emys Duméril, 1805
Emys orbicularis Linnaeus, 1758
Fig. 2-5

Description: Nearly all elements of the shell are represented in the Franchthi material (Table 1; Figs. 2-5; blue color, online version). The vast majority of the material is fragmented, and no evidence of articulated specimens was observed. Most of the specimens are fragments of costal plates, some of which were complete in juvenile specimens (Units 155, 158), or almost complete in adult ones (e.g. Unit 160) (Fig. 4). These costals are in some cases crossed by the pleural sulci and their medial border has a short anterior and a longer posterior side, as it is typical of the costals that articulate with hexagonal neurals. The second best represented elements are the peripherals. In all the identified peripherals, the pleurals cover the medial parts of the plates. Few elements are preserved from the remaining parts of the carapace. Two nuchal plates exhibit a lateral covering of the first pleurals (Units 160, 161; Fig. 3). The cervical scute is long and rather narrow. Interestingly, the neural series is very well represented by at least 29 specimens. Some of these are the rectangular (longer than wide), first neurals (Units 160, 161; Fig. 3), and are crossed by a vertebral sulcus. The remaining neurals are typically hexagonal, with short anterior lateral sides. Some of these are crossed by the sulcus between the vertebrals (e.g. Units 160, 161; Fig. 3), whereas others are not crossed by sulci (e.g. Unit 160, Fig. 3). Two suprapygals were identified (Unit 160; Fig. 3). One of them, a second suprapygal, is much wider than it is long with a narrow anterior side; it is not crossed by any sulci, being identified as a second suprapygal. The other suprapygal (probably the second as well) is fragmented and exhibits a dorsal carina. One pygal plate has been identified (Unit 161; Fig. 4), and is slightly wider than it is long. It is overlapped anteriorly by the fifth vertebral, and is covered by the twelfth marginal on its posterior side. The plastron is significantly less common in the studied material than the carapace. The right xiphiplastron (Unit 137; Fig. 2) among the best-preserved specimens, showing a rounded posterior outline for the lobe that indicates that an anal notch is absent. The plate is crossed only by the femoro-anal sulcus. The femorals are medially short and laterally long, whereas the anals are medially long and laterally short. Few, fragmented, hyoplastra are preserved, neither being crossed by the pectoro-abdominal sulcus.

Taxonomy: Stiner & Munro (2011) preliminarily identified the chelonians from Franchthi Cave as *Emys/Mayrymys* (sic) and *Testudo* sp. This re-examination of the material, enabled a more accurate identification. Although very fragmentary, the material presents some elements diagnostic of *Emys orbicularis*. The nuchal plate (160; Fig. 3) is wide and overlapped on the lateral side by the first pleural scute. Although it is incomplete, the lyre-shape is apparent in the first vertebral of *E. orbicularis*. In contrast, in *Mauremys* spp. the nuchal is narrower and the pleurals do not overlap with the lateral side. Additionally, the xiphiplastron (Unit 137; Fig. 2) lacks an anal notch and a long anal covering on the ventral side, further confirming the presence of *Emys*. Moreover, none of the hyoplastra are marked by a pectoro-abdominal sulcus, as is typical of *E. orbicularis* since it has a hyo-hypoplastral hinge. Finally, the presence of *E. orbicularis* is clearly demonstrated by the relatively small pygal, wider than long, hosting both the sagittal sulcus between the two last marginals and the transversal sulcus between the last marginals and the fifth vertebral. The pygal does not host the latter sulcus in both *Testudo* and *Mauremys* (and is longer than wide in *Testudo*). The remaining diagnostic elements (neurals, entoplastron, suprapygals) are consistent with *E. orbicularis* as well.

Testudinidae Batsch, 1788

Testudo Linnaeus, 1758 sensu lato or Pan-*Testudo* (sensu Joyce et al., 2004 and Parham et al., 2006)

Testudo hermanni Gmelin, 1789

Fig. 2,3,5

Description: In the material of *Testudo* from Franchthi Cave many diagnostic elements are missing (Figs. 2-5; brown color, online version). The best-preserved specimen is a partial carapace (Unit 168; Fig. 5) that preserves most of the anterior rim and the nuchal, the second neural and the corresponding costals. The nuchal is hexagonal and shows a narrow and long cervical scute. The carapace is covered by narrow vertebrals, much narrower than the pleurals. The second neural is octagonal. The costals indicate the alternating pattern of testudinids, with medially short and laterally long elements alternating with medially long and laterally short elements (also seen in the neural/costal association of Unit 160, Fig. 3). In the preserved part there is good overlap between the pleuro-marginal sulci and the costo-peripheral sutures. From the remaining specimens, few show some characters of potential diagnostic value. The neural 5 (Unit 160, Fig. 3) is rectangular, wider than long, crossed transversely by the vertebral sulci. The complete entoplastron (Unit 166, Fig. 5) is rather flat and shows gulars that overlap the anterior part of the entoplastron. Also, the humero-pectoral sulcus does not cross the entoplastron, a condition also indicated by an hyoplastron fragment (Unit 164; Fig. 5).

Taxonomy: All the above-mentioned characters are consistent with *Testudo.* Franchthi Cave is within the range of extant *T. h. boettgeri*, whereas *Testudo graeca ibera* is mainly found in Northeastern Greece. Additionally, we did not find any specimens indicative of *Testudo marginata*, i.e. posteriorly flared peripherals. Based on the available material, we cannot confirm or refute the presence of a hypo-xiphiplastral hinge (that is characteristic of *Testudo*), as the relevant hypoplastra and xiphiplastra are missing in the studied material. However, the preserved specimens are consistent with *Testudo hermanni* based on the narrow vertebrals and the flat entoplastron.

Distribution and human interaction: As far as temporal distribution of the chelonians in the cave is concerned, we are able to update the distribution shown in Fig. 12 of Stiner & Munro (2011). The main change concerns the first record of *Emys orbicularis*. The costal specimen from Unit 173 (Fig. 5) is attributable to *Testudo* and not to a freshwater taxon, since its medial side corresponds to the rectangular/octagonal neural pattern of *Testudo.* Therefore, the oldest remains of *Emys* at the site are the two peripherals from the Epigravettian (Units 165 and 166; Fig. 5), as indicated by the diagnostic overlap of the pleural scutes.

The chelonian specimens from Franchthi Cave represent the small prey of the early humans who inhabited the cave. Stiner & Munro (2011) noted the interesting fact that the chelonian exploitation starts first with tortoises and then shifts towards the aquatic taxa in the Epigravettian. This shift is accompanied by very high cultural inputs relative to sedimentation rate, high burning rates and further focus towards marine prey and fishing (Stiner & Munro, 2011). The small changes in the identification of some specimens herein make the distinction between tortoise/turtle exploitation even clearer. The European pond turtle shows an impressive expansion in the stratigraphy of the site during the occupation phase 5 (Epigravettian), somewhat between 13,300 and 12,700 BP, and is absent before 15,000 BP. On the contrary, *Testudo* is present since the “Gravettoid” period, showing its maximum expansion during the occupation phase 4 (Epigravettian), prior to the presence of *Emys* (Fig. 6). The interpretation of this distribution is tricky. First and foremost, this distribution primarily reflects the changes in dietary preferences of humans and their foraging strategy, and does not necessarily reflect the relative abundances of these taxa in the environment. However, these results clearly indicate the presence of *Emys* in the area at least since the latest Pleistocene during one of the coldest periods of the Quaternary for Europe. Given that the humans from Franchthi focused on aquatic niches in that period for the first time, and as a result *Emys* appears on the deposits of the cave, it is possible that the European pond turtle was present in the area even earlier.

Given the significant evidence for human involvement in the accumulation of turtle material at Franchthi Cave, some important conclusions can be inferred that can aid the interpretation of chelonian assemblages from other localities (Table 1). First in the case of *Emys*, elements of the appendicular skeleton (n=30, mostly humeri; 8%) are scarce compared to shell remains (n=350; 92%). The proportion of *Testudo* appendicular elements is even lower (3%). Moreover, the material is highly disarticulated; there are no articulated specimens of *Emys* and only two articulated specimens of *Testudo* [a neural articulated with two costals (Unit 160) and a partial anterior part of the carapace (Unit 168)]. In a complete skeleton of *Emys* and *Testudo* the analogies between carapacial/plastral isolated plates is 80% / 20% (47-48/9). In the Franchthi material the analogies of emydid material are slightly tipped towards the carapace (*Emys*=324, 92%; *Testudo*=105, 83%), which could be an effect of fragmentation as well. Finally, evidence of human interaction is confirmed based on the presence of burned specimens of both taxa (see Stiner & Munro, 2011:table 3) and on evidence for striations on the visceral face of some carapace specimens such as the partially articulated neural/costals of *Testudo* from Unit 160. Minimum Number of Individuals data (MNI; see Material & Methods) reveals that no more than one individual per taxon is necessary to account for all of the recovered material in most units. In Units 158-162, where *Emys* is most common, 7 *Emys* individuals and 2

Testudo individuals could account for all of the specimens. Given the disarticulated nature of the material (especially the peripherals which are difficult to identify when disarticulated), our estimations of MNI are conservative and the actual number of individuals could be slightly greater. If we assume that the material found in each unit is discrete (i.e. the same turtle individual is present only in one unit), then the MNI exploited at Franchthi Cave is 20 *Emys* and 22 *Testudo*.

THE CHELONIANS FROM MEGALOPOLIS

Emydidae Bell, 1825

Emys Duméril, 1805

Emys orbicularis Linnaeus, 1758

Fig. 6,7

Material published by Melentis (1966): AMPG 1966/47, left hyoplastron; AMPG 1966/48, left hypoplastron; AMPG 1966/49, left xiphiplastron; AMPG 1966/50, left hypoplastron; AMPG 1966/53, left hyoplastron. New material: UU MEG 501, neural; UU MEG 502, peripheral; UU MEG 503, peripheral; UU MEG 504, right epiplastron; UU MEG 513, right epiplastron; UU MEG 505, entoplastron; UU MEG 512, right hyoplastron; UU MEG 507, left hypoplastron; UU MEG 506, right xiphiplastron.

Description: The following description integrates the information coming from the lost material originally described and figured by Melentis (1966), here re-figured with interpretative drawings (Fig. 7), and unpublished material that is here described for the first time (Fig. 8).

The only carapace fragments clearly referable to *Emys* are few peripherals (Fig. 8A-C) characterized by a distinct pit for the reception of the costal distal process and by the broad overlap of the pleural shield (leaving a sulcus on a the peripheral far from the costo-peripheral suture). One peripheral element from the bridge region clearly shows the scar of the plastral hinge on its internal surface (Fig. 8A).

The epiplastra (Fig. 8D) are crossed by the gulo-humeral sulcus (the area formerly covered by the gular is much smaller than that covered by the humeral shield) and have a very small gular pad that is medially very narrow in dorsal view, and flat in anterior view. Due to the underdevelopment of the gular pad there is no hint of gular pocket; the surface covered by the gular shield does not protrude from the anterolateral profile of the bone. The entoplastron (Fig. 8D) is rounded in shape, rather flat, and crossed by both the gulo-humeral and humero-pectoral sulci.

Two hyoplastra were figured by Melentis (Fig. 7A,D) and are also present in the unpublished material. Thanks to them it is possible to characterize this element as being crossed by the humero-pectoral sulcus in its anterior region (so that it crossed also the neighboring entoplastron) and by the pectoro-abdominal sulcus nearly overlapping the posterior edge of the bone, indicating the presence of the hyo-hypoplastral hinge. The hypoplastra are also well represented in both the samples (Fig. 7B,E; see also fig. 3B in Melentis, 1966). Particularly informative is AMPG 1966/48 that corresponds to an almost complete left hypoplastron, with only the antero-lateral corner missing. It is slightly wider than long. It is crossed only by the abdomino-femoral sulcus in the posterior half of the plate. The anterior border appears to be the coincidence of the anterior hypoplastral suture and the anterior abdominal sulcus, resembling the condition noted by the presence of a hyo-hypoplastral hinge. As shown by AMPG 1966/49, the xiphiplastra (Fig. 7C; see also fig. 3C in Melentis, 1966) are crossed only by the femoro-anal sulcus, which is sigmoid in shape (because the femorals are medially short and laterally long, whereas the anals are medially long and laterally short), and do not have a significant anal notch. The lateral edge of the element is not significantly notched in correspondence of the femoro-anal sulcus (Fig. 8F).

Geoemydidae Theobald, 1868

Mauremys Gray, 1869

Mauremys rivulata Valenciennes *in* Bory de Saint-Vincent, 1833

Material published by Melentis (1966): AMPG 1966/45, right xiphiplastron; AMPG 1966/46, left xiphiplastron; left xiphiplastron; AMPG 1966/51, left hyoplastron; AMPG 1966/52, right hyoplastron; AMPG 1966/54, right epiplastron. New material: UU MEG 508, peripheral; UU MEG 509, right epiplastron; UU MEG 510, left epiplastron; UU MEG 511, right xiphiplastron.

Description: as for the remains of *Emys*, for the sake of completeness this description combines the morphological characters of both the old and new materials.

The only carapace element referable to this taxon is an isolated peripheral showing the transversal pleuro-marginal sulcus very far from the costo-peripheral suture and the absence of any distinct pit for the corresponding costal process.

More informative are the plastral elements. The epiplastra (Fig. 7F, 8I,J; see also fig. 7 in Melentis, 1966) are about as long as wide and show a variably expressed constriction at the level of the gulo-humeral sulcus. The area formerly covered by the gular shield is modestly protruding anteriorly in AMPG 1966/54 (Fig. 7F) and UU

MEG 512 [Fig. (J), but extremely in the very large (35 mm long and broad) UU MEG 509 (Fig. 8I)]. However, the gular pad is markedly flat in all the three available epiplastra and does not give origin to any gular pocket. Due to position of the gulo-humeral sulcus is clear that the gulars covered also part of the entoplastron.

The two hyoplastra described by Melentis (Fig. 7G,H; see also fig. 5A in Melentis, 1966) are longer than wide (slightly in the case of AMPG 1966/51, significantly in the case of AMPG 1966/52) and crossed by the humero-pectoral sulcus anteriorly and by the pectoro-abdominal sulcus posteriorly. Based on the morphology of the hyoplastra it can be estimated that the entoplastron was rather wide and crossed by the humero-pectoral sulcus posteriorly.

The three complete xiphiplastra (Fig. 7I,J, 8K; see also fig. 2A in Melentis, 1966) are crossed in their posterior half by a rather straight femoro-anal sulcus. The latter corresponds to a significant constriction at the lateral edge of the element. Posteriorly, a variably expressed but comparatively wide, deep and angular notch is present. At least in UU MEG 511, the posterior tip is ventrally tilted.

Comments: The specimens published by Melentis (1966) have been identified by him as ‘*Clemmys*’ *caspica*, an identification that has been followed in the revision of Georgalis & Kear (2013) as *Mauremys caspica*. However, half of these specimens preserved several characters that allow the attribution to the European pond turtle, *Emys orbicularis*. Worth mentioning are the presence of a hyo-hypoplastral hinge, overlap of the pectoral scutes on the entoplastron, absence of anal notch with a rounded posterior lobe of the plastron, and medially long anal scutes. It should be remarked here, however, that direct observations on these specimens are not possible, but these characters are clearly seen in the detailed drawings of Melentis (1966) and were confirmed by the unpublished material here described for the first time. Findings of the European pond turtle are not unexpected in Megalopolis basin, as such findings have been listed (but not studied in detail) by van Vugt et al. (2000). The remaining specimens are attributed to *Mauremys rivulata* (following the distribution of the extant taxa as stated in the section Materials and Methods), on the absence of hyo/hypoplastral hinge and the deep rounded anal notch. This identification is confirmed also by the new specimens from Megalopolis from the Utrecht collection that are congruent with the morphology of the ones formerly described by Melentis (1966). Worth noting is that the anterior protrusion variably expressed by the epiplastra, in the area corresponding to the gulars, falls within the range of morphologies shown by extant *Mauremys*, with the possible exception of the specimen from MTH 3 that could represent and extreme condition still unreported in extant *Mauremys* from the Mediterranean region.

OTHER MATERIAL FROM PELOPONNESUS

Schleich (1982) described *Testudo marginata* specimens from the Pleistocene Epoch in Laconia (Peloponnesus). The material consists of sections of a shell, such as the left posterior carapacial rim, peripherals, costal fragments, the right epiplastron and parts of the hyoplastra, which could belong to the same individual. According to the author the original material is stored in the Institute of Geology and Subsurface Research (Athens; now Institute of Geology and Mineral Exploration, IGME), whereas casts of these specimens are stored in BSPG. Personal communication (EV; 2014) with IGME failed to locate these specimens. Personal observations (EV; 2012) on the casts in BSPG however, confirm the Schleich's (1982) identification of *T.*

marginata, on the basis of the posteriorly flared carapacial rim. The presence of this taxon in this locality falls within the extant range of the marginated tortoise.

DISCUSSION

Several papers have reconstructed the mitochondrial phylogeography of *Emys orbicularis* and indicate that the Balkans provided a glacial refuge for this taxon. Lenk et al. (1999) suggested the existence of several refuges during the last glacial period in Europe, south of 40°N latitude and subsequent range expansions of this taxon in the Holocene. A few years later, Fritz et al. (2007) improved the sampling of Lenk et al. (1999), and suggested that glacial refuges also existed in the Black Sea region. They also suggested that smaller refuges (with smaller scale range expansions) of *Emys orbicularis hellenica* existed in south Italy and southern Greece. The mitochondrial lineage IV of *E. o. hellenica* (sensu Fritz et al., 2007) also suggests that the two refuges where distinct from one-another (one in southern Italy and another in Peloponnesus) and that the Greek occurrences of *Emys* in Corfu and Evvia probably originate from the Italian populations (Fig. 9). These results are further corroborated by population genetic approaches (Pedall et al., 2011 and Vamberger et al., 2015), who indicate a glacial refuge of *E. o. hellenica* in south Greece. Sommer et al. (2007, 2009) used absolute dates of sub-fossil remains of *Emys* from various European localities to reconstruct the expansion of this taxon into central and northern Europe during favorable warm periods within the Holocene. According to Sommer et al. (2007), the mitochondrial lineage II (sensu Fritz et al., 2007) of *Emys* reached northern Europe before 11,000 BP (Fig. 9) and even as far north as in Sweden few thousand years later (Sommer et al., 2009).

The *E. orbicularis* records from Franchthi Cave and Megalopolis are important, because they constitute the oldest confirmed records of this taxon in Greece. The systematic revision of the chelonian remains from Greece (Vlachos, 2015) showed that, besides Peloponnesus, *Mauremys rivulata* was also present during the Pleistocene in Crete and on the island of Kos (Aegean), but no evidence has been found on Central and North Greece at that time. Geoemydids were present in North Greece in Pliocene (Vlachos, 2015; Vlachos & Tsoukala, 2016) and Miocene times (e.g. Georgalis & Kear, 2013; Vlachos, 2015; Vlachos et al., 2015) but emydids are not known from that period (Vlachos, 2015). The antiquity and different distribution of *Mauremys* (as compared to *Emys*) in Greece could provide support to the suggestion in Vamberger et al. (2014 and reference therein) about capability of transoceanic gene flow between *Mauremys*. Briefly, mitochondrial differentiation between Greek and Turkish populations is weak for this taxon, contrary to the pattern seen in *Emys*, suggesting that the biogeographical barriers of the region (e.g. Mid-Aegean trench) do not affect the two taxa in the same way (Vamberger et al., 2014). It seems likely that the tolerance of *Mauremys rivulata* against salty water could allow transoceanic dispersal throughout the region (Vamberger et al., 2014). A detailed study of other material from Greek paleontological and Paleolithic sites is needed to revise the current picture, as chelonian remains have received little attention.

Emys orbicularis first appears at Franchthi Cave after the end of the Last Glacial Maximum and increases during the Epigravettian (Late Pleistocene) and towards the Final Paleolithic (Latest Pleistocene). The climatic reconstruction of the Aegean region during this period (Dormoy et al., 2009 and references therein) shows that temperatures were rising at this time (Fig. 6). Between 14,700 and 12,500 BP (Bølling/Allerød period), the marine pollen records record a temperate phase, with warm (mean annual warm temperatures up to 25°C; mean annual cold temperatures down to -5°C) and moist conditions (mean annual precipitation from 350 to 550 mm), and evidence of a sub-seasonal "Mediterranean" rainfall regime similar to the modern conditions (Dormoy et al., 2009; Fig. 6). These conditions would favor the survival, diversification and expansion of the pond turtle in Greece. Indeed, during this period we notice the maximum number of findings from this taxon in Franchthi Cave. The Late Pleistocene remains from Megalopolis are also in accordance with those findings, establishing the presence of *E. orbicularis* in Peloponnesus during the Pleistocene. As such, the emerging picture of the geographical and temporal distribution of emydids and geoemydids in Greece is certainly congruent with recent hypotheses from genetic studies.

Other zooarchaeological sites with chelonian remains from Peloponnesus peninsula include: cave Alpha in Apidima, Klissoura Cave 1, Kalamakia, and Marathousa 1 (respectively Pitsios, 1999 and Tsoukala, 1999; Starkovich, 2012; Harvati et al., 2013; Panagopoulou et al., 2015 and references therein). The caves in Apidima (south Peloponnesus) are famous for the human skull findings (see Pitsios, 1999), but they also contain a rich vertebrate fauna, from which the mammalian remains were studied by Tsoukala (1999). Both authors report the presence of turtle specimens in the assemblage. Especially Pitsios (1999:4-5) reports *in situ* observations that a turtle specimen could have been involved in the burial of one of these skulls, as it was found covering the missing base of a human skull (the skull was in an inverted position). Klissoura Cave 1, just northwest of Franchthi Cave, contains layers dated from the Middle Paleolithic to the Mesolithic (roughly between 50,000 and 9,000 BP) from which Starkovich (2012) reported several hundreds of chelonian remains. It is not clear whether the attribution by Starkovich (2012) of this material as “tortoise” refers to the presence of only testudinid taxa, or there is a potential presence of *Emys* as well. Recently, Harvati et al. (2013) reported their results from the study of the assemblage from Kalamakia, in the southern part of Peloponnesus. This site is dated in the Middle Paleolithic, roughly between 100,000 and 39,000 BP, with significant Neanderthal remains. Interestingly, they report tortoise specimens as well, attributed to *Testudo marginata* and *Testudo hermanni*, which are modified both by humans and carnivores; no evidence of the European pond turtle is reported from Kalamakia. Lately, Panagopoulou et al. (2015), reported their first finds from a new Middle Pleistocene site near Megalopolis, called Marathousa 1, with remains of the straight-tusked elephant and lithic specimens that suggest human modification in the assemblage. Among the findings they also report turtle specimens without further identification. Herein we review the previously published material and new specimens from Megalopolis, which are the result of natural accumulation and not human interaction; two aquatic species have been identified, *E. orbicularis* and *M. rivulata*. These specimens are only dated to the Late Pleistocene and future works should focus on providing more detailed dating, but certainly our findings provide information about the chelonian taxa that were living in the area of Megalopolis at that time. In all cases mentioned above the chelonian material needs revision in the light of our results, especially to find evidence of the oldest record of *E. orbicularis* in the area.

Relatively few works have focused in detail in the morphology of turtle remains in sites with human interaction, like the recent works of Smith et al. (2016) and Blasco et al. (2016) from the Middle Pleistocene Qesem Cave in Israel. In this site only the presence of tortoise taxa has been confirmed, *Testudo graeca* and *Testudo* sp. (Smith et al. 2016). Blasco et al. (2016; and references therein) reviewed a number of factors that make turtles as an important small-game target of human foraging. Briefly, hunting turtles and tortoises is ideal for the following reasons: low technological costs; decreased predation risk; vulnerability; low mobility; easy transportation; storage when alive; high nutrition in protein and fat; non-edible resources, e.g. shell (Blasco et al., 2016 and references therein).

CONCLUSIONS

Although the fossil/subfossil record of the European pond turtle (*Emys orbicularis*) in Greece is limited compared to *Mauremys* and *Testudo*, the preserved material from Franchthi Cave and Megalopolis basin confirms the presence of this taxon in Greece from the Late Pleistocene onwards. Here we describe new material from these sites and revise previously published available material from the Peloponnesus peninsula. Humans that inhabited Franchthi Cave for several thousand years turned to small game resources such as turtles and tortoises during the latest Pleistocene. From their "leftovers" several diagnostic parts have been preserved and recognized allowing the identification of *E. orbicularis* and *Testudo hermanni* close to the Pleistocene/Holocene boundary. Further specimens of *E. orbicularis* and *Mauremys rivulata* have been identified from the Late Pleistocene of Megalopolis.

These findings provide solid evidence supporting previous claims of a glacial-pleniglacial refuge of *E. orbicularis* in South Greece. From such refuges, *E. orbicularis* experienced significant range expansion during the warmer parts of the Holocene, resulting in a wide patchy distribution over Europe shaped by the numerous biogeographic barriers (e.g. mountain chains). Based on mitochondrial research, it seems most probable that the range expansion from the southern Greece refuge was small in scale, especially compared to the large-scale expansions from the

Black Sea area. We hope that the findings presented here will spur the detailed description of more specimens, especially from archaeological sites. Also, any absolute dates on chelonian bones will help to refine some of the conclusions mentioned above.

ACKNOWLEDGEMENTS

We deeply thank N. Munro and M. Stiner for their help and support and for useful comments on an earlier version of the manuscript. We deeply thank D. Schreve for editorial assistance and the reviewers H.-A. Blain and U. Fritz for useful comments that greatly improved this manuscript. For providing access to study material included in this study and comparative specimens we would like to thank G. Theodorou and S. Roussiakis (AMPG), M. Moser (BSPG), E. Tsoukala (LGPUT), K. Vitelli and the D' Ephorate of Nafplion, W. Wessels and H. de Brujin (Utrecht), C.S. Doukas (Athens). MD was supported by Università di Torino (Fondi di Ateneo 2014, 2015), Synthesys (AT-TAF-1281) and Generalitat de Catalunya (2014 SGR 416 GRC).

REFERENCES

Batsch, A.J., 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528 pp.

Bell, T., 1825. A monograph of the tortoises having a moveable sternum with remarks on their arrangement and affinities. Zoological Journal, 2, 299–310.

Blain, H.A., Gleed-Owen, C.P., López-García, J.M., Carrión, J.S., Jennings, R., Finlayson, G., Finlayson, C., Giles-Pacheco, F., 2013. Climatic conditions for the last Neanderthals: Herpetofaunal record of Gorham's Cave, Gibraltar. Journal of Human Evolution, 64(4), 289–299.

Blasco, R., Rosell, J., Smith, K. T., Maul, L. C., Sañudo, P., Barkai, R., Gopher, A., 2016. Tortoises as a dietary supplement: A view from the Middle Pleistocene site of Qesem Cave, Israel. Quaternary Science Reviews, 133, 165–182.

Bory de Saint–Vincent, J., 1833. Vertébrés à sang froid. Reptiles et poissons.: Geoffroy Saint–Hilaire, E., Ed.). Expédition Scientifique de Morée, Vol. 3, Part 1, Atlas, pl. 6.

Bour, R., 1996. Une nouvelle espèce de tortue terrestre dans le Péloponnèse (Grèce). Dumerilia, 2, 23–54.

Cope, E.D., 1868. On the Origin of Genera. Proceedings of the Academy of Natural Sciences of Philadelphia, 20, 242–300.

Dormoy, I., Peyron, O., Combourieu Nebout, N., Goring, S., Kotthoff, U., Magny, M., Pross, J., 2009. Terrestrial climate variability and seasonality changes in the Mediterranean region between 15000 and 4000 years BP deduced from marine pollen records. Climate of the Past, 5, 615–632.

Duméril, A.M., 1805. Zoologie Analytique, ou Méthode Naturelle de Classification des Animaux. Paris: Perronneau, 344 pp.

Farrand, W.R., 2000. Depositional History of Franchthi Cave: Stratigraphy, Sedimentology, and Chronology, in: Excavations at Franchthi Cave, Greece, fasc. 12. Indiana University Press, Indiana.

Fritz, U., Fattizzo, T., Guicking, D., Tripepi, S., Pennisi, M. G., Lenk, P., Joger, U., Wink, M., 2005a. A new cryptic species of pond turtle from southern Italy, the hottest spot in the range of the genus *Emys*. Zoologica Scripta, 34, 351–371.

Fritz, U., Široký, P., Kami, H., Wink, M., 2005b. Environmentally caused dwarfism or a valid species—Is *Testudo weissingeri* Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. Molecular Phylogenetics and Evolution, 37, 389–401.

Fritz, U., Auer, M., Bertolero, A., Cheylan, M., Fattizzo, T., Hundsdörfer, A. K., Sampayo, M.M., Pretus, J., Široký, P., Wink, M., 2006. A rangewide phylogeography of Hermann's tortoise, *Testudo hermanni* (Reptilia: Testudines: Testudinidae): implications for taxonomy. Zoologica Scripta, 35, 531–543.

Fritz, U., Guicking, D., Kami, H., Arakelyan, M., Auer, M., Ayaz, D., Fernández, C., Bakiev, A., Celani, A., Džukic, G., Fahd, S., Havaš, P., Joger, U., Khabibullin, V., Mazanaeva, L., Široký, P., Tripepi, S., Vélez, A., Antón, G., Wink, M., 2007.

Mitochondrial phylogeography of European pond turtles (*Emys orbicularis*, *Emys trinacris*)–an update. Amphibia Reptilia, 28, 418–426.

Fritz, U., Ayaz, D., Buschbom, J., Kami, H.G., Mazanaeva, L.F., Aloufi, A.A., Auer, M., Rifai, L., Šilić, T., Hundsdörfer A.K., 2008. Go east: Phylogeographies of *Mauremys caspica* and *M. rivulata* - discordance of morphology, mitochondrial and nuclear genomic markers and rare hybridization. Journal of Evolutionary Biology, 21, 527–540.

Fritz, U., Harris, J.D., Fahd, S., Rouag, R., Gracià Martinez, E., Giménez Casalduero, A., Široký, P., Kalboussi, M., Jdeidi, T., Hundsdörfer, A.K., 2009. Mitochondrial phylogeography of *Testudo graeca* in the Western Mediterranean: Old complex divergence in North Africa and recent arrival in Europe. Amphibia– Reptilia, 30, 63–80.

Fritz, U., Schneeweiß, N., Podloucky, R., 2015. Die Europäische Sumpfschildkröte – Reptil des Jahres 2015. Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V., 39 pp.

Georgalis, G., Kear, B., 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios, 46, 299–311.

Gmelin, J., 1789. Caroli a Linné, Systema Naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 13. Tom. I. Pars III. Leipzig: G.E. Beer, Ed. 13, 1(3), 1033–1516.

Gray, J.E., 1869. Description of *Mauremys laniaria*, a new freshwater tortoise. Proceedings of the Zoological Society of London, 1869, 499–500.

Harvati, K., Darlas, A., Bailey, S. E., Rein, T. R., El Zaatari, S., Fiorenza, L., Kullmer, O., Psathi, E., 2013. New Neanderthal remains from Mani peninsula, southern Greece: the Kalamakia middle Paleolithic cave site. Journal of Human Evolution, 64(6), 486–499.

Jacobsen, T.W., 1981. Franchthi Cave and the beginning of settled village life in Greece. Hesperia, 50, 303–319.

Jiménez-Fuentes, E., 1986. Los quelonios de la Cueva de Nerja, in: Jordá Pardo, J.F. (ed.), La Prehistoria de la Cueva de Nerja (Málaga). Patronato de la Cueva de Nerja, Málaga, pp. 135–143.

Joyce, W.G., Parham, J.F., Gauthier, J.A., 2004. Developing a protocol for the conversion of rank–based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology, 78, 989–1013.

Lenk, P., Fritz, U., Joger, U., Wink, M., 1999. Mitochondrial phylogeography of the European pond turtle, *Emys orbicularis* (Linnaeus, 1758). Molecular Ecology, 8, 1911–1922.

Linnaeus, C., 1758. Systema Naturae, per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima, Reformata. [10th Ed.]. Holmiae [Stockholm]: Laurentii Salvii, 824 pp.

Melentis, J. K., 1966. *Clemmys caspica* aus dem Pleistozän des Beckens von Megalopolis im Peloponnes (Griechenland). Annales Géologiques des Pays Helléniques, 17, 169–181.

Panagopoulou, E., Tourloukis, V., Thompson, N., Athanassiou, A., Tsartsidou, G., Konidaris, G. E., Giusti, D., Karkanas, P., Harvati, K., 2015. Marathousa 1: a new Middle Pleistocene archaeological site from Greece. Antiquity, 343.

Parham, J.F., Macey, J.R., Papenfuss, T.J., Feldman, C.R., Türkozan, O., Polymeni, R., Boore, J., 2006. The phylogeny of Mediterranean tortoises and their close relatives based on complete mitochondrial genome sequences from museum specimens. Molecular Phylogenetics and Evolution, 38, 50–64.

Pedall, I., Fritz, U., Stuckas, H., Valdeón, A., Wink, M., 2011. Gene flow across secondary contact zones of the *Emys orbicularis* complex in the Western Mediterranean and evidence for extinction and re- introduction of pond turtles on Corsica and Sardinia (Testudines: Emydidae). Journal of Zoological Systematics and Evolutionary Research, 49(1), 44–57.

Pérez-García, A., Boneta, I., Alday, A., Murelaga, X., 2015. The oldest Quaternary turtle remains from the Basque-Cantabrian Basin (Atxoste, Álava, Spain). Comptes Rendus Palevol, 14(6), 605–611.

Pitsios, T.K., 1999. Paleoanthropological research at the cave site of Apidima and the surrounding region (South Peloponnese, Greece). Anthropologischer Anzeiger, 1-11.

Schleich, H., 1982. *Testudo marginata* Schoepff aus plio/pleistozänen ablagerungen SE–Lakoniens (Peloponnes, Griechenland). Paläontologische Zeitschrift, 56(3), 259–264.

Smith, K.T., Maul, L.C., Flemming, F., Barkai, R., Gopher, A., 2016. The microvertebrates of Qesem Cave: A comparison of the two concentrations. Quaternary International, 135, 165–182.

Sommer, R.S., Persson, A., Wieseke, N., Fritz, U., 2007. Holocene recolonization and extinction of the pond turtle, *Emys orbicularis* (L., 1758), in Europe. Quaternary Science Reviews, 26(25), 3099–3107.

Sommer, R. S., Lindqvist, C., Persson, A., Bringsøe, H., Rhodin, A. G., Schneeweiss, N., Široký, P., Bachmann, L., Fritz, U., 2009. Unexpected early extinction of the European pond turtle (*Emys orbicularis*) in Sweden and climatic impact on its Holocene range. Molecular Ecology, 18(6), 1252–1262.

Starkovich, B.M., 2012. Intensification of small game resources at Klissoura Cave 1 (Peloponnese, Greece) from the Middle Paleolithic to Mesolithic. Quaternary International, 264, 17–31.

Stiner, M.C., Munro, N.D., 2011. On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchthi Cave (Peloponnese, Greece). Journal of Human Evolution, 60, 618–636.

Theobald, W., 1868. Catalogue of Reptiles in the Museum of the Asiatic Society of Bengal. Journal of the Asiatic Society, Extra Number, 88 pp.

Tsoukala, E., 1999. Quaternary large mammals from the Apidima Caves (Lakonia, S. Peloponnese, Greece). Beitraege zur Palaeontologie, 24, 207–229.

Tsoukala, E., Mol, D., Pappa, S., Vlachos, E., van Logchem, W., Vaxevanopoulos, M., Reumer, J., 2011. *Elephas antiquus* in Greece: New finds and a reappraisal of older material (Mammalia, Proboscidea, Elephantidae). Quaternary International, 245(2), 339–349.

Vamberger, M., Stuckas, H., Ayaz, D., Lymberakis, P., Široký, P., Fritz, U., 2014. Massive transoceanic gene flow in a freshwater turtle (Testudines: Geoemydidae: *Mauremys rivulata*). Zoologica Scripta, 43(4), 313–322.

Vamberger, M., Stuckas, H., Sacco, F., D'Angelo, S., Arculeo, M., Cheylan, M., Corti, C., Lo Valvo, M., Marrone, F., Wink, M., Fritz U., 2015. Differences in gene flow in a twofold secondary contact zone of pond turtles in southern Italy (Testudines: Emydidae: *Emys orbicularis galloitalica*, *E. o. hellenica*, *E. trinacris*). Zoologica Scripta, 44, 233–249.

van Dijk, P.P., Iverson, J.B., Shaffer, H.B., Bour, R., Rhodin, A.G.J. Turtle Taxonomy Working Group: Turtles of the world, 2012 update. Annotated checklist of taxonomy, synonymy, distribution, and conservation status. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No, 5.

Vlachos, E., 2015. The fossil chelonians of Greece. Systematics - Evolution - Stratigraphy – Palaeoecology. PhD dissertation, Scientific Annals of the School of Geology, Aristotle University of Thessaloniki, Greece, 173, 479 pp.

Vlachos, E., Tsoukala, E., 2016. The diverse fossil chelonians from Milia (late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae). Papers in Palaeontology, 2(1), 71–86.

Vlachos, E., Kotsakis, T., Delfino, M., 2015. The chelonians from the Latest Miocene–Earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia, Greece). Comptes Rendus Palevol, 14(3), 187–205.

Vugt van N., Bruijn de H., Kolfschoten van M., Langereis G.G., 2000. Magneto- and cyclostratigraphy and mammal-fauna's of the Pleistocene lacustrine Megalopolis Basin, Peloponnesos, Greece, in: Vugt van N. (ed.), Orbital forcing in late Neogene lacustrine basins from the Mediterranean. A magnetostratigraphic and cyclostratigraphic study. Geologica Ultraiectina, 189, pp. 69–92.

Zangerl, R., 1969. The turtle shell, in: A. d'A. Bellairs and T. S. Parsons (Eds.), The Biology of the Reptilia 1, Morphology A, Academic Press, London and New York, pp. 311–339.

Figure Captions

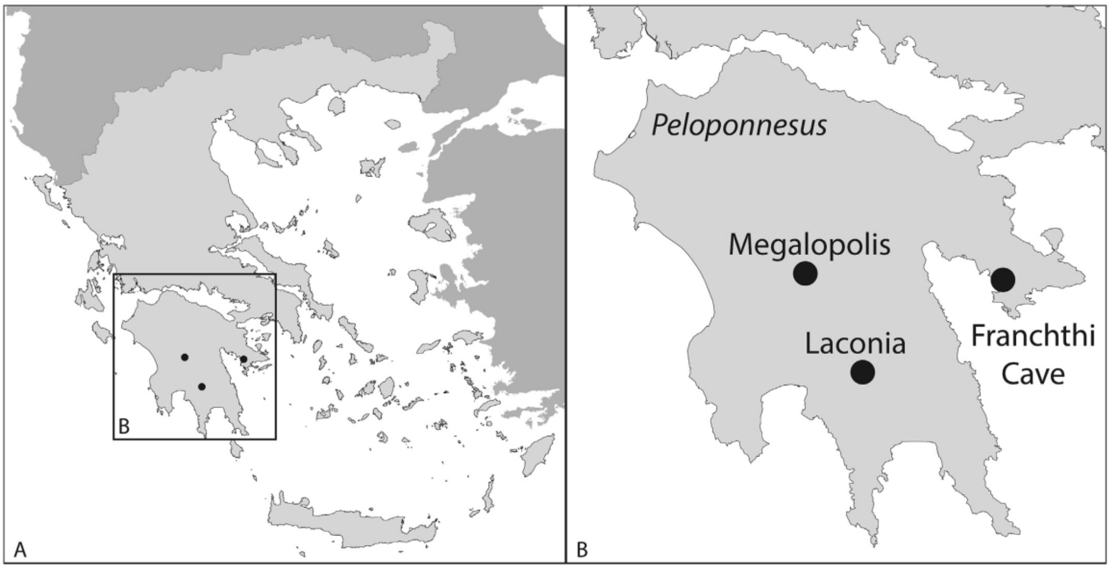

Figure 1. Map of Greece (A), showing the localities discussed in this paper (B).

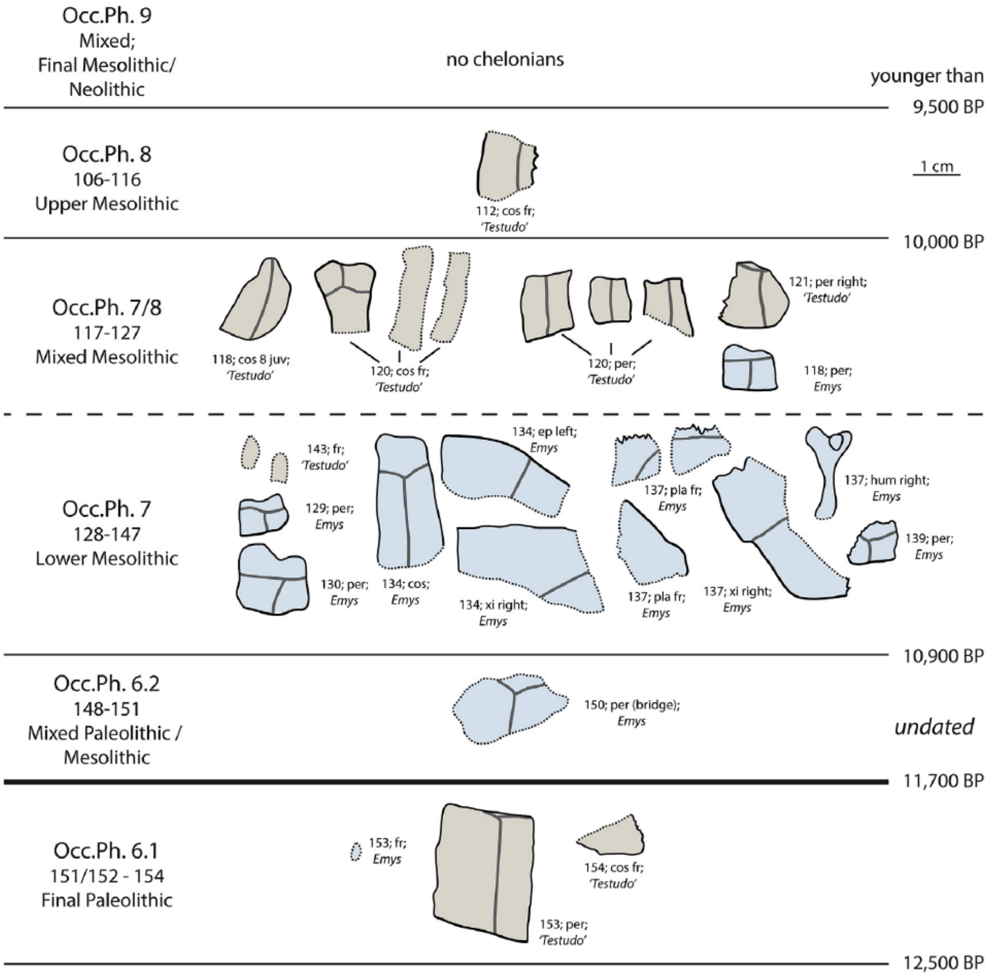

Figure 2. *Emys orbicularis* Linnaeus, 1758 (blue, online version) and *Testudo hermanni* Gmelin, 1789 (brown, online version), from the Pleistocene – Holocene times of Franchthi Cave (Peloponnesus, Greece). Occupational phases 9-6, from Final Mesolithic/Neolithic till Final Paleolithic times. Scale bar equals 1 cm.

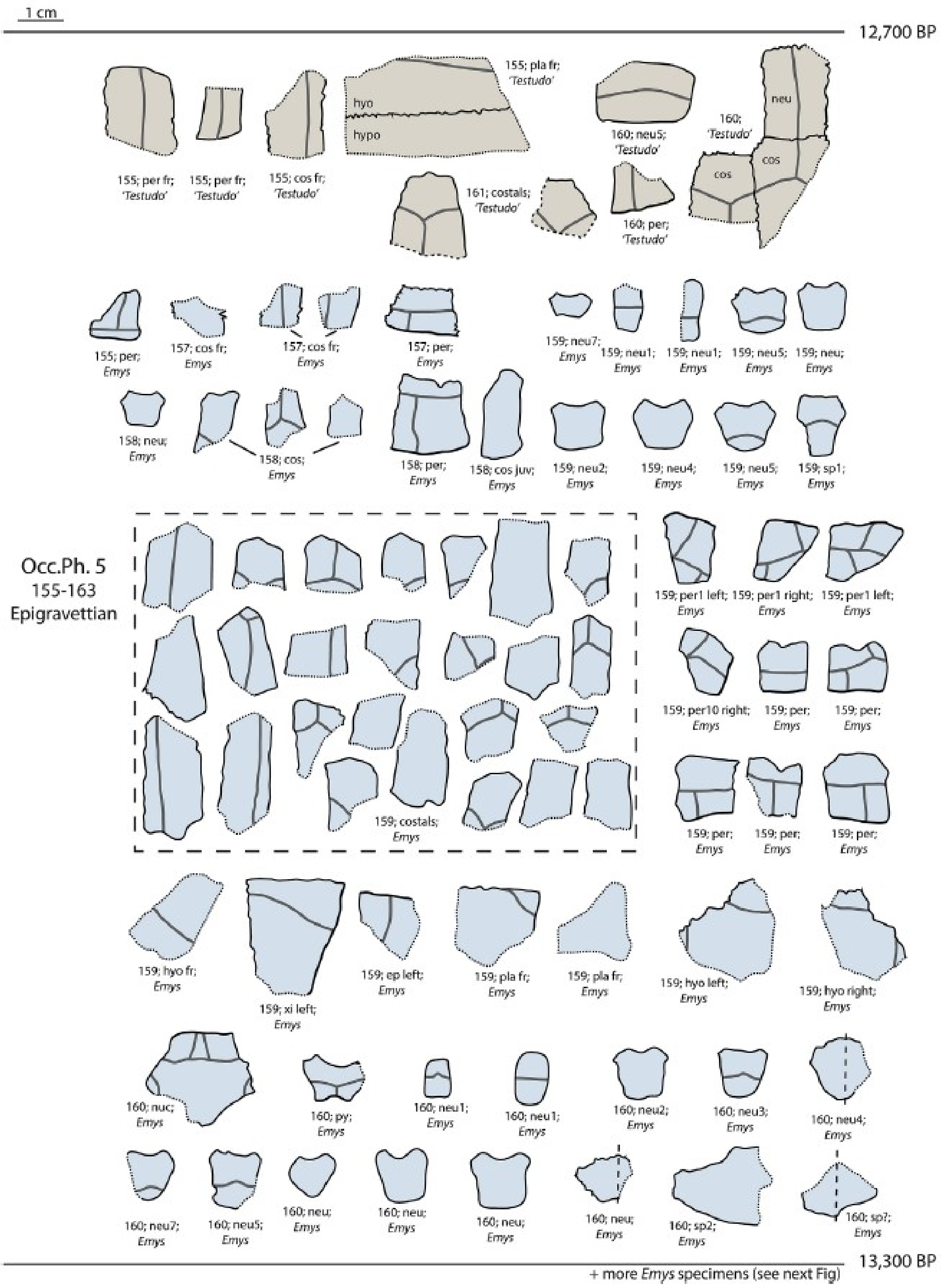

Figure 3. *Emys orbicularis* Linnaeus, 1758 (blue, online version) and *Testudo hermanni* Gmelin, 1789 (brown, online version), from the Pleistocene – Holocene times of Franchthi Cave (Peloponnesus, Greece). Occupational phase 5, from the Epigravettian times. Scale bar equals 1 cm.

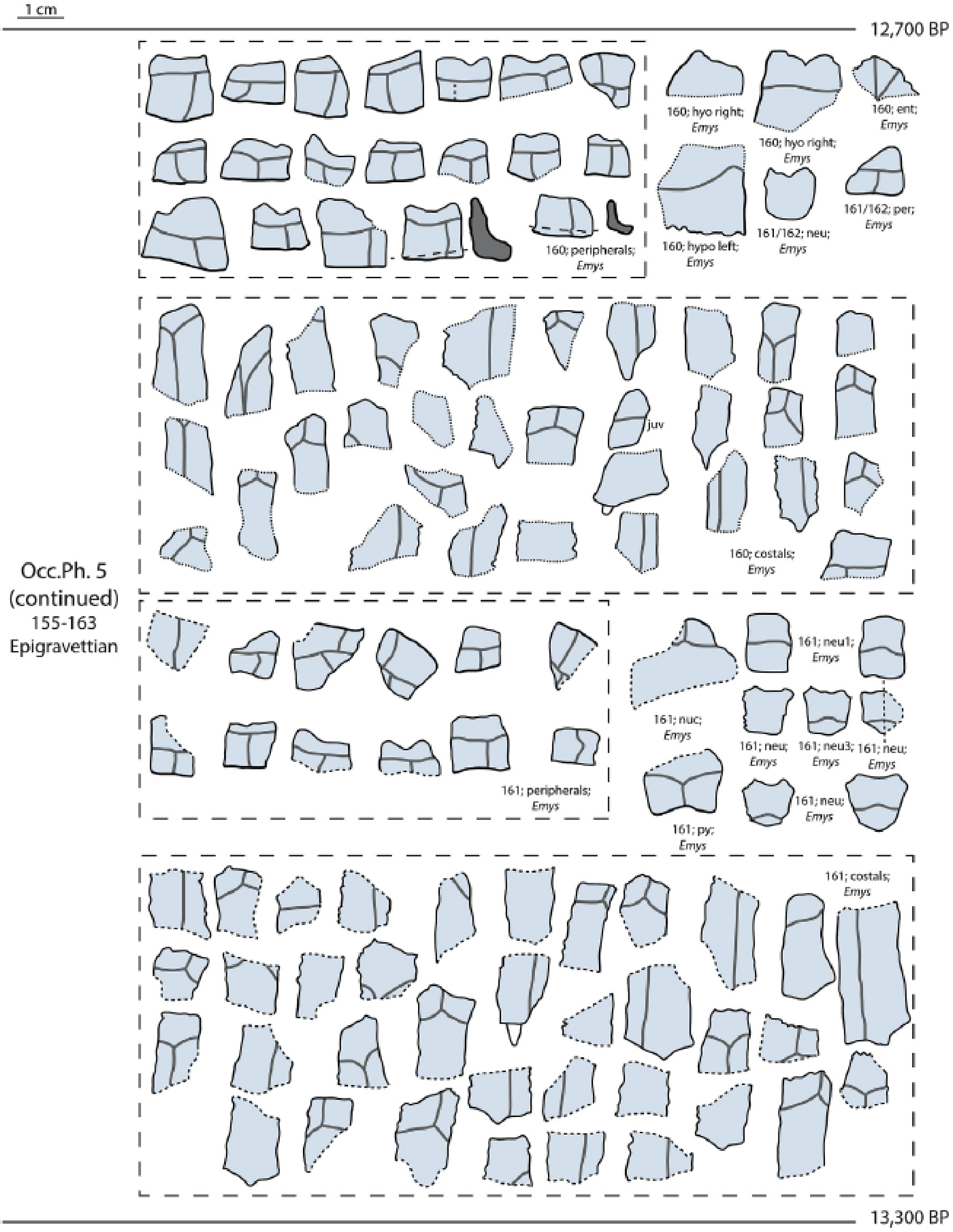

Figure 4. *Emys orbicularis* Linnaeus, 1758 (blue, online version), from the Pleistocene – Holocene times of Franchthi Cave (Peloponnesus, Greece). Occupational phase 5, from the Epigravettian times (continued from previous figure). Scale bar equals 1 cm.

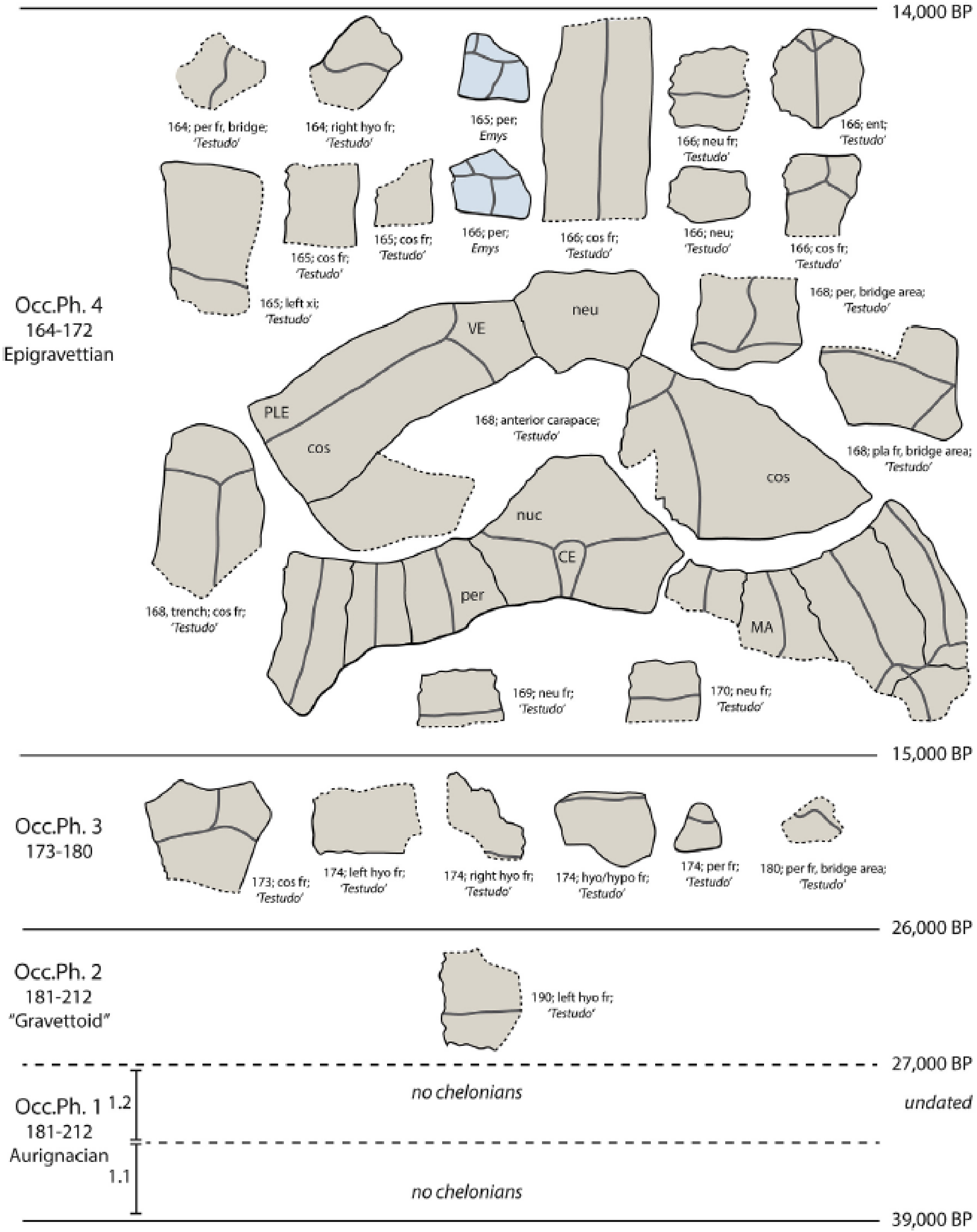

Figure 5. *Emys orbicularis* Linnaeus, 1758 (blue, online version) and *Testudo hermanni* Gmelin, 1789 (brown, online version), from the Pleistocene – Holocene times of Franchthi Cave (Peloponnesus, Greece). Occupational phases 4-2, from the Epigravettian till the "Gravettoid" times. Scale bar equals 1 cm.

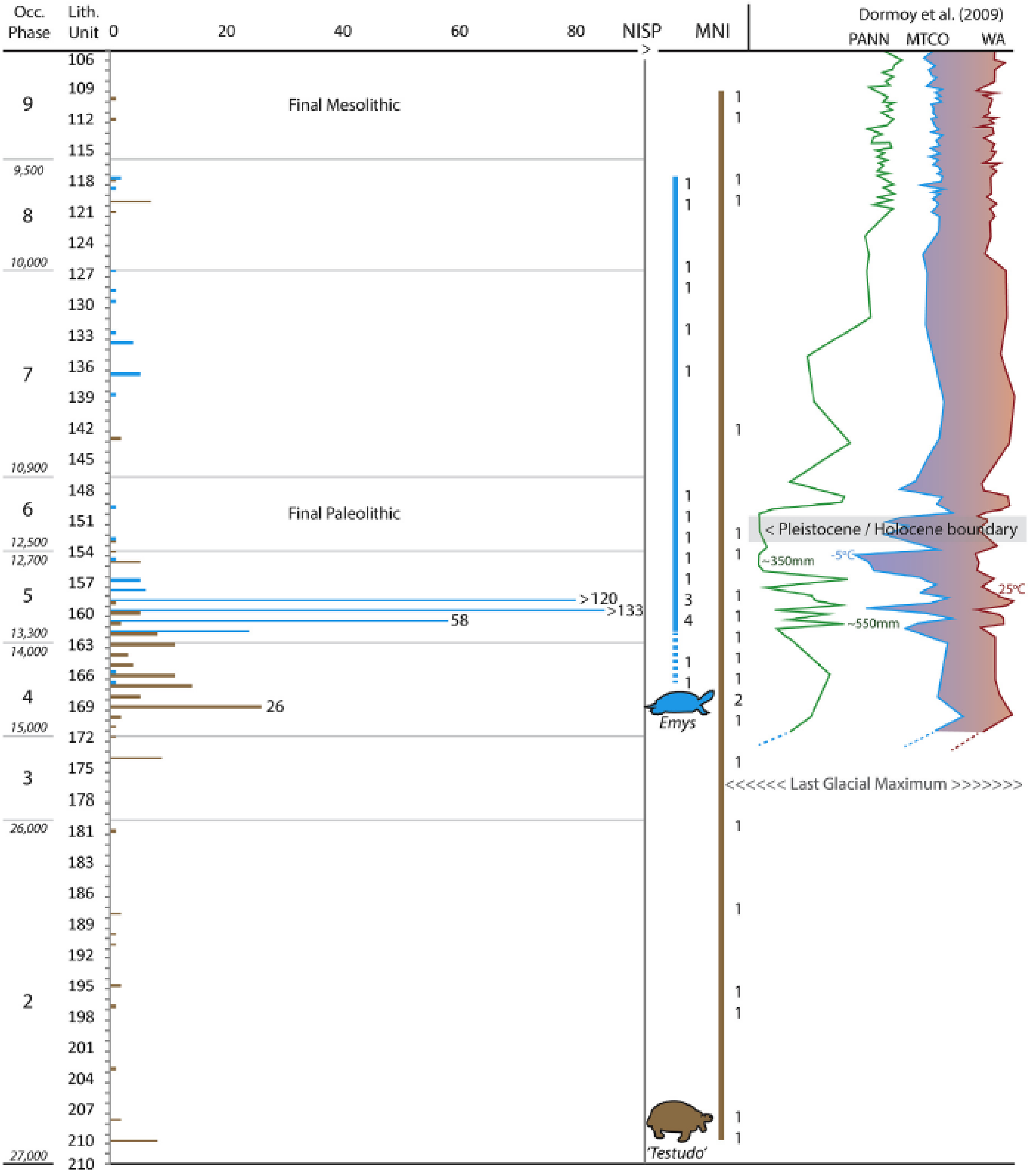

Figure 6. Temporal distribution of the chelonians from Franchthi Cave (Peloponnesus, Greece), based on the number of identified specimens and estimation of the minimum number of individuals. Curves follow Dormoy et al. (2009). Abbreviations: MNI, Minimum Number of Individuals; MTCO, mean temperature of the coldest month; MTWA, mean temperature of the warmest month; NISP, Number of identified specimens; PANN, annual precipitation.

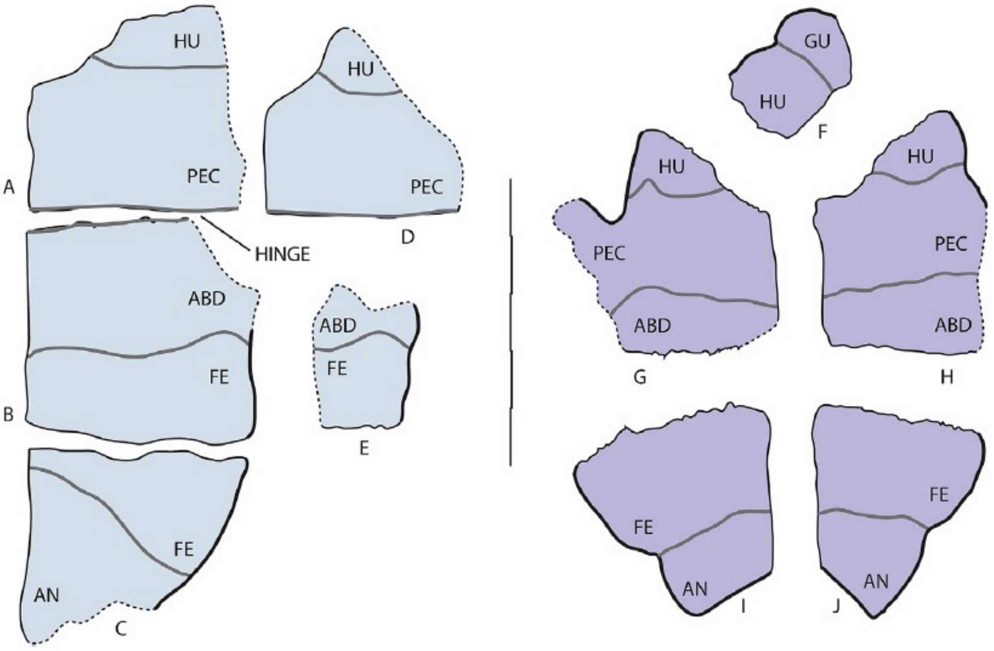

Figure 7. Fossil turtle material from the Pleistocene of Megalopolis (Peloponnesus, Greece) described by Melentis (1966). *Emys orbicularis* Linnaeus, 1758 (blue, online version): A, AMPG 1966/47, left hyoplastron. B, AMPG 1966/48, left hypoplastron. C, AMPG 1966/49, left xiphiplastron. D, AMPG 1966/53, left hyoplastron. E, AMPG 1966/50, left hypoplastron. *Mauremys rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833 (purple, online version). F, AMPG 1966/54, right epiplastron. G, AMPG 1966/51, right hyoplastron. H, AMPG 1966/52, left hyoplastron. J, AMPG 1966/45, right xiphiplastron. K, AMPG 1966/46, left xiphiplastron. Scale bar equals 5 cm. Modified from the drawings of the ventral views by Melentis (1966).

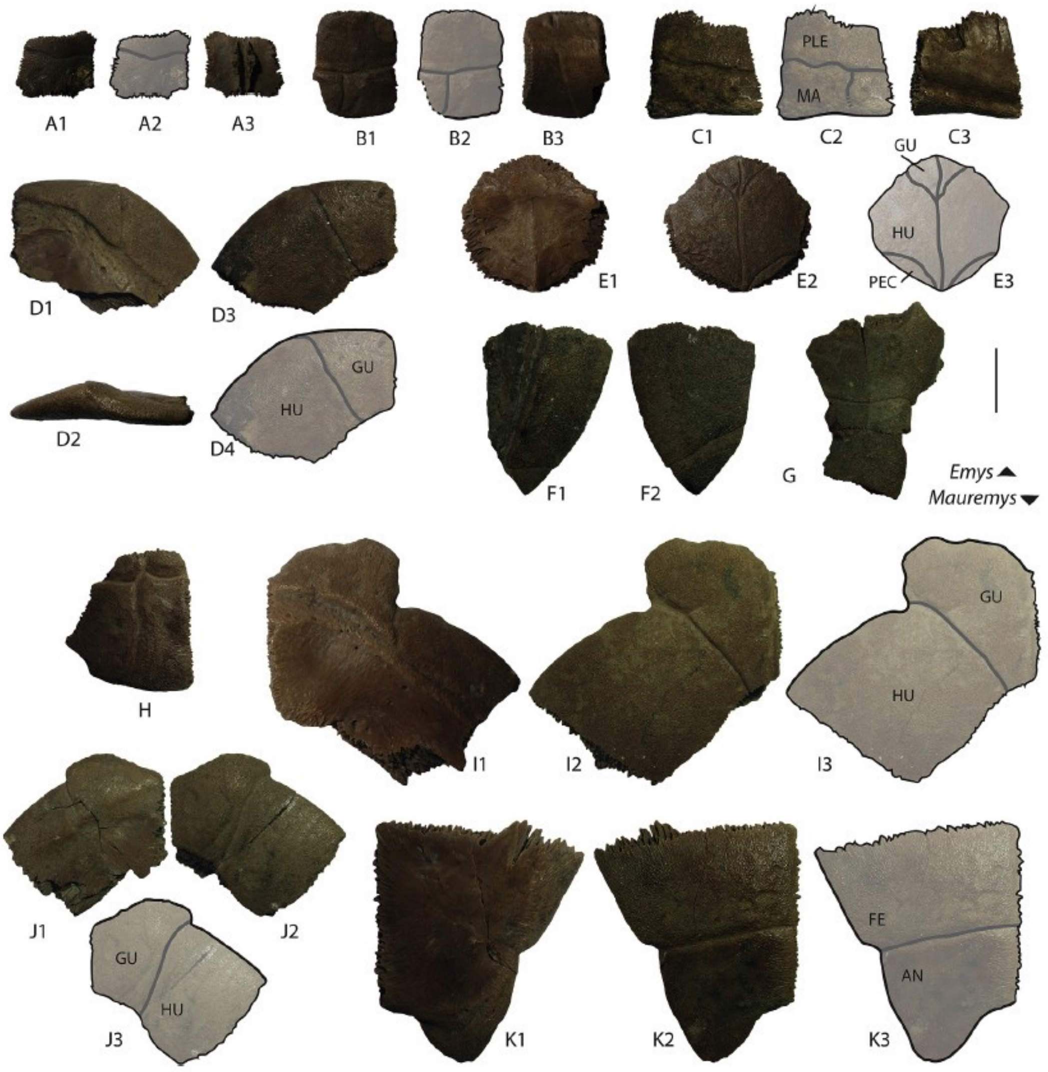

Figure 8. Formerly unpublished fossil turtle material from the Pleistocene of Megalopolis (Peloponnesus, Greece). *Emys orbicularis* Linnaeus, 1758: A, UU MEG 501, neural in (A1) dorsal, (A2) drawing of the dorsal and (A3) visceral views; B, UU MEG 502, peripheral in (B1) dorsal, (B2) drawing of the dorsal and (B3) visceral views; C, UU MEG 503, peripheral in (C1) dorsal, (C2) drawing of the dorsal and (C3) visceral views; D, UU MEG 504, right epiplastron in (D1) visceral, (D2) lateral, (D3) ventral and (D4) drawing of the ventral views; E, UU MEG 505, entoplastron in (E1) visceral, (E2) ventral and (E3) drawing of the ventral views; F, UU MEG 506, right xiphiplastron in (F1) visceral and (F2) ventral views; G, UU MEG 507, left

hypoplastron in ventral view. *Mauremys rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833: H, UU MEG 508, peripheral in dorsal view; I, UU MEG 509, right epiplastron in (I1) visceral, (I2) ventral and (I3) drawing of the ventral views; J, UU MEG 510, left epiplastron in (J1) visceral, (J2) ventral and (J3) drawing of the ventral views; K, UU MEG 511, right xiphiplastron in (K1) visceral, (K2) ventral and (K3) drawing of the ventral views. Scale bar equals 1 cm.

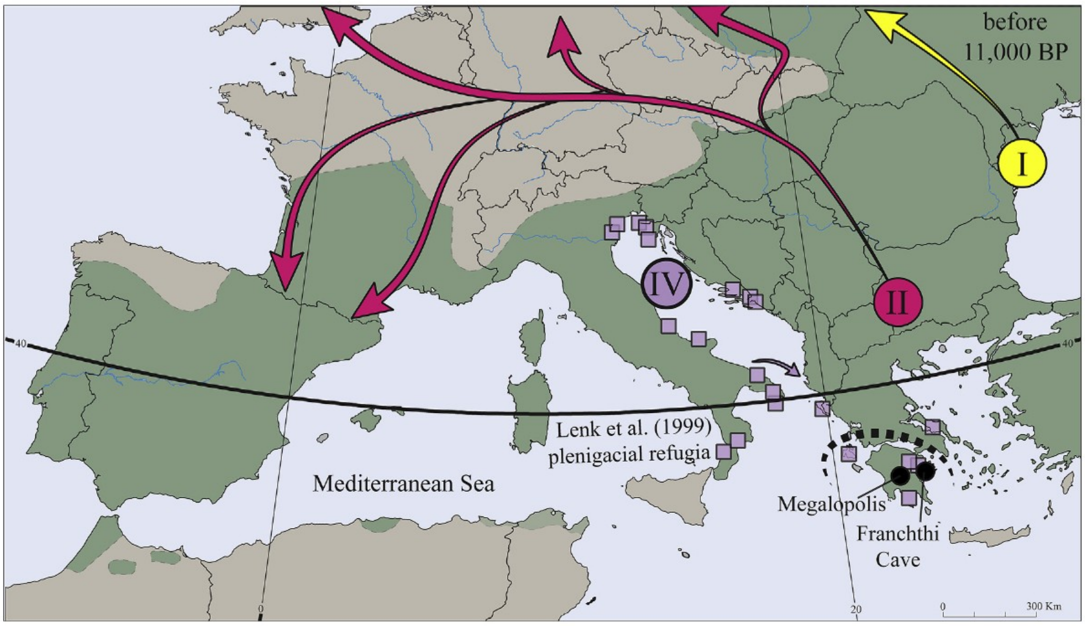

Figure 9. (color online) Map of Europe, showing the sites with *Emys orbicularis* discussed in this paper (Franchthi Cave and Megalopolis; filled circles) in Peloponnesus peninsula (S. Greece). Dark green color indicates the extant range of *Emys* based on Fritz et al. (2015). Yellow and violet arrows indicate the expansion of *Emys* already before 11,000 BP from Glacial refuges (mitochondrial lineages I and II sensu Fritz et al., 2007), based on Sommer et al. (2007; 2009). Open purple squares indicate the *Emys* occurrences of the mitochondrial lineage IV (from Fritz et al., 2007), with a purple arrow indicating the postulated colonization of Corfu and Evvia from the southern Italy populations (see Fritz et al., 2007 and references therein). Coloration of the lineages in online version follows Sommer et al. (2009). Dashed line indicates the boundaries of the possible Glacial refuge of *Emys* in southern Greece.

Table 1. Skeletal element representation of *Emys* and *Testudo* specimens from Franchthi Cave (Peloponnesus, Greece).

Emys Shell Remains:						**352**
Nu	Ne	Cos	Per	Sp/Py	Indet	Total Car
2	27	134	68	6	87	324
Ep	En	Hyo	Hypo	Xi	Indet	Total Pla
2	1	7	1	3	14	28
Appendicular Elements						**30**
Total of *Emys*						**382**

Testudo Shell Remains:						**123**
Nu	Ne	Cos	Per	Sp/Py	Indet	Total Car
1	7	25	23	0	49	105
Ep	En	Hyo	Hypo	Xi	Indet	Total Pla
0	1	6	1	1	9	18
Appendicular Elements						**4**
Total of *Testudo*						**127**
Grant Total						**509**