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Abstract

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: one alytid anuran, one crocodylian, two turtles (one pan-trionychid and one geoemydid) and two squamates (one amphisbaenian and one colubroid snake). The crocodylian 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 the 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.

Keywords:

Anura

Testudines

Crocodylia

Amphisbaenia

Serpentes

Miocene

1. Introduction

Miocene herpetofaunas from Europe are relatively well understood (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 towards 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 have taken place during this time interval (Rögl, 1999; Koufos et al., 2005). As such, the study of southeastern European localities could clarify significant 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, and references therein). However, mammal finds were almost always the main focus of these studies, thereby neglecting other important tetrapod groups, such as amphibians and reptiles. Nevertheless, important fossil finds 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; Georgalis and Kear, 2013; Vlachos and Tsoukala, 2014; Vlachos et al., 2015b; Garcia et al., 2016; Georgalis et al., 2016b), whereas amphibian remains are practically unknown from this time interval from Greece, with only few, sporadic, published occurrences (Sanchiz, 1998; Rage and Roček, 2003).

Here we describe new amphibian and reptile finds 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 designation to the species level. Higher level taxonomic determination of the specimens was possible, however, revealing an unexpectedly diverse assemblage consisting of anurans, pan-trionychids, geoemydids, crocodylians, 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 cannot confirm, neither 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 crocodylians are better represented in early and middle Miocene localities of Europe, rather than late Miocene ones (Karl, 1999; Delfino and Rossi, 2013). However, since none among the Plakias representatives of the

herpetofauna can be attributed to the species level, no further age correlations 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, crocodylians 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 Bruijn and Meulenkamp (1972) from the first period of field work 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 S. Kuss in the 1970's. This material was originally in the Geologisch-Paläontologisches Institut der Universität Freiburg, Germany, and later formed part 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 crocodylians, 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 crocodylians, Estes (1983) for amphisbaenians, and Rage (1984) for snakes.

4. Systematic Palaeontology

AMPHIBIA Linnaeus, 1758

ANURA Fischer von Waldheim, 1813

ALYTIDAE Fitzinger, 1843

cf. Alytidae indet.

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

Description: UU PL 701 (Fig. 2): 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 it as "Platkia (sic), Greece, Neogene: Discoglossinae indet. (Sanchiz, unpublished)" (Borja Sanchiz, pers. commun. 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).

REPTILIA Laurenti, 1768

TESTUDINES Batsch, 1788

PAN-TRIONYCHIDAE Joyce et al., 2004

Pan-Trionychidae indet.

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. 3A): 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. 3B): 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. 3C): 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 with the previously described specimen (UU PL 703), but a larger part of the costal is preserved.

NHMC 21.7.3.1671 (Fig. 3D): 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.

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 Gefira pan-trionychid, they are mostly coalesced, forming continuous grooves. As was mentioned above, however, the extreme variability of sculpturing that is 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

Mauremys Gray, 1869

Mauremys sp.

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, neural; NHMC 21.7.3.1623, neural; NHMC 21.7.3.1624, neural; NHMC 21.7.3.1625, left hyoplastron fragment; NHMC 21.7.3.1626, left hypoplastron fragment; 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, costal fragment; NHMC 21.7.3.1631, costal fragment; 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, left epiplastron; NHMC 21.7.3.1637, left epiplastron; NHMC 21.7.3.1638, costal fragment; NHMC 21.7.3.1639, costal fragment; 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, costal fragment; NHMC 21.7.3.1646, costal fragment; NHMC 21.7.3.1647, costal fragment; 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, costal fragment; NHMC 21.7.3.1653, costal fragment; NHMC 21.7.3.1654, costal fragment; NHMC 21.7.3.1655, costal fragment; NHMC 21.7.3.1656, costal fragment; NHMC 21.7.3.1657, costal fragment; NHMC 21.7.3.1658, costal fragment; NHMC 21.7.3.1659, costal fragment; NHMC 21.7.3.1660, costal fragment; NHMC 21.7.3.1661, costal fragment; NHMC 21.7.3.1662, costal fragment; NHMC 21.7.3.1663, costal fragment; NHMC 21.7.3.1664, costal fragment; NHMC 21.7.3.1665, costal fragment; NHMC 21.7.3.1666, peripheral fragment; NHMC

21.7.3.1667, peripheral fragment; NHMC 21.7.3.1668, peripheral fragment; 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 (Figs. 4A–J):

NHMC 21.7.3.1623 (Fig. 4A): 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 (Fig. 4C) shows a similar morphology.

NHMC 21.7.3.1622 (Fig. 4B): 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. 4D): 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. 4E): 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. 4F): 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. 4G): 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. 4H): 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. 4I): 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. 4J): 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 (Figs. 4K–S)

NHMC 21.7.3.1618 (Fig. 4K): 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. 4L): 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 gularscutes 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. 4M): 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 gularscutes 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. 4N): 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. 4O): 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. 4P),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. 4P): 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. 4Q): This specimen corresponds to an almost complete rightxiphiplastron. 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. 4R): 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.

UU PL 705 (Fig. 4S): 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 with 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 *Mauremys rivulata* (Valenciennes, 1833), as also from the extinct *Mauremys 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. *Mauremys 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 *Mauremys 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 (latest Miocene) forms (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.

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

Description: UU PL 706 - UU PL 732 (Fig. 5): Several isolated teeth preserve only a crown that is characterized by being 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 - UU PL 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 crocodylians, but does not allow a more precise identification, since in most cases crocodylian 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 crocodylian morphology. They are referred to the same taxon as the teeth. The Plakias specimens constitute the first

fossils of crocodylians 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.

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 (Fig. 6). 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 in Biogeography), 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.

Interestingly also, the vertebra UU PL 733 represents the sole non-snake squamate from Plakias, as other lizards are cospicuously 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.

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

Description: The vertebra is fragmentary, with the prezygapophyses, part of the cotyle and part of the neural spine being eroded (Fig. 7). 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 could belong 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 fresh-water 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 Crocodylia 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 crocodylian 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 and references therein). The presence 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 Papanikolaou, 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 up to date. Turtles, in general, 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 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), 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.

Crocodylians 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 crocodylians 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 so-called 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 crocodylian 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 crocodylians from Greece to be formally described and one of only 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, 1862-67; 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 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 Tauţ, 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: *Blanus alexandri* Sindaco, Kornilios, Sacchi and Lymberakis, 2014, and *Blanus aporus* Werner, 1898. 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 Plakias specimen represents a species of *Blanus*, cannot be evaluated on the basis of vertebral characters. It is, however, probable that the Plakias amphisbaenian belongs indeed 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 once 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), but such hypothesis is 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 crocodylians are the first such described faunal elements 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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References

Abbazzi, L., Delfino, M., Gallai, G., Trebini, L., Rook, L., 2008. New data on the vertebrate assemblage of Fiume Santo (North-western Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinia paleobioprovince. Palaeontology 51, 425–451.

Alexander, A.A., 1966. Taxonomy and variation of *Blanus strauchi* (Amphisbaenia, Reptilia). Copeia 1966, 205–224.

Antunes, M.T., 1994. On Western Europe Miocene gavials (Crocodylia): their paleogeography, migrations and climatic significance. Comunicações do Instituto Geológico e Mineiro 80, 57–69.

Augé, M., 2005. Evolution des lézards du Paléogène en Europe. Publications Scientifiques du Muséum, Mémoires du Muséum national d'histoire naturelle, Paris 192, 1–369.

Bachmayer, F., 1967. Eine Riesenschildkröte aus den altpliozänen Schichten von Pikermi (Griechenland). Annales Géologiques des Pays Helléniques 19, 512–526.

Bachmayer, F., Brinkerink, J., Symeonidis, N., 1975.Pleistozäne Schildkröten aus Höhlen der Insel Kreta.Annales Géologiques des Pays Helléniques 27, 110–121.

Bailon, S., 1999. Diférenciation ost éologique des anoures (Amphibia, Anura) de France. Fiches d'osteologie animale pour l'archeologie (C: Varia) 1, 1–41.

Batsch, A.J.G.C., 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Erster Theil. Allgemeine Geschichte der Natur; besondre der Säugthiere, Vögel, Amphibien und Fische. Akademische Buchhandlung, Jena.

Bedriaga J. 1884 Nachträgliche Bemerkung über *Amphisbaena strauchi* v. Bedr. Zoologischer Anzeiger 7, 346.

~~Boettger, O., 1883. Herpetologische Mittheilungen. Berichte des Offenbacher Vereins für Naturkunde (1880–1882) 22–23, 147–156.~~

Böhme, M., 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 195, 389–401.

Bolet, A., Delfino, M., Fortuny, J., Almécija, S., Robles, J.M., Alba, D.M., 2014. An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards. PLoS One 9, e98082.

Bonaparte, C.L. 1832–1841. Iconographia della fauna Italica per le quattro classi degli animali vertebrati. 2. Anfibi. Tipografia Salviucci, Roma.

Brinkerink, H.P., 1996. Tortoises and turtles from the Pleistocene of Crete, in: Reese, D.S. (Ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28, Prehistory Press, 207–210.

Britton, A.R.C., Whitaker, R., Whitaker, N., 2012. Here be a Dragon: exceptional size in a saltwater crocodile (*Crocodylus porosus*) from the Philippines. Herpetological Review 43, 541–546.

Brochu, C.A., 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. Copeia 2000, 657–673.

Busack, S.D., Ernst, C.H., 1980. Variation in Mediterranean populations of *Mauremys* Gray 1869 (Reptilia, Testudines, Emydidae). Annals of the Carnegie Museum 49, 251–264.

Caloi, L., Kotsakis, T., Palombo, M.R., 1986. La fauna a vertebrati terrestri del Pleistocene delle isole del Mediterraneo. Geologia Romana 25, 235–256.

Capellini, G., 1890. Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel 1868. Rendicondi Reale Accademia Lincei (ser. 4) 6 (I sem.), 149–151.

Čerňanský, A., Rage, J.-C., Klembara, J., 2015. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. Journal of Systematic Palaeontology 13, 97–128.

Chesi, F., Delfino, M., Abbazzi, L., Carboni, S., Lecca, L., Rook, L., 2007. New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last

Mauremys (Reptilia, Testudines) in the central Mediterranean. Rivista Italiana di Paleontologia e Stratigrafia 113, 287–297.

Chesi, F., Delfino, M., Rook, L., 2009. Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. Journal of Paleontology 83, 379–388.

Claude, J., Tong, H., Suteethorn, V., 2007. Turtles from the late Eocene–early Oligocene of the Krabi Basin (Thailand).Bulletin de la société géologique de France, Série 1, 178, 305–316.

Danilov, I.G., 2005. Die fossilen Schildkröten Europas. Part 9, in: Fritz, U. (Ed.), Handbuch der Reptilien und Amphibien Europas. Part 3/IIIB: Schildkröten (Testudines) II.AULA-Verlag GmbH, Wiebeisheim, pp. 329–448.

Daza, J.D., Bauer, A.M., Snively, E., 2014. On the gekkotan fossil record. Anatomical Record 297, 433–462.

de Bruijn H., Doukas, C.S., van den Hoek Ostende, L.W., Zachariasse, W.J., 2012. New finds of rodents and insectivores from the Upper Miocene at Plakias (Crete, Greece). Swiss Journal of Palaeontology 131, 61–75.

de Bruijn, H., Meulenkamp, J.E.,1972. Late Miocene rodents from the Pandanassa formation (Prov. Rethymnon), Crete, Greece.Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B 75, 54–60.

de Bruijn, H., van der Meulen, A.J., Katsikatsos, G., 1980.The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 1: The Sciuridae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B 83, 241–261.

Delfino, M., 1997.*Blanus* from the early Pleistocene of southern Italy: another small tessera from a big mosaic, in: Böhme, I.W., Bischoff, W., Ziegler, T., (Eds.), Herpetologica Bonnensis. SEH, Bonn, pp. 89–97.

Delfino, M., 2003.A Pleistocene amphisbaenian from Sicily. Amphibia-Reptilia 24, 407–414.

Delfino, M., Bailon, S., 2000.Early Pleistocene herpetofauna from Cava Dell' Erba and Cava Pirro (Apulia, Southern Italy). Herpetological Journal 10, 95–110.

Delfino, M., Böhme, M., Rook, L., 2007. First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). Zoological Journal of the Linnean Society, London 149, 293–307.

Delfino, M., Rook, L., 2008. African crocodylians in the late Neogene of Europe: a revision of *Crocodylus bambolii* Ristori, 1890. Journal of Paleontology 82, 336–343.

Delfino, M., Rossi, M.A., 2013. Fossil crocodylid remains from Scontrone (Tortonian, Southern Italy) and the late Neogene Mediterranean biogeography of crocodylians. Geobios 46, 25–31.

Delfino, M., Segid, A., Yosief, D., Shoshani, J., Rook, L., Libsekal, Y., 2004. Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression), in: Abbate, E., Woldehaimanot, B., Libsekal, Y., Tecle, T.M., Rook, L., (Eds.), A step towards human origins. The Buia *Homo* one-million-years ago in the Eritrean Danakil Depression (East Africa). Rivista Italiana di Paleontologia e Stratigrafia 110(supplement), 51–60.

Depéret, C., 1885. Description géologique du bassin tertiare du Roussillon. Annales des Sciences Géologiques 17, 1–272.

Dermitzakis, D.M., Papanikolaou, D.J., 1981. Paleogeography and geodynamics of the Aegean region during the Neogene.Annales Géologiques des Pays Helléniques 30, 245–289.

Estes, R., 1983. Sauria Terrestria, Amphisbaenia, in: Wellnhofer, P., (Ed.), Encyclopedia of Paleoherpetology, part 10a. G. Fischer Verlag, Stuttgart.

Fischer von Waldheim, G., 1813. Zoognosia. Tabulis Synopticis Illustrata, in: Usum Praelectionum Academiae Imperialis Medico-Chirurgicae Mosquensis Edita. Ed. 3. Volume 1. Nicolai Sergeidis Vsevolozsky, Moscow.

Fitzinger, L.J.F.J., 1843. Systema Reptilium. Fasciculus Primus. Braumüller et Seidel, Vienna.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P.E., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C., 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History 297, 1–370.

Gad, J., 1990. Nachweis einer Schildkröte des *Mauremys–Ocadia*–Komplexes aus dem Obermiozän von Nordgriechenland. Salamandra 26, 311–313.

Garcia, G., Kostopoulos, D.S., Valentin, X., Koufos, G.D., 2016. Testudines, in: Koufos, G.D., Kostopoulos, D.S., (Eds.), Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49, 23–27.

Gardner, J.D., Russell, A.P., 1994. Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen 193, 209–244.

Gaudry, A., 1862–1867. Animaux fossiles et géologie de l'Attique. Savy, Paris.

Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behike, A.D.B., 2012.Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History 53, 3–308.

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

Georgalis, G.L., Szyndlar, Z., Kear, B.P., Delfino, M., 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109, 103–116.

Georgalis, G.L., Velitzelos, E., Velitzelos, D.E., Kear, B.P., 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the lower Miocene of northern Greece, in: Brinkman, D.B., Holroyd, P.A., Gardner, J.D., (Eds.), Morphology and Evolution of Turtles. Springer, Dordrecht, pp. 277–287.

Georgalis, G.L., Villa, A., Delfino, M., 2016b. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103, 12.

Ginsburg, L., Bulot, C., 1997. Les *Diplocynodon* (Reptilia, Crocodylia) de l'Orléanien (Miocène inférieur à moyen) de France. Geodiversitas 19, 107–28.

Gmelin, J.F., 1789. Tom. I. Pars III, in: Caroli a Linné, Systema Naturae. Beer, G.E. Leipzig. pp. 1033–1516.

Gmelin, S.G., 1774. Reise durch Rußland zur Untersuchung der drey Natur-Reiche. Kaiserliche Akademie der Wissenschaften, St. Petersbourg.

Gray, J.E., 1844. Catalogue of the tortoises, crocodiles, and amphisbaenians, in the collection of the British Museum. Trustees of the British Museum, London.

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

Hadjisterkotis, E., Kassapis, I., Klerides, N., 2000. Paleontological evidence for the presence of *Trionyx* sp. on Cyprus, with new information on living and alien species of terrapins. Newsletter, Hellenic Zoological Society 33, 8–10.

Hervet, S., 2003. Le groupe "*Palaeochelys* sensu lato–*Mauremys*" dans le contexte systématique des Testudinoidea aquatiques du Tertiaired'Europe occidentale: Apports à

la biostratigraphie et à la paléobiogéographie. Ph.D. thesis, Muséum National d' Histoire Naturelle, Paris.

Holman, A.J., 1998. Pleistocene amphibians and reptiles in Britain and Europe. Oxford Monographs on Geology and Geophysics 38, Oxford University Press, New York, Oxford.

Huene, F., von., Nikoloff, I., 1963. Ein pliozänes krokodil in Bulgarien. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 118, 266–271.

Hummel, K.,1932. Trionychia fossilia, in: Questedt, W., (Ed.), Fossilium Catalogus I: Animalia, Junk, W., Berlin.

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.

Karl, H.V., 1999. Die Zoogeographie der känozoischen Weichschildkröte *Trionyxtriunguis* Forskål, 1775 (Testudines: Trionychidae). JoanneaGeologie und Paläontologie, Graz 1, 27–60.

Kearney, M., 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17, 1–74.

Kotsakis, T., 1977. I resti di anfibi e rettili pleistocenici della grotta 'Bate' (Rethymnon, Creta). Atti della Accademia Nazionale dei Lincei 63, 571–582.

Kotsakis, T., 1985. Les Trionychidae (Testudinata, Reptilia) fossiles de l'Italie. Bollettino della SocietàPaleontologica Italiana 24, 161–168.

Kotsakis, T., Delfino, M., Piras, P., 2004. Italian Cenozoic crocodilians: taxa, timing and biogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 210, 67–87.

Koufos, G.D., 2006. The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. Annales Géologiques des Pays Helléniques 4, 183–214.

Koufos, G.D., Kostopoulos, D.S., 2013. First report of *Brachypotherium* Roger, 1904 (Rhinocerotidae, Mammalia) in the Middle Miocene of Greece. Geodiversitas 35, 629–641.

Koufos, G.D., Kostopoulos, D., Vlachou, T., 2005. Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belgian Journal of Zoology 135, 181–190.

Lapparent de Broin, F., de, 2000. African chelonians from the Jurassic to present: phases of development and preliminary catalogue of the fossil record. Palaeontologia Africana 36, 43–82.

Laurenti, J.N., 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Joan. Thomae, Vienna.

Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Laurenti Salvii, Holmiae 1, 1–823.

Longrich, N.R., Vinther, J., Pyron, R.A., Pisani, D., Gauthier, J.A., 2015. Biogeography of worm lizards (Amphisbaenia) driven by end-Cretaceous mass extinction. Proceedings of the Royal Society B: Biological Sciences 282, 20143034.

Martin, J.E., 2010. A new species of *Diplocynodon* (Crocodylia, Alligatoroidea) from the Late Eocene of the Massif Central, France, and the evolution of the genus in the climatic context of the Late Palaeogene. Geological Magazine 147, 596–610.

Martin, J.E., Gross, M., 2011. Taxonomic clarification of *Diplocynodon* Pomel, 1847 (Crocodilia) from the Miocene of Styria, Austria.Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen 261, 177–193.

Ménouret, B., Mein, P., 2008. Les vertébrés du miocène supérieur de Soblay (Ain, France) Document des Laboratoires de Géologie de Lyon, UFR des sciences de la terre, Université Claude Bernard-Lyon 1 165, 1–97.

Młynarski, M., 1976. Testudines,in: Kuhn, O., (Ed.), Encyclopedia of Paleoherpetology, part 7. G. Fischer Verlag, Stuttgart.

Oppel, M., 1811. Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, München.

Pamouktchiev, A., de Lapparent de Broin, F., Anguelov, A., 1998. Nouvelle trouvaille de tortue fossile en Bulgarie. Annuaire de l'Université de Sofia "St. Kliment Ohridski" Faculté de Géologie et Géographie, Livre 1, Géologie 90, 5–8.

Paraskevaidis, I., 1955. Zwei Schildkröten reste aus dem Obermiozän von Chios. Annales Géologiques des Pays Helléniques 6, 133–141.

Poulakakis, N., Lymberakis, P., Tsigenopoulos, C.S., Magoulas, A., Mylonas, M., 2005. Phylogenetic relationships and evolutionary history of snake-eyed skink *Ablepharus kitaibelii* (Sauria: Scincidae). Molecular Phylogenetics and Evolution 34, 245–256.

Purschke, C.A., 1885. *Clemmys sarmatica* n. sp. aus dem Tegel von Hernals bei Wien.Denkschriften der Kaiserlichen Akademie der Wissenschaften / Mathematisch-Naturwissenschaftliche Classe 50, 185–192.

Pyron, R.A., Reynolds, R.G., Burbrink, F.T., 2014. A taxonomic revision of boas (Serpentes, Boidae). Zootaxa 3846, 249–260.

Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution 61, 543–583.

Rage J.-C., 1984. Serpentes,in: Wellnhofer, P., (Ed.), Encyclopedia of Paleoherpetology, part 11. G. Fischer Verlag, Stuttgart, New York.

Rage, J.-C., 2003.Squamate reptiles from the early Miocene of Arrisdrift (Namibia).Memoir of the Geological Society of Namibia (Ministry of Mines and Energy), Windhoek 19, 43–50.

Rage, J.-C., 2013. Mesozoic and Cenozoic squamates of Europe. Palaeobiodiversity and Palaeoenvironments 93, 517–534.

Rage, J.-C., Augé, M., 1993. Squamates from the Cenozoic of the western part of Europe.A review. Revue de Paléobiologie, volume spécial 7, 199–216.Rage, J.-C., Roček, Z., 2003.Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. Amphibia-Reptilia 24, 133–177.

Rage, J.-C., Sen, S.,1976.Les Amphibiens et les Reptiles du Pliocène supérieur de Calta (Turquie). Géologie méditerranéenne 3, 127–134.

Richter, A., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian–Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). Münchner Geowissenschaftliche Abhandlungen 28, 35–38.

Roček, Z., 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia).Rozpravy Ceskoslovenské Akademie Ved, Rada Matematickych a prírodních Ved 94, 3–69.

Rögl, F., 1999.Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologia Carpathica 50, 330–349.

Römer, F., 1870.Über *Python euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea.Zeitschrift der Deutschen Geologischen Gesellschaft 22, 582–590.

Rook, L., Delfino, M., Sami, M., 2015. I vertebrati fossili della cava del Monticino di Brisighella: una finestra sui popolamenti continentali del Mediterraneo nel Miocene

superiore. I gessi di Brisighella e Rontana. Memorie dell'Istituto Italiano di Speleologia s. II 28, 79–100.

Rustioni, M., Mazza, P., Azzaroli, A., Boscagli, G., Cozzini, F., Di Vito, E., Masseti, M., Pisano, M., 1993. Miocene vertebrate remains from Scontrone, National Park of Abruzzi, Central Italy. Rendiconti della Accademia Nazionale dei Lincei, Classe di Scienze Fisiche Matematiche e Naturali 9, 227–237.

Sanchiz, B., 1998. Salientia, in: Wellnhofer, P., (Ed.), Encyclopedia of Paleoherpetology, part 4.Friedrich Pfeil, Munich.

Sen, S., Antoine, P.O., Varol, B., Ayyildiz, T., Sözeri, K., 2011. Giant rhinoceros *Paraceratherium* and other vertebrates from Oligocene and middle Miocene deposits of the Kağızman-Tuzluca Basin, Eastern Turkey. Naturwissenschaften 98, 407–423.

Sindaco, R., Jeremčenko, V., 2008. The reptiles of the western Palearctic. Vol. 1: annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. Monografie della Societas Herpetologica Italica I, Belvedere, Latina.

Sindaco, R., Kornilios, P., Sacchi, R., Lymberakis, P., 2014: Taxonomic reassessment of *Blanus strauchi* (Bedriaga, 1884) (Squamata: Amphisbaenia: Blanidae), with the description of a new species from south-east Anatolia (Turkey). Zootaxa 3795, 311–326.

Staesche, K., Karl, H.-V., Staesche, U., 2007.Fossile Schildkröten aus der Türkei.Geologisches Jahrbuch Reihe B 98, 91–149.

Steel, R., 1973. Crocodylia, in: Kuhn, O., (Ed.), Encyclopedia of Paleoherpetology, part 16. G. Fischer Verlag, Stuttgart, Portland.

Szalai, T., 1931. Schildkrötenstudien: I. *Testudo schafferi* nov. sp., eine Riesenschildkröte aus dem Pliozän von Samos.Annalen des Naturhistorischen Museums in Wien 46, 153–157.

Szyndlar, Z., 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47, 103–126.

Szyndlar, Z., 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estudios Geológicos 47, 237–266.

Szyndlar, Z., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian–Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). Münchner Geowissenschaftliche Abhandlungen 28, 35–39.

Szyndlar, Z., Rage, J.-C., 2002. Fossil record of the true vipers, in: Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W., (Eds.), Biology of the vipers. Eagle Mountain Publicing, Eagle Moutain, pp. 419–444.

Szyndlar, Z., Rage, J.-C., 2003.Non-erycine Booidea from the Oligocene and Miocene of Europe.Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow.

Szyndlar, Z., Zerova, G., 1990. Neogene cobras of the genus *Naja* (Serpentes: Elapidae) of East Europe. Annalen des Naturhistorischen Museums in Wien 91A, 53–61.

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

Valakos, E.D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., Foufopoulos, J., 2008. Amphibians and Reptiles of Greece. Edition Chimaira, Serpents Tale, Frankfurt.

Valenciennes, A., 1833. *Chelonia pelasgorum*, *Emys hellenica*, *Emys iberica*, *Emys rivulata*, in: Bory de Saint-Vincent, J.B., (Ed.), Expédition Scientifique de Morée. Travaux de la Section des Sciences Physiques. Zoologie. Levrault, F.G., Paris.

van der Made, J., 1996. Pre–Pleistocene land mammals from Crete, in: Reese, D.S., (Ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28, Prehistory Press, pp. 69–79.

Venczel, M., Ştiucă, E., 2008. Late middle Miocene amphibians and squamate reptiles from Tauţ, Romania. Geodiversitas 30, 731–763.

Vianna, A., Moraes, A., 1945. Sur un craˆne de crocodile fossile découvert dans le Miocène de Lisbonne. Boletim de la Sociedade Geológica de Portugal 4, 161–170.

Viriot, L., Pelaez-Campomanes, P., Vignaud, P., Andossa, L., Mackaye, H.T., Brunet, M., 2011. A new xerinae (Rodentia, Sciuridae) from the late Miocene of Toros-Menalla (Chad). Journal of Vertebrate Paleontology 31, 844–848.

Vitek, N.S., Joyce, W.G., 2015. A review of the fossil record of New World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 56, 185–244.

Vitt, L.J., Caldwell, J.P., 2014. Herpetology.An introductory biology of amphibians and reptiles.Fourth edition.Academic Press, Elsevier, Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Sydney, Tokyo.

Vlachos, E., 2015. The fossil chelonians of Greece. Systematics - evolution - stratigraphy - palaeoecology. Ph.D. thesis, Aristotle University of Thessaloniki, Greece.

Vlachos, E., Cerda, I., Tsoukala, E., 2015a. The first record of a soft-shelled turtle (Testudines: *Pan-Trionychidae*) from southern Balkans (Pliocene, Gefira, N. Greece) and new information from bone histology. The Science of Nature 102, 45.

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

Vlachos, E., Tsoukala, E., 2014. *Testudo* cf. *graeca* from the new Late Miocene locality of Platania (Drama basin, N. Greece) and a reappraisal of previously published specimens. Bulletin of the Geological Society of Greece XLVIII, 27–40.

Wallach, V., Williams, K.L., Boundy, J., 2014. Snakes of the world: a catalogue of living and extinct species. CRC Press, Boca Raton.

Weithofer, A., 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen.Beiträge zur Paläontologie Österreich-Ungarns 6, 225–292.

Werner, F., 1898.Über einige neue Reptilien und einen neuen Frosch aus dem cilicischen Taurus. Zoologischer Anzeiger 21, 217–223.

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

Figure captions

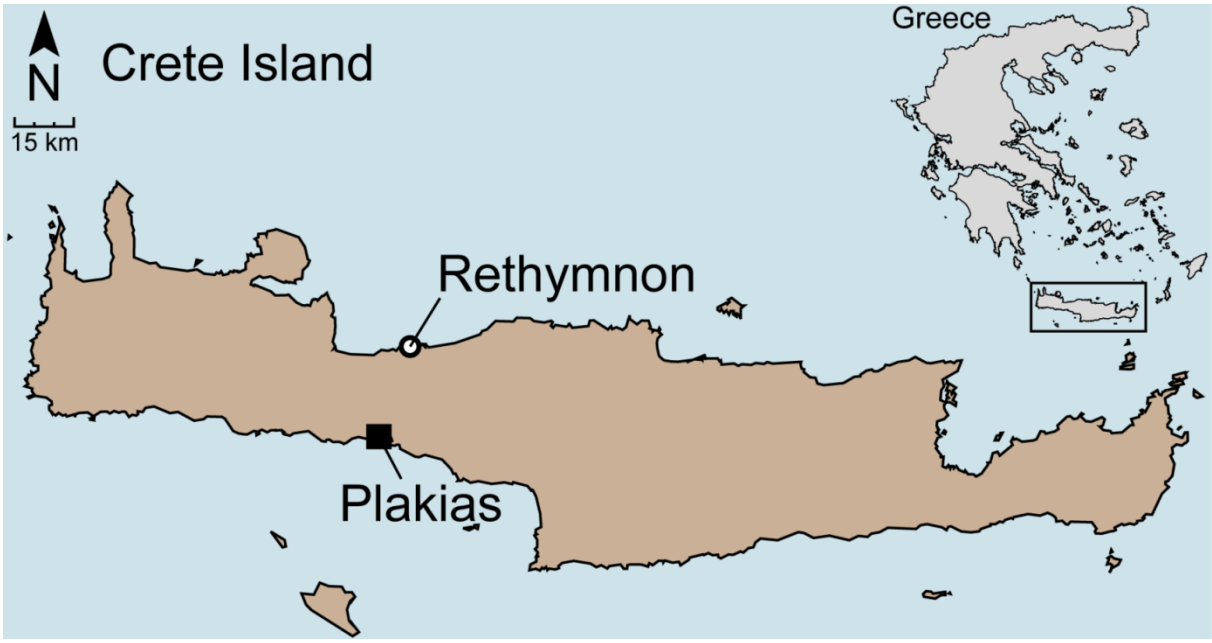

Fig. 1. Map of Crete, indicating the earliest late Miocene locality of Plakias.

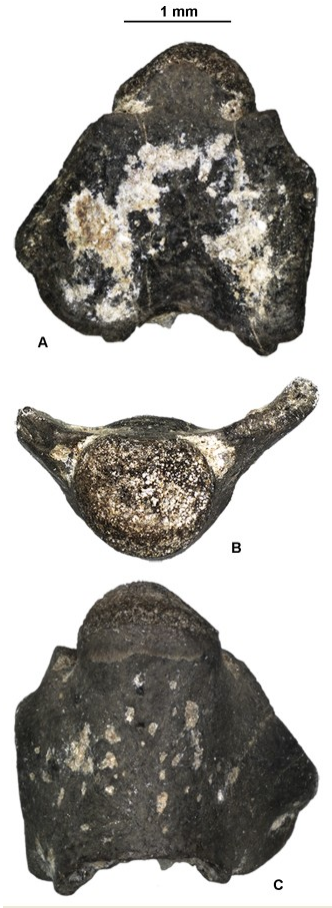

Fig. 2. cf. Alytidae from the earliest late Miocene of Plakias. UU PL 701, a trunk vertebra in dorsal (A), anterior (B) and ventral(C) views.

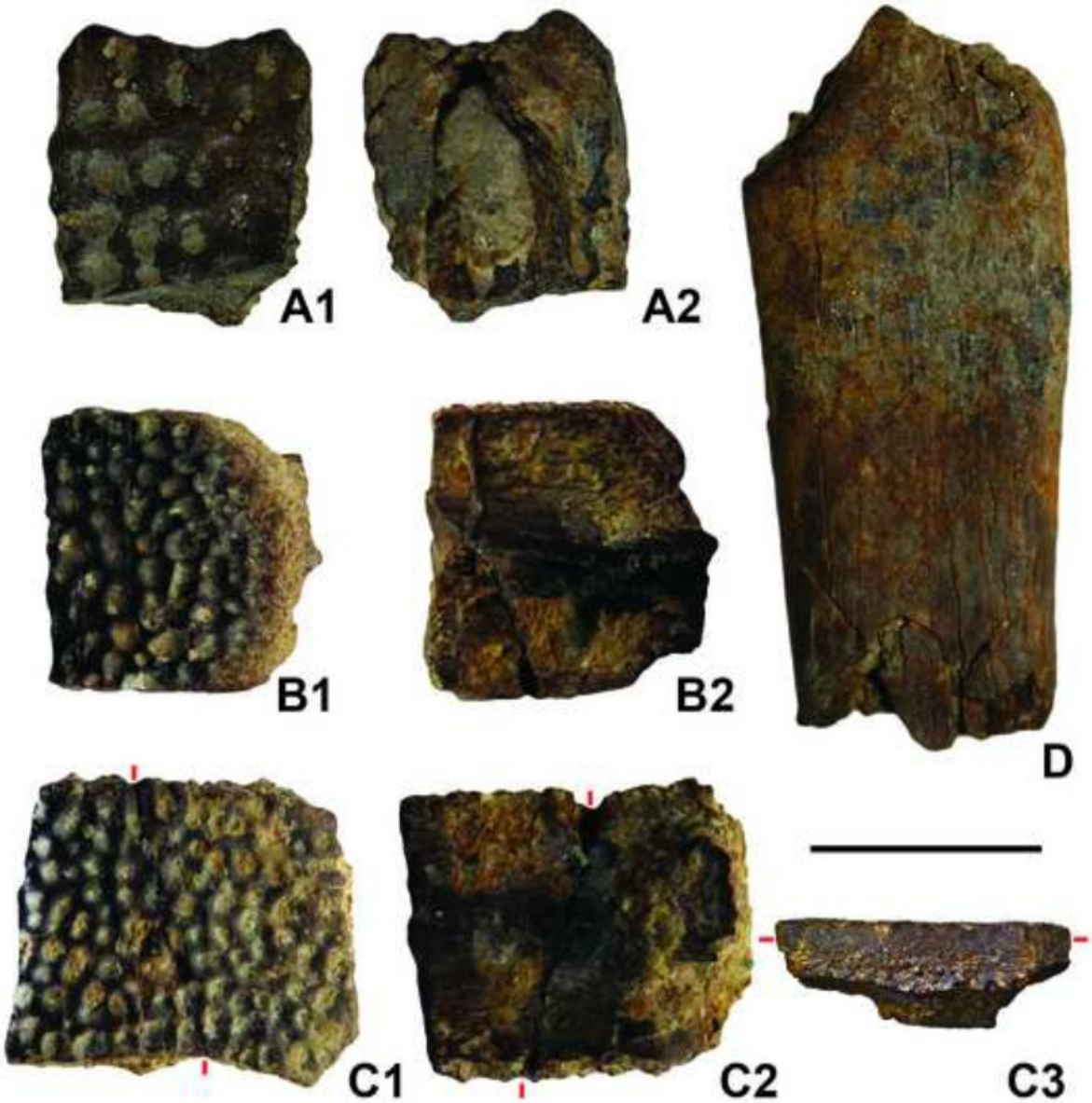

Fig. 3. Pan-Trionychidae from the earliest late Miocene of Plakias.A, NHMC 21.7.3.1670, fragment of a neural, in A1, dorsal and A2, visceral views. B, UU PL 703, fragment of a costal in B1, dorsal and B2, visceral views. C, UU PL 704, fragment of a costal in C1, dorsal and C2, visceral views. D, NHMC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

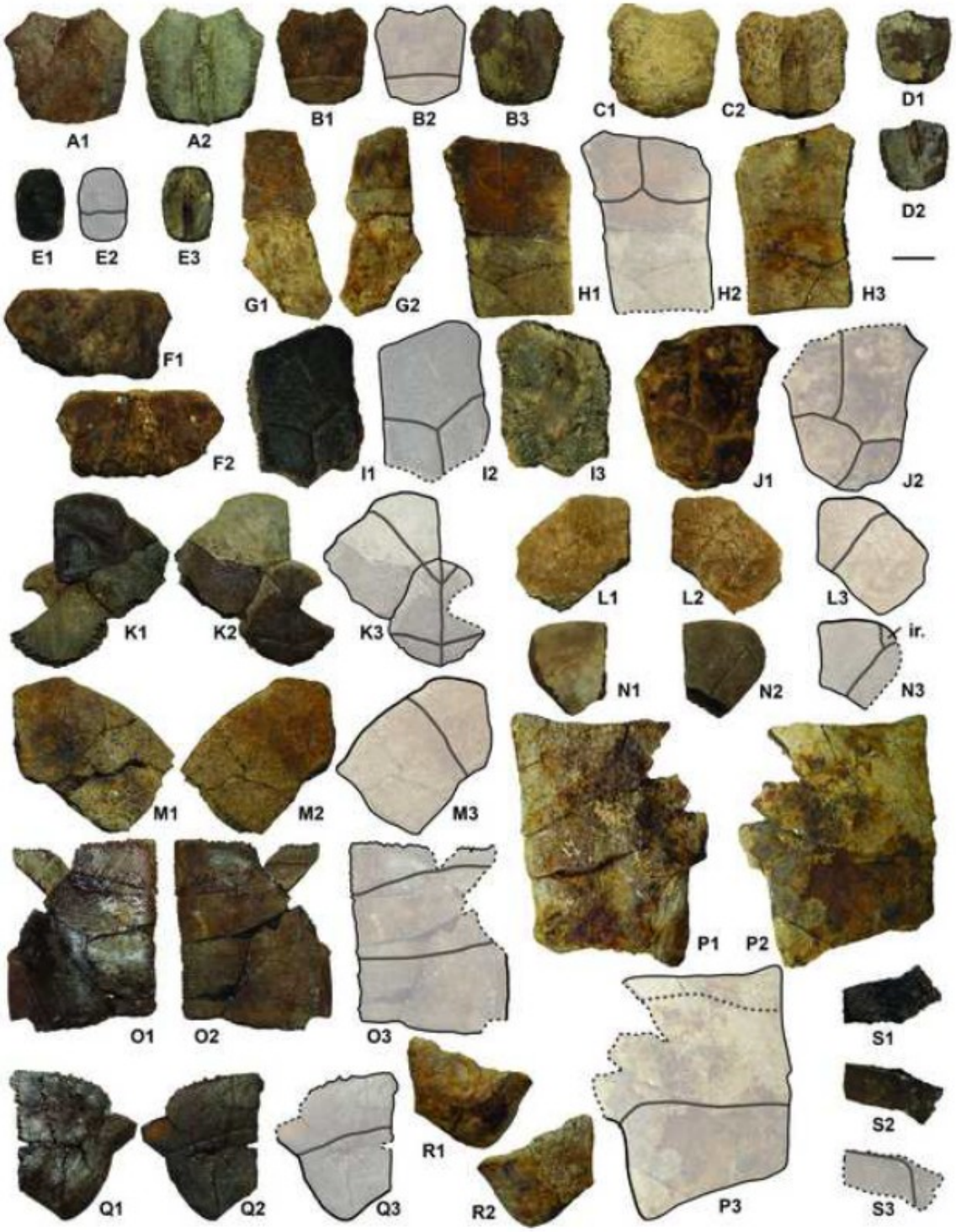

Fig. 4. *Mauremys* sp. from the earliest late Miocene of Plakias.A, NHMC 21.7.3.1623, neural in (A1) dorsal and (A2) visceral views.B, NHMC 21.7.3.1622, neural in (B1) dorsal, (B2) drawing of the dorsal and (B3) visceral views.C, NHMC 21.7.3.1645, neural in (C1) dorsal and (C2) visceral views.D, NHMC 21.7.3.1624, neural in (D1) dorsal and (D2) visceral

views.E, NHMC 21.7.3.1651, neural in (E1) dorsal, (E2) drawing of the dorsal and (E3) visceral views. F, NHMC 21.7.3.1649, neural fragment in (F1) dorsal (F3) visceral views. G, NHMC 21.7.3.1640, two successive costals in (G1) dorsal and (G2) visceral views.H, NHMC 21.7.3.1638, costal in (H1) dorsal, (H2) drawing of the dorsal and (H3) visceral views. I, NHMC 21.7.3.1639, costal fragment in (I1) dorsal, (I2) drawing of the dorsal and (I3) visceral views. J, NHMC 21.7.3.1641, peripheral in (J1) dorsal and (J2) drawing of the dorsal views. K, NHMC 21.7.3.1618, right epiplastron and entoplastron in (K1) visceral, (K2) ventral and (K3) drawing of the ventral views. L, NHMC 21.7.3.1637, left epiplastron in (L1) visceral, (L2) ventral and (L3) drawing of the ventral views. M, NHMC 21.7.3.1635, right epiplastron in (M1) visceral, (M2) ventral and (M3) drawing of the ventral views. N, NHMC 21.7.3.1632, left epiplastron fragment in (N1) visceral, (N2) ventral and (N3) drawing of the ventral views. O, NHMC 21.7.3.1620, left hypoplastron in (O1) visceral, (O2) ventral and (O3) drawing of the ventral views. P, NHMC 21.7.3.1643, right hypoplastron in (P1) visceral, (P2) ventral and (P3) drawing of the ventral views. Q, NHMC 21.7.3.1619, right xiphiplastron in (Q1) visceral, (Q2) ventral and (Q3) drawing of the ventral views. R, NHMC 21.7.3.1642 right xiphiplastron fragment in (R1) visceral and (R2) ventral views. S, UU PL 705, possible hyoplastron fragment in (S1) visceral, (S2) ventral and (S3) drawing of the ventral views. Abbreviation: ir, irregular scute growth.

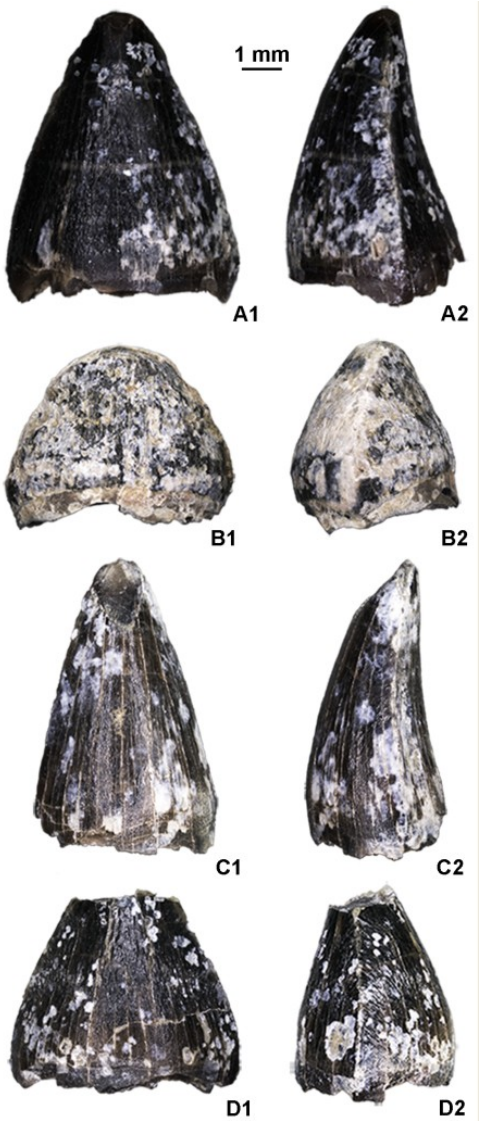

Fig. 5. Crocodylia from the earliest late Miocene of Plakias. A,UU PL 706, isolated tooth in labial (A1) and mesial (A2) views.B, UU PL 707, isolated tooth in labial (B1) and mesial (B2) views.C, UU PL 708, isolated tooth in labial (C1) and mesial (C2) views.D, UU PL 709, isolated tooth in labial (D1) and mesial (D2) views.

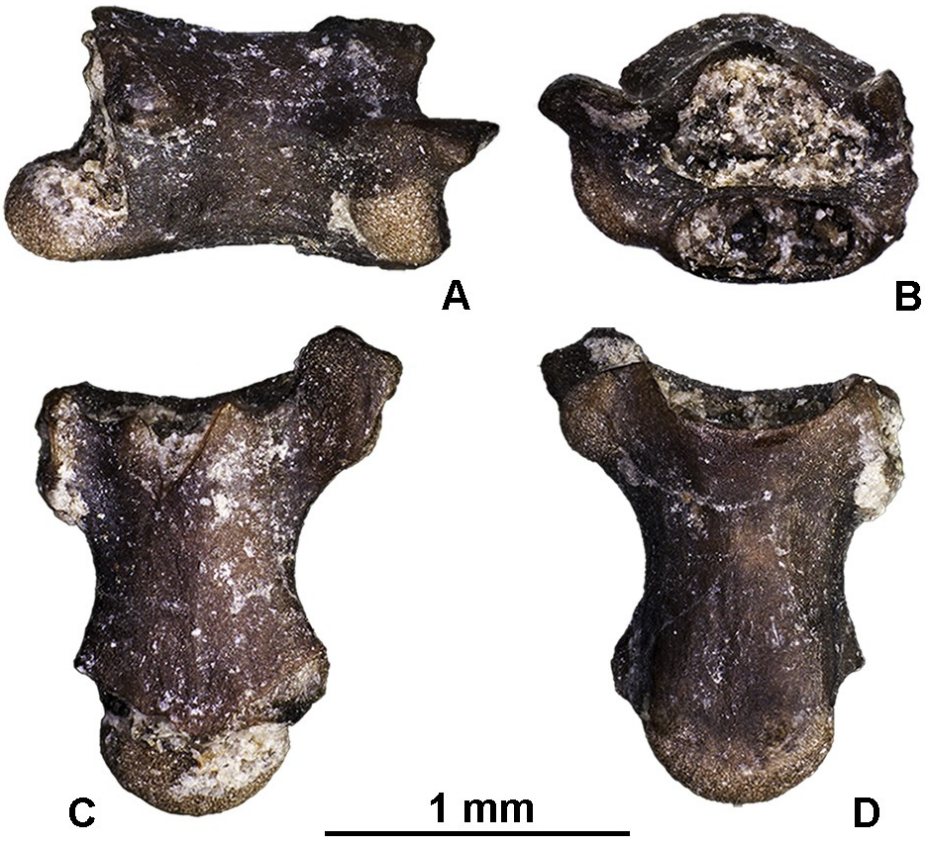

Fig. 6. Amphisbaenia from the earliest late Miocene of Plakias. UU PL 733, presacral vertebra in right lateral (A), dorsal (B), ventral (C) and anterior (D) views.

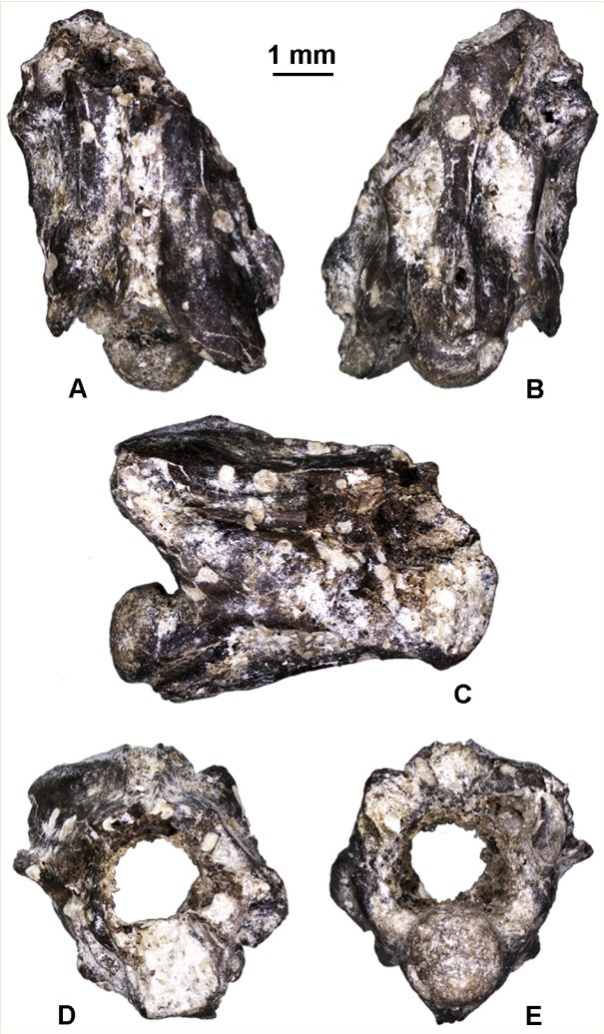

Fig. 7. ?Natricinae from the earliest late Miocene of Plakias. UU PL 734, precloacal vertebra in dorsal (A), anterior (B), right lateral (C), posterior (D) and ventral (E) views.

Table 1

The youngest occurrences of crocodylians in Europe.

Taxon	**Age**	**Locality**	**Reference**
Crocodylus sp.	latest Messinian (or even early Zanclean,	Gargano, Apulia, Italy	Delfino et al., 2007

	depending on the age of the Terre Rosse from Gargano)		
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; Delfino and Rossi, 2013

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