Fossil amphibians and reptiles from Plakias, Crete: A glimpse into the earliest late Miocene herpetofaunas of southeastern Europe[☆]

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Fossil amphibians and reptiles from the earliest late Miocene (early Tortonian, MN 9) of Plakias (Crete, Greece) are described in this paper. Most of the material is fragmentary, precluding precise taxonomic assignment. Nevertheless, the herpetofauna of Plakias is here shown to be diverse, comprising at least six different taxa: an alytid anuran, a crocodilian, two turtles (a pan-trionychid and a geoemydid) and two squamates (an amphisbaenian and a colubroid snake). The crocodilian material represents the first such fossils described from Greece and furthermore, one of the latest occurrences of this group in Europe. The pan-trionychid and the geoemydid represent the oldest occurrences of these groups in Greece and further add to their scarce Miocene record from this country. The first description of a fossil amphisbaenian from Greece is also provided. The new specimens from Plakias add to our knowledge of the Miocene herpetofaunas of southeastern Europe.

1. Introduction

Miocene herpetofaunas from Europe are relatively well known (Rage and Augé, 1993; Sanchiz, 1998; Rage and Roček, 2003; Szyndlar and Rage, 2003; Augé, 2005; Danilov, 2005). However, the focus of previous studies is heavily unbalanced toward the herpetofaunas of the western and central parts of the continent, whereas only few papers have dealt with the eastern European ones (Szyndlar and Zerova, 1990; Szyndlar, 1991a,b; Rage and Augé, 1993; Antunes, 1994; Rage and Roček, 2003; Danilov, 2005; Daza et al., 2014). On the other hand, even less is known about the Miocene amphibians and reptiles from southeastern Europe, despite the fact that this region played a pivotal biogeographic role during that period: several dispersals events from both Africa and Asia occurred during this time interval (Rögl, 1999; Koufos et al., 2005). As such, the study of southeastern European localities

could clarify important aspects about the biogeography, evolutionary history and extinction events of certain European groups.

Greece harbors a large number of Miocene localities, of which several have been well known and studied for more than a century (Koufos, 2006). However, mammal findings were almost always the main focus of these studies, thereby neglecting other important tetrapod taxa such as amphibians and reptiles. Nevertheless, important fossil findings during the last 160 years have shown a diverse array of Miocene reptiles (Gaudry, 1862–1867; Römer, 1870; Weithofer, 1888; Szalai, 1931; Paraskevaidis, 1955; Bachmayer, 1967; Richter, 1995; Szyndlar, 1995; Georgalis et al., 2013, 2016b; Georgalis and Kear, 2013; Vlachos and Tsoukala, 2014; Vlachos et al., 2015b; Garcia et al., 2016), whereas amphibian fossils remain practically unknown from this time interval in Greece, with only few, sporadic published occurrences (Sanchiz, 1998; Rage and Roček, 2003).

Here we describe new amphibian and reptile findings from the earliest late Miocene (early Tortonian, MN 9) locality of Plakias, on the Island of Crete, southern Greece. The fragmentary nature of these fossils precludes any taxonomic assignment at the species level. Higher level taxonomic determination was possible,

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however, revealing an unexpectedly diverse assemblage consisting of anurans, pan-trionychids, geoemydids, crocodilians, amphisbaenians, and snakes.

Institutional Abbreviations: **NHMC**, Natural History Museum and University of Crete, Greece; **UU**, Department of Earth Sciences, University of Utrecht, The Netherlands.

2. Geological framework

All specimens described herein were collected from the locality of Plakias (also known under the spelling Plakia). This is an earliest late Miocene locality, situated in the Agios Vasileios municipality, Rethymnon periphery, Island of Crete (Fig. 1). Its exact age was initially believed to be younger than late Astaracian (late MN 7/MN 8; de Bruijn and Meulenkamp, 1972), a suggestion that was tentatively followed by van der Made (1996) and Koufos (2006). However, it was recently shown that the fauna pertains to the Vallesian (early Tortonian, MN 9), with an age of approximately 9.9 Ma (de Bruijn et al., 2012; Koufos and Kostopoulos, 2013). The Plakias Basin is filled with continental deposits characterized by alternations of silty clays, silts, sandstones and conglomerates (de Bruijn et al., 2012). Fossils originate from grayish clays overlying beige to brown clays with calcretes in a shallow gully complex, southeast of Plakias (de Bruijn et al., 2012).

The palaeoherpetofauna of Plakias can neither confirm nor dispute with certainty the suggested age of the locality as Vallesian (MN 9), earliest late Miocene (de Bruijn et al., 2012). However, it is noted that pan-trionychids and crocodilians are better represented in early and middle Miocene localities of Europe, rather than late Miocene ones (Karl, 1999; Delfino and Rossi, 2013). Since none among the Plakias representatives of the herpetofauna can be attributed to the species level, no further age correlation can be safely made. In any case, the age information on the basis of micromammals allows referring the whole faunal assemblage to the earliest late Miocene (MN 9; de Bruijn et al., 2012).

3. Material and methods

All the amphibians, crocodilians and squamates, and part of the pan-trionychid and geoemydid material described in this study is housed in the collections of the University of Utrecht (UU). This amphibian and reptile material was collected along with the fossil micromammals that were described by de Bruijn and Meulenkamp (1972) from the first period of fieldwork at Plakias. Part of the geoemydid and the pan-trionychid material belongs to the collections of the Natural History Museum of Crete (NHMC) and represents material that was collected by Kuss in the 1970s. This material was originally in the Geologisch-Paläontologisches Institut der Universität Freiburg, Germany, and later formed part

Fig. 1. Map of Crete, locating the earliest late Miocene locality of Plakias.

of the collections of the Natural History Museum of Karlsruhe, Germany, before its recent return to the NHMC. This material was studied in the doctoral thesis of one of us (Vlachos, 2015) and is further presented here in the context of the whole herpetofauna of Plakias. It is not possible to determine the exact stratigraphic origin of the material collected by Kuss, as he did not publish anything about it. It has been recently noted, however, that the old (de Bruijn and Meulenkamp, 1972) and new (de Bruijn et al., 2012) micromammal collections of Plakias could "come from slightly different stratigraphic levels" (de Bruijn et al., 2012, p. 61) due to building activity in the area during the last 40 years. However, the same authors noted that "the 25 cm thick grayish silty clay sampled in 2010 seems to be the only bed that contains vertebrate remains" (de Bruijn et al., 2012, p. 61). Following this line of reasoning, and in the absence of conflicting evidence, we treat all the material described herein as originating from the same site.

Taxonomy follows Pyron and Wiens (2011) for anurans, Joyce et al. (2004) for turtles, Brochu (2000) for crocodilians, and Gauthier et al. (2012), Pyron et al. (2014), and Wallach et al. (2014) for squamates. Anatomical terminology follows Sanchiz (1998) for anurans, Zangerl (1969) for turtles, Steel (1973) for crocodilians, Estes (1983) for amphisbaenians, and Rage (1984) for snakes.

4. Systematic paleontology

Amphibia Linnaeus, 1758
Anura Fischer von Waldheim, 1813
Alytidae Fitzinger, 1843
cf. Alytidae indet.
Fig. 2

Referred specimens: UU PL 701, a fragmentary trunk vertebra; UU PL 702, a single, partial tibiofibula.

Description: UU PL 701: This trunk vertebra preserves only the centrum and, on both sides, a small, basal portion of the neural arch. The centrum is roughly 2.8 mm long and slightly dorsoventrally flattened. The condyle bears a small, but well-defined condylar neck that is typical of opisthocoelous vertebrae and therefore characterizes the anterior extremity of the centrum. The anterior condyle and the posterior cotyle are rather subcircular.

UU PL 702: The preservational status of this tibiofibula fragment is poor. It preserves only a terminal portion, showing the presence of the two fused elements. Moreover, the fact that this skeletal element has limited diagnostic value hinders a precise identification.

Remarks: UU PL 701 can be tentatively referred to the Alytidae on the basis of the condylar neck that marks the condyle. This character has not been described in the literature (e.g., Bailon, 1999) but in our experience, this trait is characteristic for this group of frogs, which at least in some cases have also a comparable size. UU PL 702 is here tentatively referred to the same taxon represented by the co-occurring vertebra. Most probably, the amphibian material presented herein is the same that Sanchiz (1998, p. 168) referred to as "Platkia (sic.), Greece, Neogene: Discoglossinae indet. (Sanchiz, unpublished)" (Borja Sanchiz, pers. comm. to GLG, February 2016).

It is beyond the scope of this paper to evaluate the taxonomic affinities of European painted frogs and we follow Frost et al. (2006) in using the term Alytidae for all these amphibians. Despite their confined extant distribution, alytids were once widespread in Europe (Rage and Roček, 2003). In Greece, other fossils attributed to this group have been briefly reported from the Miocene of Aliveri, Ano Metochi, Biodrak, Lefkon, Maramena, Monasteri and Pikermi, the Pliocene of Kardia, Ptolemais and Spilia, and the Miocene or Pliocene of Rema Aslan and Rema Marmara (Rage and Roček, 2003).

Fig. 2. cf. Alytidae from the earliest late Miocene of Plakias: UU PL 701, a trunk vertebra in dorsal (**A**), anterior (**B**) and ventral (**C**) views. Scale bar: 1 mm.

Reptilia Laurenti, 1768
Testudines Batsch, 1788
Pan-Trionychidae Joyce et al., 2004
Pan-Trionychidae indet.
Fig. 3

Referred specimens: UU PL 703, costal fragment; UU PL 704, costal fragment; NHMC 21.7.3.1670, neural; NHMC 21.7.3.1671, plastron fragment.

Description: NHMC 21.7.3.1670 (Fig. 3(A)): This specimen corresponds to an almost complete neural. Although the specimen is eroded, the shape of the neural appears to be hexagonal with short lateral sides. Dorsally, the distinctive sculpturing is visible, consisting mainly of small pits. Viscerally, the attachment for the vertebra is preserved.

UU PL 703 (Fig. 3(B)): This specimen corresponds to a fragment of a costal, as is shown by the presence of a rib on the visceral part. On the distal side, a part of the rib is apparent as well. Dorsally, the distinctive sculpturing is visible, consisting of small pits that are mainly separated from one another. The anterior and posterior margins of the costal are developed parallel to each other on the preserved part.

UU PL 704 (Fig. 3(C)): This specimen corresponds to a fragment of a costal, as is shown by the presence of the rib on the visceral part. Its morphology is similar to the previously described specimen (UU PL 703), but a larger part of the costal is preserved.

NHMC 21.7.3.1671 (Fig. 3(D)): This specimen most probably corresponds to a process of the plastron. It is long and flattened, with an elliptical cross-section. Further identification is not possible.
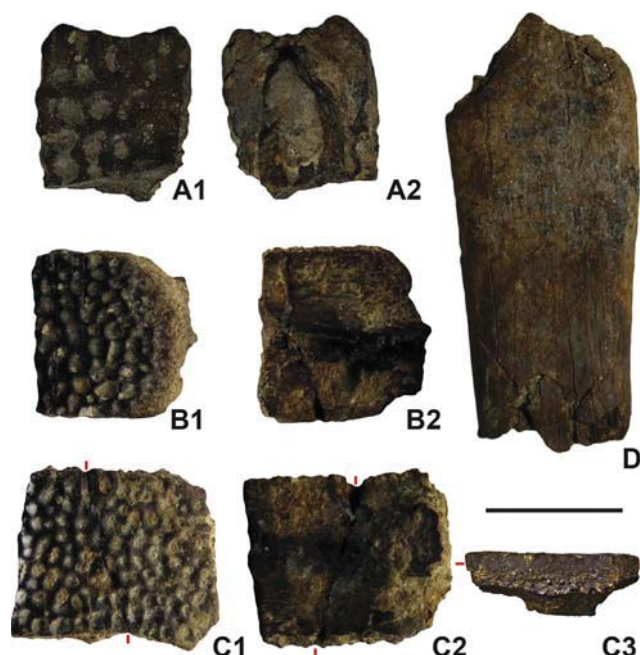

Fig. 3. Pan-Trionychidae from the earliest late Miocene of Plakias. **A**. NHMC 21.7.3.1670, fragment of a neural, in dorsal (A1) and visceral (A2) views. **B**. UU PL 703, fragment of a costal in dorsal (B1) and visceral (B2) views. **C**. UU PL 704, fragment of a costal in dorsal (C1) and visceral (C2) views. **D**. NHMC 21.7.3.1671, fragment of plastron in dorsal view. Scale bar: 10 mm.

Remarks: The available specimens can be attributed to Pan-Trionychidae based on the presence of sculpturing that covers all metaplastic portions of the shell bones (Vitek and Joyce, 2015). The preserved pan-trionychid material from Plakias consists mainly of carapace fragments and a possible plastron element. Given that the sculpturing pattern is highly variable among soft-shelled turtles, even within individuals of the same species (Gardner and Russell, 1994; Vitek and Joyce, 2015), further identification is not possible. Compared to the only other known fossil pan-trionychid from Greece from the Pliocene of Gefira, northern Greece (Vlachos et al., 2015a), the Plakias specimens pertain to a smaller-sized form, both in regards of carapacial disk length and thickness of the carapace. Another difference between these two Greek occurrences is noted in the sculpturing of the two forms: on the basis of the commonly preserved distal part of the costal, the pits on the Plakias pan-trionychid are mainly separated, whereas in the pan-trionychid from Gefira, they are mostly coalesced, forming continuous grooves. As mentioned above, however, the extreme variability of sculpturing observed within pan-trionychids does not allow us to determine taxonomic differences between the two Greek forms on the basis of this character.

Geoemydidae Theobald, 1868
Genus *Mauremys* Gray, 1869
Mauremys sp.
Fig. 4

Referred specimens: NHMC 21.7.3.1618, part of anterior lobe; NHMC 21.7.3.1619, right xiphiplastron; NHMC 21.7.3.1620, left hypoplastron; NHMC 21.7.3.1621, group of 15 plastral fragments; NHMC 21.7.3.1622-1624, three neurals; NHMC 21.7.3.1625-1626, left hyoplastron fragments; NHMC 21.7.3.1627, right hypoplastron fragment; NHMC 21.7.3.1628, costal fragment; NHMC 21.7.3.1629, right hypoplastron fragment; NHMC 21.7.3.1630-1931, two costal fragments; NHMC 21.7.3.1632, left epiplastron; NHMC 21.7.3.1633, left hyoplastron fragment; NHMC 21.7.3.1634, group of 23 shell fragments; NHMC 21.7.3.1635, right epiplastron; NHMC

21.7.3.1636-1937, two left epiplastra; NHMC 21.7.3.1638-1939, two costal fragments; NHMC 21.7.3.1640, two costals in association; NHMC 21.7.3.1641, right peripheral 1; NHMC 21.7.3.1642, right xiphiplastron fragment; NHMC 21.7.3.1643, right hypoplastron fragment; NHMC 21.7.3.1644, left hyoplastron fragment; NHMC 21.7.3.1645-1947, three costal fragments; NHMC 21.7.3.1648, group of approximately 80 shell fragments; NHMC 21.7.3.1649, neural fragment; NHMC 21.7.3.1650, group of 10 shell fragments; NHMC 21.7.3.1651, neural I; NHMC 21.7.3.1652-1665, 14 costal fragments; NHMC 21.7.3.1666-1668, three peripheral fragments; NHMC 21.7.3.1669, group of 50 shell fragments; UU PL 705, possible hyoplastron fragment.

Description: The material consists of numerous shell fragments of relatively good preservation. Most specimens preserve sufficient anatomical information, but several remain indeterminate. The description of the most complete specimens is given below.

Carapace elements (Fig. 4(A–J)). NHMC 21.7.3.1623 (Fig. 4(A)): This specimen corresponds to a complete neural. It is hexagonal, with short anterior lateral sides. It is not crossed by any vertebral sulci, suggesting that it is the second or fourth neural. NHMC 21.7.3.1645 shows a similar morphology (Fig. 4(C)).

NHMC 21.7.3.1622 (Fig. 4(B)): This is a complete neural that is hexagonal, with short lateral sides. It is crossed by the vertebral sulci in the posterior part, suggesting that it is the third or fifth neural.

NHMC 21.7.3.1624 (Fig. 4(D)): This complete neural is quadrangular to rounded, with the anterior part being slightly wider. It is not crossed by any vertebral sulci. Its size is rather small, in comparison to the other neurals described. A dorsal keel is noted longitudinally, suggesting that it could belong to a young individual.

NHMC 21.7.3.1651 (Fig. 4(E)): This specimen corresponds to a complete first neural. It is quadrangular with rounded edges, being longer than wide. The posterior part is crossed by the vertebral sulcus that is not straight.

NHMC 21.7.3.1649 (Fig. 4(F)): This specimen corresponds to a fragment of a neural. It is much wider than long, hexagonal in shape, with shorter anterior lateral sides. As such, it is most probably one of the posterior neurals. Viscerally, the attachment for the vertebra is visible. As it is not crossed by any sulci; it could be either the sixth or seventh neural.

NHMC 21.7.3.1640 (Fig. 4(G)): This specimen corresponds to the medial parts of two successive left costals in association. Both show the long and short medial sutures for the corresponding hexagonal neurals. In the preserved part, the sulci between the vertebrals and the pleurals can be observed.

NHMC 21.7.3.1638 (Fig. 4(H)): This specimen corresponds to an almost complete right costal, missing only the distal part. In medial side, two sutured surfaces are visible, one long and the other short, corresponding to an hexagonal neural. Dorsally, the sulci between the vertebrals are visible, suggesting that this could be the third or fifth costal.

NHMC 21.7.3.1639 (Fig. 4(I)): This specimen corresponds to the medial part of a left costal. In medial side, two sutured surfaces are visible, one long and one short, corresponding to an hexagonal neural. Dorsally, the sulci between the pleurals cross the medial part of this costal, suggesting that this could be the second, fourth or sixth costal.

NHMC 21.7.3.1641 (Fig. 4(J)): This specimen corresponds to an almost complete right peripheral I. Based on the preserved anterior border we can estimate the presence of a wide nuchal notch affecting also the first peripherals. The peripheral is long and narrow. Medially, the vertebral I and the pleural I show a long overlap on the peripheral, whereas the vertebral I contacts marginal II.

Plastron elements (Fig. 4(K–S)). NHMC 21.7.3.1618 (Fig. 4(K)): This specimen corresponds to the right part of the anterior lobe of the plastron, consisting of the right epiplastron and most of the entoplastron. The epiplastron is long and narrow. Viscerally, a long but shallow lip is formed, being concave medially and convex laterally. Anteriorly, a shallow notch is noted. The entoplastron is hexagonal and rounded, being wider posteriorly. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gular/humeral sulcus is slightly convex laterally, and causes a slight constriction in the anterior part of the lobe. The humerals are medially short and laterally longer. The entoplastron is also overlapped by the anterior part of the pectorals. The humero-pectoral sulcus is slightly concave medially.

NHMC 21.7.3.1637 (Fig. 4(L)): This specimen corresponds to a left epiplastron. The epiplastron is long and rather wide. Viscerally, a long lip is formed, being concave medially and convex laterally. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gularo/humeral sulcus is slightly convex laterally. The left epiplastron NHMC 21.7.3.1636 shows a similar morphology.

NHMC 21.7.3.1635 (Fig. 4(M)): This specimen corresponds to a right epiplastron. It is long and rather wide. Viscerally, a long and shallow lip is formed, being concave medially and convex laterally. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is slightly convex laterally and causes a slight constriction in the anterior part of the lobe.

NHMC 21.7.3.1632 (Fig. 4(N)): This is an almost complete left epiplastron, rather long and wide. Viscerally, a short, shallow and slightly concave lip is formed. It is covered medially by the gulars. An irregular growth of a small scute is noted in the anterior end of the gularo-humeral sulcus.

NHMC 21.7.3.1620 (Fig. 4(O)): This specimen corresponds to an almost complete left hypoplastron. The anterior suture, which connects it to the hyoplastron, is straight, whereas the posterior one, which connects it to the xiphiplastron, is slightly convex. The hypoplastron is rather flat. Viscerally, the abdominal forms a wide and slightly convex lip on the posterior lobe. Ventrally, an unusual morphology is noticed. Although the posterior part of the hypoplastron is covered by the abdominal scute, anteriorly there is another sulcus. Such sulcus is apparent also in another specimen from Plakias (NHMC 21.7.3.1643; Fig. 4(P)), a morphology that has not been previously noted in geoemydids. However, the absence of corresponding hyoplastra and the disarticulated nature of the material do not allow us to clarify this character.

NHMC 21.7.3.1643 (Fig. 4(P)): This specimen corresponds to an almost complete right hypoplastron. The anterior suture, which connects it to the hyoplastron, is straight, whereas the posterior one, which connects it to the xiphiplastron, is slightly convex. The hypoplastron is rather flat. Viscerally, the abdominal forms a wide and slightly convex lip on the posterior lobe. In the posterior part, the abdomino-femoral sulcus is clearly visible, whereas in the anterior part the sulcus is not clear as a result of erosion.

NHMC 21.7.3.1619 (Fig. 4(Q)): This specimen corresponds to an almost complete right xiphiplastron. The lateral sides of the posterior lobe are converging posteriorly. On the posterior part, a deep and wide anal notch is formed. The xiphiplastral extremities are rounded. The femorals cover the anterior part of the xiphiplastron, whereas the anals show a somewhat long covering on the posterior part of the lobe. The femoro-anal sulcus is slightly convex, being oriented antero-medially.

NHMC 21.7.3.1642 (Fig. 4(R)): This specimen corresponds to a fragment of the right xiphiplastron. On the basis of the preserved part, the presence of a wide angular anal notch can be estimated. In the anterior part, a short part of the femoro-anal sulcus is noted.

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UU PL 705 (Fig. 4(S)): In the collections of UU, this small-sized specimen probably represents a fragment of the left hyoplastron. It preserves a curved sulcus that could be identified as the pectoro-abdominal one. Further identification is not possible, but it is overall similar to the respective material from NHMC and can be attributed to the same taxon as well.

Remarks: The specimens can be attributed to Geoemydidae on the basis of the following characters: first neural quadrangular, remaining neurals hexagonal with short anterolateral sides, pectorals medially shorter than the gulars, and deep anal notch. They can be further identified as a member of *Mauremys* on the basis of the contact between vertebral I with marginal II and the entoplastron being crossed by the gulars and the humero-pectoral sulcus (Claude et al., 2007). The *Mauremys* material from Plakias suggests attribution to a single taxon, on the basis of the similar size, surface sculpturing and overall morphology. The combined information of the preserved elements allows the documentation of the morphology of most parts of the shell, indicating a confident assignment to *Mauremys*, but no species determination can be made with certainty.

Based on the available epiplastra, at least three adult individuals are preserved, and a juvenile individual is also present. The unusual morphology noted in the hypoplastra (NHMC 21.7.3.1620 and NHMC 21.7.3.1643) needs to be further investigated, as it has not previously been observed in other geoemydids. However, the absence of corresponding hyoplastra and the disarticulated nature of the material do not allow us to interpret this character. The extended covering of the pleural I and vertebral I on peripheral I distinguishes the Plakias *Mauremys* from the extant *Mauremys caspica* (Gmelin, 1774) and *M. rivulata* (Valenciennes, 1833), as also from the extinct *M. gaudryi* (Depéret, 1885) (Pliocene, France; Hervet, 2003). As such, the Plakias *Mauremys* is more similar to other Miocene terrapins from central and eastern Mediterranean (e.g., *M. campanii* Chesi et al., 2009, from Tuscany, Italy). The narrower neural I, the shape of the entoplastron, having the posterior part shorter than the anterior one, and the shorter pectoral covering on the entoplastron differentiate the Plakias geoemydid from *M. campanii*. The angular anal notch also differentiates the Plakias geoemydid from the roughly similar *M. sarmatica* (Purschke, 1885) from the Miocene of Germany, which has a rounded anal notch (Hervet, 2003). The Plakias terrapin represents the oldest described occurrence of Geoemydidae from Greece, being older than the Allatini (Miocene/Pliocene boundary; Vlachos et al., 2015b) and the Maramena forms (latest Miocene; Gad, 1990; Georgalis and Kear, 2013; Vlachos et al., 2015b), both recovered from northern Greece. All other fossil geoemydid occurrences from Greece are only known from Pleistocene and Holocene remains (Chesi et al., 2007; Georgalis and Kear, 2013).

Crocodylia Gmelin, 1789
Crocodylia indet.
Fig. 5

Referred specimens: UU PL 706 to UU PL 732, 27 isolated teeth; UU PL 735 and UU PL 736, two phalanges.

Description: UU PL 706-732: Several isolated teeth preserve only a crown that is conical, variably pointed apically, and regularly concave basally. Some of the teeth are only partially preserved; the largest crown is 8.3 mm long. Mesiodistal carinae separate a lingual, slightly concave surface from a labial, slightly convex surface. The carinae are not serrated. Both lingual and labial surfaces can be slightly wrinkled and bear longitudinal ridges. Some of the teeth are slender, long, and pointed, whereas others are more massive and apically blunt.

UU PL 735-736: These two phalanges are elongated elements showing a single roundish articular surface proximally. The best

preserved element (UU PL 735) is 18 mm long. Its distal portion is dorsoventrally flattened and laterally provided, on both sides, with a sort of weak keel.

Remarks: The morphology of the teeth is fully congruent with that of generalized crocodilians, but does not allow a more precise identification, since in most cases crocodilian teeth are not diagnostic. These are, however, congruent with the morphology of the *Crocodylus* teeth from the late Miocene of Italy (Delfino et al., 2007). Not much can be said about the phalanges, except for the fact that they show standard crocodilian morphology. They are referred to the same taxon as the teeth. The Plakias specimens constitute the first fossils of crocodilians described from Greece, as also one of the last occurrences of this group in the European continent (Table 1).

Squamata Oppel, 1811
Amphisbaenia Gray, 1844
Amphisbaenia indet.
Fig. 6

Referred specimen: UU PL 733, a single presacral vertebra.

Description: The specimen is a rather small, procoelous vertebra with a centrum length of only 1.2 mm. A slight degree of deformation is recognizable in anterior view. The centrum is dorsoventrally compressed and has a flattened ventral surface and subparallel lateral margins. A massive and rounded synapophysis is visible on the right side of the vertebra. In dorsal view, the neural arch is constricted in the middle. Its dorsal surface is flattened and the neural spine is lacking, as well as the zygosphene. Only the right prezygapophysis is preserved: it is roughly sub-elliptical and tilted dorsally about 30°. The prezygapophyseal process is rather short. Neither the posterior end of the neural arch nor the postzygapophyses are preserved.

Remarks: The specimen can be attributed to Amphisbaenia on the basis of the combination of the following characters: small size, dorsoventrally compressed centrum with a flattened ventral surface and roughly parallel lateral margins, short and robust prezygapophyses, massive and rounded synapophyses, absence of zygosphene, and a dorsally flattened neural arch lacking a neural spine (Estes, 1983; Delfino, 2003). Amphisbaenians are present in the extant herpetofauna of Greece, with *Blanus* occurring in the Dodecanese Islands (see below, Section 5.2), but they were totally absent in the fossil record of the country. As such, the specimen described herein represents the first known fossil amphisbaenian from Greece. Its affinities with Blanidae, which are the only extant amphisbaenians inhabiting Europe, cannot be tested on the basis of the vertebral morphology: isolated vertebrae of Amphisbaenia do not show significant diagnostic features that would allow for a more precise identification (Estes, 1983). The sole other known fossil amphisbaenian from the Aegean region has been recovered from the Pliocene of Çalta, Turkey (Rage and Sen, 1976). The Çalta amphisbaenian is represented by three vertebrae, none of which was figured or described in detail. As a matter of fact, no further comparison between these specimens can be made.

Also interesting, the vertebra UU PL 733 represents the sole non-snake squamate from Plakias, as other lizards are conspicuously absent. We consider that this absence is due to taphonomic or collection biases and does not reflect the actual lizard palaeodiversity of Plakias.
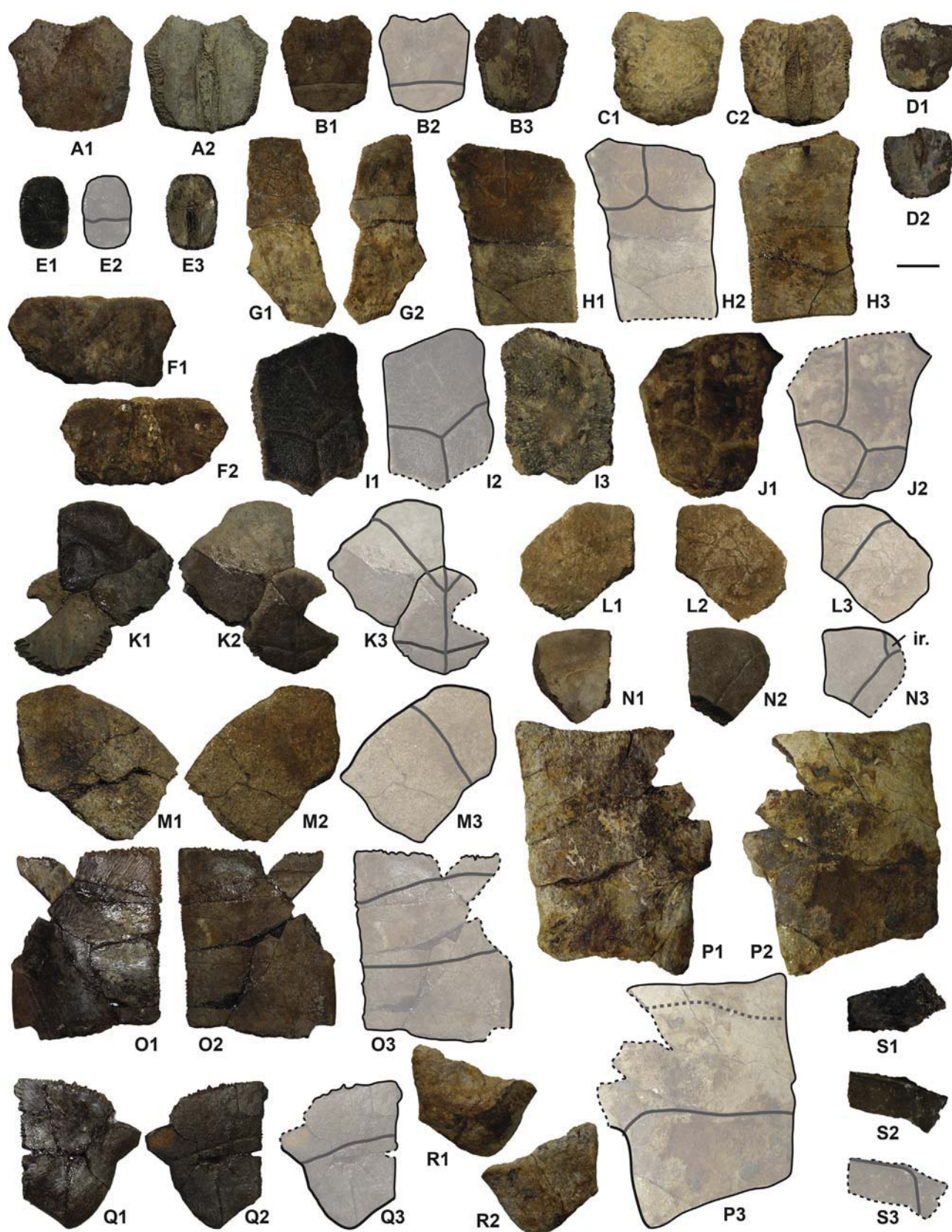
Serpentes Linnaeus, 1758
Colubroidea Oppel, 1811
?Natricinae Bonaparte, 1838 (*sensu* Szyndlar, 1991b)
?Natricinae indet.
Fig. 7

Referred specimen: UU PL 734, a single precloacal vertebra.

Description: The vertebra is fragmentary, with the prezyga-pophyses, part of the cotyle and part of the neural spine being eroded. The vertebra is procoelous, relatively large and proportionally elongate, with a centrum length of 5.5 mm. The prezygapophyseal processes are not clearly visible, due to the fact that the anterior portion of the vertebra is not well preserved. The cotyle is rather incomplete but appears to be relatively rounded. Only part of the zygosphene is preserved. The condyle is spherical and rather robust, and protrudes significantly from the posterior part of the vertebra. The roof of the zygantrum is visible and appears to be relatively thick. The neural canal is rather large, almost equal in size to the condyle. Synapophyses are divided in diapophyses and parapophyses. The neural spine is broken. The hypapophysis was probably present, however, this cannot be evaluated with certainty. In ventral view, a subcentral foramen is also visible at mid centrum length of the vertebra.

Remarks: The specimen can be attributed to Serpentes on the basis of the general vertebral shape and especially the presence of zygantrum and zygosphene (Rage, 1984). The single snake vertebra from Plakias is fragmentary, thus precluding the evaluation of exact taxonomic affinities. However, the probable presence of hypapophysis could indicate that this specimen belongs to either natricines, viperids or elapids. All these three groups have been recorded in the Miocene of Greece (Szyndlar, 1991a,b, 1995; Szyndlar and Rage, 2002; Georgalis et al., 2016a). The combination, however, of a rather elongate centrum, strong subcentral ridge and, probably, a posteriorly vaulted neural spine, prompts us to consider natricine affinities as the most plausible for the Plakias snake. This identification is further supported by direct comparison with numerous skeletons of extant natricine snakes.

5. Discussion

5.1. Palaeoecology of Plakias

The locality of Plakias is mostly known for its micromammal assemblage (de Bruijn and Meulenkamp, 1972; de Bruijn et al., 2012). This is comprised of erinaceomorphs and soricomorphs eulipotyphlans, and eomyid, sciurid, glirid and murid rodents, whereas larger mammals are known only by an indeterminate suid similar to *Propotamochoerus* (van der Made, 1996; Koufos, 2006; de Bruijn et al., 2012). The presence of at least three distinct taxa of sciurids (Koufos, 2006) indicates the likely presence of a forested environment (de Bruijn et al., 1980), although we acknowledge that several fossil and extant sciurids are ground dwellers (e.g., Viriot et al., 2011). Plant remains and invertebrates are also known from Plakias (de Bruijn et al., 2012). Fossil invertebrates include freshwater gastropods such as *Planorbis* and *Brotia* (de Bruijn et al., 2012), which further suggest the presence of a river or lake system.

The new amphibian and reptile finds from Plakias allow us to draw further conclusions regarding the palaeoecology of this locality. The presence of an alytid frog implies wet habitats, which is the common environment for the extant members of the group (Vitt and Caldwell, 2014). All extant crocodilians are known to be water dwellers, inhabiting river systems, lakes, and even venture

into the open sea (Steel, 1973; Britton et al., 2012). The fragmentary nature of the Cretan crocodilian does not allow us to make a proper specific or generic identification, but as the teeth from Plakias bear strong resemblance with certain Neogene finds from the Mediterranean that are assigned to Crocodyloidea or Alligatoroidea, we can infer a similar lifestyle. All extant pan-trionychids are known to be strictly aquatic, and a similar or identical life strategy has been proposed for all fossil taxa of this group as well (Vitek and Joyce, 2015). The occurrence of a geoemydid further indicates the presence of lake and river systems (Busack and Ernst, 1980). The amphisbaenian vertebra is fragmentary and cannot be assigned to the specific level. However, the vast majority of amphisbaenians are fossorial (Kearney, 2003) and as such, a similar, burrowing lifestyle is also proposed for the Cretan representative of this clade. Additionally, the presence of a natricine snake adds a further aquatic or semi-aquatic taxon to the locality (Vitt and Caldwell, 2014).

5.2. Biogeography

At least until the late Serravallian (middle Miocene), Crete was located at the southern part of Aegäis, the continental area that united modern Greece with Anatolia, but it was most probably already isolated as an island by the Tortonian (late Miocene), after the opening of the Proto-Aegean Sea (Dermitzakis and Papaniko-laou, 1981; Poulakakis et al., 2005). The suggested age of the Plakias fauna as early Tortonian (de Bruijn et al., 2012) coincides with the breakup of the southern Aegean landmass and the early formation of Crete as an island (Poulakakis et al., 2005; fig. 4). As such, we cannot determine with certainty whether Plakias hosted a truly continental fauna or an insular fauna at least partly deriving from the former continental assemblages. However, even if the fauna was an insular one, it should have strong biogeographic affinities with coeval mainland Aegäis faunas.

The micromammal fauna of Plakias bears strong affinities with coeval ones from Central Europe (de Bruijn et al., 2012). The amphibian and reptile fossils described herein provide additional information about the palaeobiogeography of this part of southeastern Europe, as Miocene herpetofaunas are not well documented in that region (Georgalis et al., 2013; Georgalis and Kear, 2013).

The presence of an alytid frog in the late Miocene of Crete is not of biogeographic importance, as this group was widespread throughout Europe during that time interval and has been also found from several other Neogene localities from Greece (Rage and Roček, 2003). All other fossil amphibians from Crete are of Quaternary age (Caloi et al., 1986; Sanchiz, 1998).

The two distinct turtle taxa recovered from Plakias represent the oldest turtles from Crete, as also the oldest occurrences of Geoemydidae and Pan-Trionychidae from Greece known up to date. Overall, turtles were considered up to now to be absent from Neogene localities of Crete, with their only remains known from Pleistocene and Holocene sediments (Bachmayer et al., 1975; Kotsakis, 1977; Brinkerink, 1996; Chesi et al., 2007; Georgalis and Kear, 2013). Although Brinkerink (1996, p. 208) noted that no

Fig. 4. *Mauremys* sp. from the earliest late Miocene of Plakias. **A**. NHMC 21.7.3.1623, neural in dorsal (A1) and visceral (A2) views. **B**. NHMC 21.7.3.1622, neural in dorsal (B1), drawing of the dorsal (B2) and visceral (B3) views. **C**. NHMC .7.3.1645, neural in dorsal (C1) and visceral (C2) views. **D**. NHMC .7.3.1624, neural in dorsal (D1) and visceral (D2) views. **E**. NHMC 21.7.3.1651, neural in dorsal (E1), drawing of the dorsal (E2) and visceral (E3) views. **F**. NHMC 21.7.3.1649, neural fragment in dorsal (F1) and visceral (F3) views. **G**. NHMC 21.7.3.1640, two successive costals in dorsal (G1) and visceral (G2) views. **H**. NHMC 21.7.3.1638, costal in dorsal (H1), drawing of the dorsal (H2) and visceral (H3) views. **I**. NHMC 21.7.3.1639, costal fragment in dorsal (I1), drawing of the dorsal (I2) and visceral (I3) views. **J**. NHMC 21.7.3.1641, peripheral in dorsal (J1) and drawing of the dorsal (J2) views. **K**. NHMC 21.7.3.1618, right epiplastron and entoplastron in visceral (K1), ventral (K2) and drawing of the ventral (K3) views. **L**. NHMC 21.7.3.1637, left epiplastron in visceral (L1), ventral (L2) and drawing of the ventral (L3) views. **M**. NHMC 21.7.3.1635, right epiplastron in visceral (M1), ventral (M2) and drawing of the ventral (M3) views. **N**. NHMC 21.7.3.1632, left epiplastron fragment in visceral (N1), ventral (N2) and drawing of the ventral (N3) views. **O**. NHMC 21.7.3.1620, left hypoplastron in visceral (O1), ventral (O2) and drawing of the ventral (O3) views. **P**. NHMC 21.7.3.1643, right hypoplastron in visceral (P1), ventral (P2) and drawing of the ventral (P3) views. **Q**. NHMC 21.7.3.1619, right xiphiplastron in visceral (Q1), ventral (Q2) and drawing of the ventral (Q3) views. **R**. NHMC 21.7.3.1642, right xiphiplastron fragment in visceral (R1) and ventral (R2) views. **S**. UU PL 705, possible hyoplastron fragment in visceral (S1), ventral (S2) and drawing of the ventral (S3) views. Abbreviation: ir, irregular scute growth. Scale bar: 10 mm.
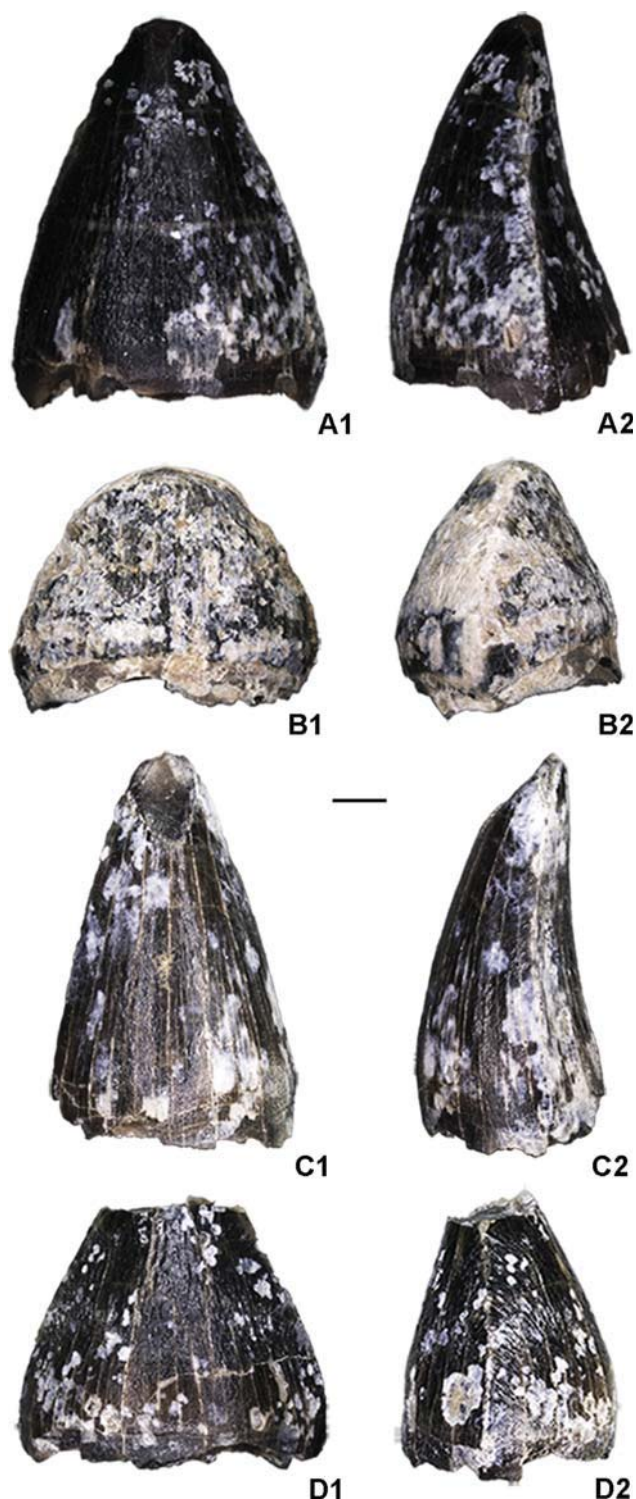
Fig. 5. Crocodylia from the earliest late Miocene of Plakias. **A**. UU PL 706, isolated tooth in labial (A1) and mesial (A2) views. **B**. UU PL 707, isolated tooth in labial (B1) and mesial (B2) views. **C**. UU PL 708, isolated tooth in labial (C1) and mesial (C2) views. **D**. UU PL 709, isolated tooth in labial (D1) and mesial (D2) views. Scale bar: 1 mm.

turtles are known from pre-Pleistocene sites from Crete, he pointed out the potential of the site of Plakias. The presence of pan-trionychids in the early late Miocene of Greece represents the oldest record and the second only occurrence of this group from the country, which was otherwise only known from the Pliocene of northern Greece (Vlachos et al., 2015a). Pan-trionychids are

widespread throughout Europe during the Neogene (Hummel, 1932; Młynarski, 1976; Danilov, 2005; Karl, 1999); however, their alpha taxonomy has not been settled with certainty, mostly because of the homoplastic characters that are observed in their morphology (Vitek and Joyce, 2015). Curiously also, Miocene pan-trionychids were totally absent until now from Greece, despite the wealth of fossil localities of that age in the country and extensive sampling (Georgalis and Kear, 2013). The new specimens from Plakias could probably indicate that this absence was not genuine and that pan-trionychids will be subsequently found in other Greek Miocene localities. This is further supported by the presence of pan-trionychids in the Miocene of Bulgaria (Pamouktchiev et al., 1998; Georgalis and Kear, 2013) and Anatolia (Staesche et al., 2007). Affinities of the new Cretan pan-trionychid with the Bulgarian and Anatolian forms cannot be established due to the fragmentary nature of the new specimens. Other, relatively geographically close Miocene pan-trionychids are also known from Cyprus (Hadjisterkotis et al., 2000), Egypt (Lapparent de Broin, 2000), and Italy and Malta (Kotsakis, 1985). The Plakias geoemydid adds to the Miocene diversity of this group in southeastern Europe. Additionally, this pre-Messinian occurrence of *Mauremys* further corroborates the suggestion of Chesi et al. (2009) for warm and wet conditions during that period in southern Mediterranean Europe.

Crocodilians are conspicuous elements in several Miocene faunas across European localities (among others, Ginsburg and Bulot, 1997; Kotsakis et al., 2004; Delfino et al., 2007; Delfino and Rook, 2008; Martin, 2010; Martin and Gross, 2011; Delfino and Rossi, 2013). However, they are relatively scarce by the late Miocene and were apparently absent from southeastern Europe and Anatolia (Böhme, 2003; Sen et al., 2011). The youngest up to date published records of crocodilians from Europe are known from the latest Miocene of Italy (Table 1), as supposed occurrences from the late Miocene and Pliocene of Spain and Portugal have not been accompanied by descriptions or figures, and are here considered anecdotal (Delfino et al., 2007). The taxon *Diplocynodon levantinicum* from Bulgaria, was initially thought to be of Pliocene age (Huene and Nikoloff, 1963), whereas it was later treated questionably as late Miocene (Delfino and Rossi, 2013), but its type locality is now believed to pertain most probably to the middle Miocene (Sen et al., 2011). With the exception of the slender snouted forms attributed to *Tomistoma* (Capellini, 1890; Vianna and Moraes, 1945), several late Miocene occurrences are considered to be members of *Crocodylus* or at least cf. *Crocodylus* (Delfino et al., 2007; Delfino and Rook, 2008; Delfino and Rossi, 2013) that possibly dispersed from Africa well before the Messinian Salinity Crisis (Delfino et al., 2007). Interestingly also, Gargano and Scontrone, that yielded *Crocodylus* remains, were palaeoislands during the latest Miocene; we can thus speculate that the Cretan crocodilian could also belong to the same lineage and had originated through a similar dispersal route from Africa. Whatever the case, the isolated teeth from Plakias represent the first crocodilians from Greece to be formally described and one of a few late Miocene occurrences of this group in Europe.

Our knowledge of squamate biogeography during the Miocene of Europe is hindered by the lack of consensus surrounding the taxonomy and phylogenetic relationships of its representatives. This is especially true for the southeastern European localities, from where only few specimens have been recovered, most of which originating from classic, well known mammal-bearing sites (Gaudry, 1862–1867; Weithofer, 1888; Richter, 1995; Georgalis et al., 2016b). The presence of a natricine in the late Miocene of Plakias adds to the already known diversity of this widespread snake group (Szyndlar, 1991b), and in fact, represents one of the southernmost fossil occurrences of colubroids in Europe. Whether the Plakias snake bears close affinities with other Neogene

Table 1
Youngest occurrences of crocodilians in Europe.

Taxon	Age	Locality	Reference
Crocodylus sp.	Latest Messinian (or even early Zanclean, depending on the age of the Terre Rosse from Gargano)	Gargano, Apulia, Italy	Delfino et al. (2007)
Crocodylia indet.	Late Messinian	Cava del Monticino, Brisighella, Emilia-Romagna, Italy	Rook et al. (2015)
Tomistoma calaritanus	Tortonian–Messinian	Is Mirrionis, Sardinia, Italy	Capellini (1890)
Crocodylia indet.	Late Tortonian	Fiume Santo, Sardinia, Italy	Abbazzi et al. (2008)
cf. *Crocodylus* sp. (type of *Crocodylus bambolii*)	Tortonian	Montabamboli-Casteani-Ribolla, Tuscany, Italy	Delfino and Rook (2008)
Tomistoma cf. *lusitanica*	Tortonian	Olhos de Agua, Algarve, Portugal	Vianna and Moraes (1945)
Crocodylia indet. (*Diplocynodon* sp.)	Tortonian	Soblay, Ain, France	Ménouret and Mein (2008)
Crocodylia indet.	Early Tortonian	Plakias, Crete, Greece	This paper
cf. *Crocodylus* sp.	Early Tortonian	Scontrone, Abruzzo, Italy	Rustioni et al. (1993) and Delfino and Rossi (2013)

natricines from southeastern Europe (e.g., the natricine from Maramena described by Szyndlar, 1995) cannot be tested due to the fragmentary nature of the single known specimen. Furthermore, the Plakias natricine represents the sole Neogene record of snakes from Crete, as all other fossil occurrences from the island are confined to Pleistocene and Holocene sediments (Holman, 1998). Amphisbaenians are well known from several Miocene European localities, but almost only from the western and central parts of the continent (Roček, 1984; Bolet et al., 2014; Čerňanský et al., 2015), whereas they have never been described from the Balkan Peninsula and eastern Europe in general (Delfino, 2003), with the single exception of a blanid from the middle Miocene of Tauṭ, Romania (Venczel and Ştiucă, 2008). After the end of the Miocene, the distribution of amphisbaenians in Europe became gradually restricted to its Mediterranean margins, becoming extinct from most regions after the Pleistocene and surviving today only in the Iberian Peninsula and few Greek Islands (Delfino, 1997; Delfino and Bailon, 2000). Amphisbaenians are represented in the Greek extant herpetofauna solely by the species *Blanus strauchi* (Bedriaga, 1884), which is distributed in the islands of Samos, Fournoi, Leros, Kos, Symi, Rhodes, and Kastellorizon (Valakos et al., 2008). *Blanus* occurs also in the adjacent Anatolia, represented by *B. strauchi* and two additional, recently described or revalidated species: *B. alexandri*

Sindaco, Kornilios, Sacchi and Lymberakis, 2014, and *B. aporus* Werner, 1898. So far, the Anatolian fossil record of amphisbaenians is also poor, consisting of only a single record from the Pliocene of Çalta (Rage and Sen, 1976; Delfino, 1997). Whether or not the
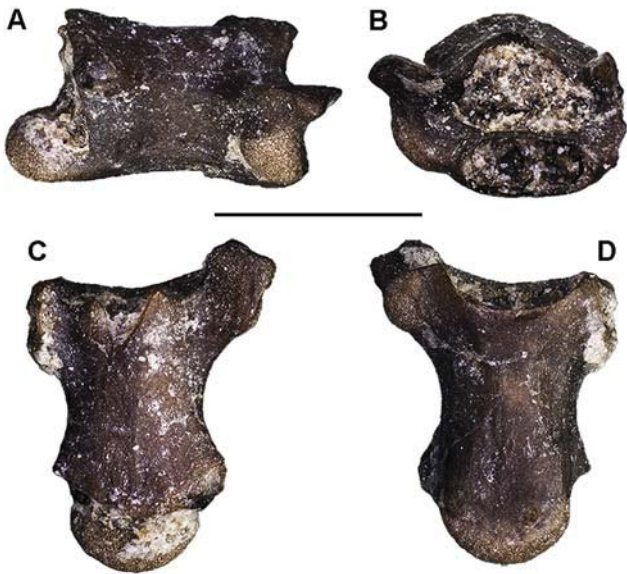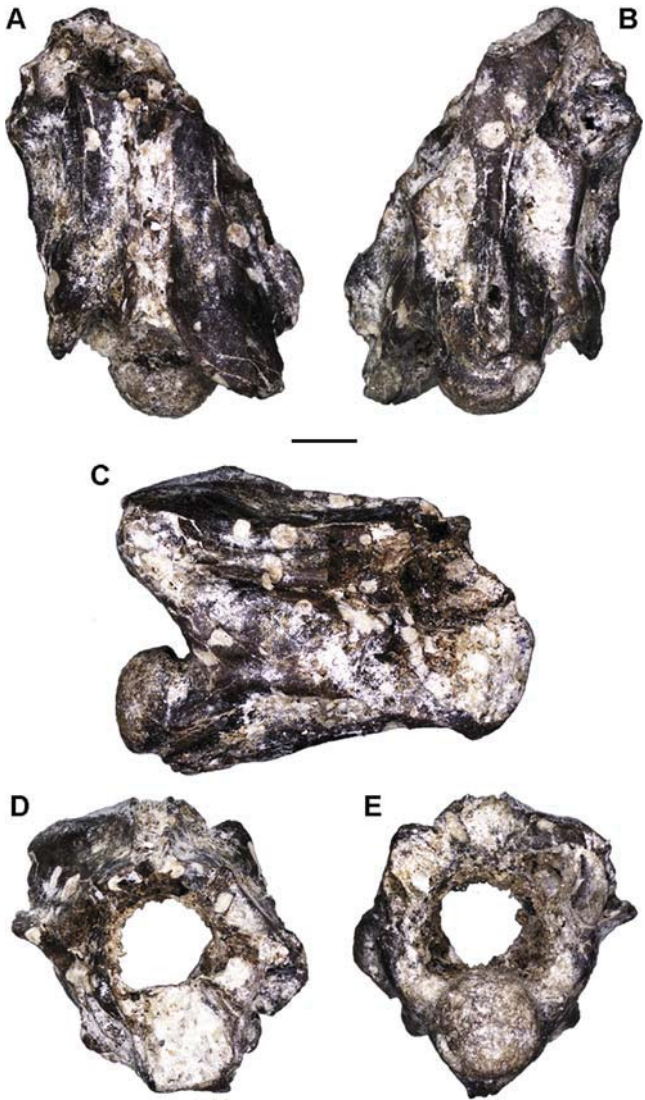

Fig. 7. ?Natricinae from the earliest late Miocene of Plakias: UU PL 734, precloacal vertebra in dorsal (**A**), ventral (**B**), right lateral (**C**), anterior (**D**) and posterior (**E**) views. Scale bar: 1 mm.

Fig. 6. Amphisbaenia from the earliest late Miocene of Plakias: UU PL 733, presacral vertebra in right lateral (**A**), anterior (**B**), dorsal (**C**) and ventral (**D**) views. Scale bar: 1 mm.

Plakias specimen represents a species of *Blanus* cannot be evaluated on the basis of vertebral characters. It is, however, probable that the Plakias amphisbaenian does belong to *Blanus*, as members of this genus have a wide Miocene distribution in western and Central Europe (Bolet et al., 2014; Čerňanský et al., 2015) and the disjunct extant restricted distribution in the western and eastern edges of the continent has been in fact interpreted as relics of an initially continuous range in southern Europe (Alexander, 1966; Delfino, 2003), a situation that has also been observed for other squamate groups such as erycid and elapid snakes (Szyndlar, 1991a,b; Rage, 2013). In fact, Greece and in general the southern Balkans have been suggested as acting as a refugium for multiple squamate groups such as scolecophidians, erycids, the large anguid *Pseudopus*, and the so called "oriental vipers" (Delfino, 2003), which all have their sole extant European populations only in that region (Sindaco and Jeremčenko, 2008). However, an alternative hypothesis of the Plakias amphisbaenian sharing affinities with African ones should also be taken into consideration, due to the geographical proximity of Crete to Africa and the unexpected but now well-known marine dispersal capabilities of these squamates (Kearney, 2003; Longrich et al., 2015). Nevertheless, such hypothesis remains severely hindered by the poor fossil record of African squamates (Rage, 2003; Delfino et al., 2004). Pending the discovery of more complete material from Plakias that could ideally comprise cranial elements that bear diagnostic features, no further biogeographic correlations of the Cretan amphisbaenian with European, Anatolian or African taxa can be made with certainty.

6. Conclusions

The herpetofauna of Plakias described in this paper includes the oldest amphibians and reptiles from the Island of Crete and represents one of the southernmost fossil herpetofaunas of Europe. The alytid frog presented herein adds to the known record of this group from the Miocene of southern Europe. The crocodilians are the first described from the country and represent one of the youngest occurrences of this group in Europe. Turtles include two distinct taxa: a geoemydid and a pan-trionychid, both representing the oldest occurrences of these groups from Greece. The single colubroid snake specimen adds further to the published record of Miocene snakes from Greece, whereas the amphisbaenian vertebra from Plakias represents the first described fossil of this group from the country, suggesting that amphisbaenians had a continuous range in the northern Mediterranean area. The herpetofauna of Plakias is shown to be diverse. Overall, it further adds to our knowledge of the Miocene herpetofaunas of southeastern Europe, a region in which amphibian and reptile fossils are still not adequately known.

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