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1 **Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the**
2 **earliest late Miocene herpetofaunas of southeastern Europe**

3

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23

24

25 **Abstract**

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

37

38 *Keywords:*

39 Anura

40 Testudines

41 Crocodylia

42 Amphisbaenia

43 Serpentes

44 Miocene

45

46 **1. Introduction**

47 Miocene herpetofaunas from Europe are relatively well understood (Rage and Augé,
48 1993; Sanchiz, 1998; Rage and Roček, 2003; Szyndlar and Rage, 2003; Augé, 2005; Danilov,
49 2005). However, the focus of previous studies is heavily unbalanced towards the
50 herpetofaunas of the western and central parts of the continent, whereas only few papers have
51 dealt with the eastern European ones (Szyndlar and Zerova, 1990; Szyndlar, 1991a, b; Rage
52 and Augé, 1993; Antunes, 1994; Rage and Roček, 2003; Danilov, 2005; Daza et al., 2014).
53 On the other hand, even less is known about the Miocene amphibians and reptiles from
54 southeastern Europe, despite the fact that this region played a pivotal biogeographic role
55 during that period: several dispersals events from both Africa and Asia have taken place
56 during this time interval (Rögl, 1999; Koufos et al., 2005). As such, the study of southeastern
57 European localities could clarify significant aspects about the biogeography, evolutionary
58 history and extinction events of certain European groups.

59 Greece harbors a large number of Miocene localities, of which several have been well
60 known and studied for more than a century (Koufos, 2006, and references therein). However,
61 mammal finds were almost always the main focus of these studies, thereby neglecting other
62 important tetrapod groups, such as amphibians and reptiles. Nevertheless, important fossil
63 finds during the last 160 years have shown a diverse array of Miocene reptiles (Gaudry, 1862-
64 1867; Römer, 1870; Weithofer, 1888; Szalai, 1931; Paraskevaidis, 1955; Bachmayer, 1967;
65 Richter, 1995; Szyndlar, 1995; Georgalis et al., 2013; Georgalis and Kear, 2013; Vlachos and
66 Tsoukala, 2014; Vlachos et al., 2015b; Garcia et al., 2016; Georgalis et al., 2016b), whereas
67 amphibian remains are practically unknown from this time interval from Greece, with only
68 few, sporadic, published occurrences (Sanchiz, 1998; Rage and Roček, 2003).

69 Here we describe new amphibian and reptile finds from the earliest late Miocene
70 (early Tortonian, MN 9) locality of Plakias, on the Island of Crete, southern Greece. The

71 fragmentary nature of these fossils precludes any taxonomic designation to the species level.
72 Higher level taxonomic determination of the specimens was possible, however, revealing an
73 unexpectedly diverse assemblage consisting of anurans, pan-trionychids, geoemydids,
74 crocodylians, amphisbaenians, and snakes.

75

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

78

79 **2. Geological framework**

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

91 The palaeoherpetofauna of Plakias cannot confirm, neither dispute with certainty the
92 suggested age of the locality as Vallesian (MN 9), earliest late Miocene (de Bruijn et al.,
93 2012). However, it is noted that pan-trionychids and crocodylians are better represented in
94 early and middle Miocene localities of Europe, rather than late Miocene ones (Karl, 1999;
95 Delfino and Rossi, 2013). However, since none among the Plakias representatives of the

96 herpetofauna can be attributed to the species level, no further age correlations can be safely
97 made. In any case, the age information on the basis of micromammals allows referring the
98 whole faunal assemblage to the earliest late Miocene (MN 9) (de Bruijn et al., 2012).

99

100 **3. Material and methods**

101 All the amphibians, crocodylians and squamates, and part of the pan-trionychid and
102 geoemydid material described in this study is housed in the collections of the University of
103 Utrecht (UU). This amphibian and reptile material was collected along with the fossil
104 micromammals that were described by Bruijn and Meulenkamp (1972) from the first period
105 of field work at Plakias.

106 Part of the geoemydid and the pan-trionychid material belongs to the collections of the
107 Natural History Museum of Crete (NHMC) and represents material that was collected by S.
108 Kuss in the 1970's. This material was originally in the Geologisch-Paläontologisches Institut
109 der Universität Freiburg, Germany, and later formed part of the collections of the Natural
110 History Museum of Karlsruhe, Germany, before its recent return to the NHMC. This material
111 was studied in the doctoral thesis of one of us (Vlachos, 2015) and is further presented here in
112 the context of the whole herpetofauna of Plakias. It is not possible to determine the exact
113 stratigraphic origin of the material collected by Kuss, as he did not publish anything about it.
114 It has been recently noted, however, that the old (de Bruijn and Meulenkamp, 1972) and new
115 (de Bruijn et al., 2012) micromammal collections of Plakias could “come from slightly
116 different stratigraphic levels” (de Bruijn et al., 2012: p. 61) due to building activity in the area
117 during the last 40 years. However, the same authors noted that “the 25 cm thick grayish silty
118 clay sampled in 2010 seems to be the only bed that contains vertebrate remains” (de Bruijn et
119 al., 2012: p. 61). Following this line of reasoning, and in the absence of conflicting evidence,
120 we treat all the material described herein as originating from the same site.

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

126

127 **4. Systematic Palaeontology**

128 AMPHIBIA Linnaeus, 1758

129 ANURA Fischer von Waldheim, 1813

130 ALYTIDAE Fitzinger, 1843

131 cf. Alytidae indet.

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

134 **Description:** UU PL 701 (Fig. 2): This trunk vertebra preserves only the centrum and, on
135 both sides, a small, basal portion of the neural arch. The centrum is roughly 2.8 mm long and
136 slightly dorsoventrally flattened. The condyle bears a small, but well-defined condylar neck
137 that is typical of opisthocoelous vertebrae and therefore characterizes the anterior extremity of
138 the centrum. The anterior condyle and the posterior cotyle are rather subcircular.

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

142 **Remarks:** UU PL 701 can be tentatively referred to the Alytidae on the basis of the condylar
143 neck that marks the condyle. This character has not been described in the literature (e.g.
144 Bailon, 1999) but in our experience, this trait is characteristic for this group of frogs, which at
145 least in some cases have also a comparable size. UU PL 702 is here tentatively referred to the

146 same taxon represented by the co-occurring vertebra. Most probably, the amphibian material
147 presented herein is the same that Sanchiz (1998: p. 168) referred to it as “Platkia (sic), Greece,
148 Neogene: Discoglossinae indet. (Sanchiz, unpublished)” (Borja Sanchiz, pers. commun. to
149 GLG, February 2016).

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

157

158 REPTILIA Laurenti, 1768

159 TESTUDINES Batsch, 1788

160 PAN-TRIONYCHIDAE Joyce et al., 2004

161 Pan-Trionychidae indet.

162 **Referred specimens:** UU PL 703, costal fragment; UU PL 704, costal fragment; NHMC
163 21.7.3.1670, neural; NHMC 21.7.3.1671, plastron fragment.

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

168 UU PL 703 (Fig. 3B): This specimen corresponds to a fragment of a costal, as is shown by the
169 presence of a rib on the visceral part. On the distal side, a part of the rib is apparent as well.

170 Dorsally, the distinctive sculpturing is visible, consisting of small pits that are mainly

171 separated from one another. The anterior and posterior margins of the costal are developed
172 parallel to each other on the preserved part.

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

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

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

194

195 GEOEMYDIDAE Theobald, 1868

196 *Mauremys* Gray, 1869

197 *Mauremys* sp.

198 **Referred specimens:** NHMC 21.7.3.1618, part of anterior lobe; NHMC 21.7.3.1619, right
199 xiphiplastron; NHMC 21.7.3.1620, left hypoplastron; NHMC 21.7.3.1621, group of 15
200 plastral fragments; NHMC 21.7.3.1622, neural; NHMC 21.7.3.1623, neural; NHMC
201 21.7.3.1624, neural; NHMC 21.7.3.1625, left hyoplastron fragment; NHMC 21.7.3.1626, left
202 hypoplastron fragment; NHMC 21.7.3.1627, right hypoplastron fragment; NHMC
203 21.7.3.1628, costal fragment; NHMC 21.7.3.1629, right hypoplastron fragment; NHMC
204 21.7.3.1630, costal fragment; NHMC 21.7.3.1631, costal fragment; NHMC 21.7.3.1632, left
205 epiplastron; NHMC 21.7.3.1633, left hyoplastron fragment; NHMC 21.7.3.1634, group of 23
206 shell fragments; NHMC 21.7.3.1635, right epiplastron; NHMC 21.7.3.1636, left epiplastron;
207 NHMC 21.7.3.1637, left epiplastron; NHMC 21.7.3.1638, costal fragment; NHMC
208 21.7.3.1639, costal fragment; NHMC 21.7.3.1640, two costals in association; NHMC
209 21.7.3.1641, right peripheral 1; NHMC 21.7.3.1642, right xiphiplastron fragment; NHMC
210 21.7.3.1643, right hypoplastron fragment; NHMC 21.7.3.1644, left hyoplastron fragment;
211 NHMC 21.7.3.1645, costal fragment; NHMC 21.7.3.1646, costal fragment; NHMC
212 21.7.3.1647, costal fragment; NHMC 21.7.3.1648, group of approximately 80 shell
213 fragments; NHMC 21.7.3.1649, neural fragment; NHMC 21.7.3.1650, group of 10 shell
214 fragments; NHMC 21.7.3.1651, neural I; NHMC 21.7.3.1652, costal fragment; NHMC
215 21.7.3.1653, costal fragment; NHMC 21.7.3.1654, costal fragment; NHMC 21.7.3.1655,
216 costal fragment; NHMC 21.7.3.1656, costal fragment; NHMC 21.7.3.1657, costal fragment;
217 NHMC 21.7.3.1658, costal fragment; NHMC 21.7.3.1659, costal fragment; NHMC
218 21.7.3.1660, costal fragment; NHMC 21.7.3.1661, costal fragment; NHMC 21.7.3.1662,
219 costal fragment; NHMC 21.7.3.1663, costal fragment; NHMC 21.7.3.1664, costal fragment;
220 NHMC 21.7.3.1665, costal fragment; NHMC 21.7.3.1666, peripheral fragment; NHMC

221 21.7.3.1667, peripheral fragment; NHMC 21.7.3.1668, peripheral fragment; NHMC
222 21.7.3.1669, group of 50 shell fragments; UU PL 705, possible hyoplastron fragment.

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

226

227 Carapace elements (Figs. 4A–J):

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

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

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

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

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

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

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

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

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

263

264 Plastron elements (Figs. 4K–S)

265 NHMC 21.7.3.1618 (Fig. 4K): This specimen corresponds to the right part of the
266 anterior lobe of the plastron, consisting of the right epiplastron and most of the entoplastron.
267 The epiplastron is long and narrow. Viscerally, a long but shallow lip is formed, being
268 concave medially and convex laterally. Anteriorly, a shallow notch is noted. The entoplastron
269 is hexagonal and rounded, being wider posteriorly. The gular scutes are wide and long,
270 overlapping the anterior part of the entoplastron. The gular / humeral sulcus is slightly convex

271 laterally, and causes a slight constriction in the anterior part of the lobe. The humerals are
272 medially short and laterally longer. The entoplastron is also overlapped by the anterior part of
273 the pectorals. The humero-pectoral sulcus is slightly concave medially.

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

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

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

288 NHMC 21.7.3.1620 (Fig. 4O): This specimen corresponds to an almost complete left
289 hypoplastron. The anterior suture, which connects it to the hyoplastron, is straight, whereas
290 the posterior one, which connects it to the xiphiplastron, is slightly convex. The hypoplastron
291 is rather flat. Viscerally, the abdominal forms a wide and slightly convex lip on the posterior
292 lobe. Ventrally, an unusual morphology is noticed. Although the posterior part of the
293 hypoplastron is covered by the abdominal scute, anteriorly there is another sulcus. Such
294 sulcus is apparent also in another specimen from Plakias (NHMC 21.7.3.1643: fig. 4P), a
295 morphology that has not been previously noted in geoemydids. However, the absence of

296 corresponding hyoplastra and the disarticulated nature of the material do not allow us to
297 clarify this character.

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

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

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

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

318 **Remarks:** The specimens can be attributed to Geoemydidae on the basis of the following
319 characters: first neural quadrangular, remaining neurals hexagonal with short anterolateral
320 sides, pectorals medially shorter than the gulars, and deep anal notch. They can be further

321 identified as a member of *Mauremys*, on the basis of the contact between vertebral I with
322 marginal II and the entoplastron being crossed by the gulars and the humero-pectoral sulcus
323 (Claude et al., 2007). The *Mauremys* material from Plakias suggests attribution to a single
324 taxon, on the basis of the similar size, surface sculpturing and overall morphology. The
325 combined information of the preserved elements allows the documentation of the morphology
326 of most parts of the shell, indicating a confident assignment to *Mauremys*, but no species
327 determination can be made with certainty. Based on the available epiplastra, at least three
328 adult individuals are preserved, and a juvenile individual is also present. The unusual
329 morphology noted in the hypoplastra (NHMC 21.7.3.1620 and NHMC 21.7.3.1643) needs to
330 be further investigated, as it has not previously been observed in other geoemydids. However,
331 the absence of corresponding hyoplastra and the disarticulated nature of the material do not
332 allow us to interpret this character. The extended covering of the pleural I and vertebral I on
333 peripheral I distinguishes the Plakias *Mauremys* from the extant *Mauremys caspica* (Gmelin,
334 1774) and *Mauremys rivulata* (Valenciennes, 1833), as also from the extinct *Mauremys*
335 *gaudryi* (Depéret, 1885) (Pliocene, France; Hervet, 2003). As such, the Plakias *Mauremys* is
336 more similar to other Miocene terrapins from central and eastern Mediterranean (e.g.
337 *Mauremys campanii* Chesi et al., 2009, from Tuscany, Italy). The narrower neural I, the shape
338 of the entoplastron, having the posterior part shorter than the anterior one, and the shorter
339 pectoral covering on the entoplastron differentiate the Plakias geoemydid from *M. campanii*.
340 The angular anal notch also differentiates the Plakias geoemydid from the roughly similar
341 *Mauremys sarmatica* (Purschke, 1885) from the Miocene of Germany, which has a rounded
342 anal notch (Hervet, 2003). The Plakias terrapin represents the oldest described occurrence of
343 Geoemydidae from Greece, being older than the Allatini (Miocene / Pliocene boundary)
344 (Vlachos et al., 2015b) and the Maramena (latest Miocene) forms (Gad, 1990; Georgalis and
345 Kear, 2013; Vlachos et al., 2015b), both recovered from northern Greece. All other fossil

346 geoemydid occurrences from Greece are only known from Pleistocene and Holocene remains
347 (Chesi et al., 2007; Georgalis and Kear, 2013).

348

349 CROCODYLIA Gmelin, 1789

350 *Crocodylia* indet.

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

353 **Description:** UU PL 706 - UU PL 732 (Fig. 5): Several isolated teeth preserve only a crown
354 that is characterized by being conical, variably pointed apically, and regularly concave
355 basally. Some of the teeth are only partially preserved; the largest crown is 8.3 mm long.
356 Mesiodistal carinae separate a lingual, slightly concave surface from a labial, slightly convex
357 surface. The carinae are not serrated. Both lingual and labial surfaces can be slightly wrinkled
358 and bear longitudinal ridges. Some of the teeth are slender, long, and pointed, whereas others
359 are more massive and apically blunt.

360 UU PL 735 - UU PL 736: These two phalanges are elongated elements showing a
361 single roundish articular surface proximally. The best preserved element (UU PL 735) is 18
362 mm long. Its distal portion is dorsoventrally flattened and laterally provided, on both sides,
363 with a sort of weak keel.

364 **Remarks:** The morphology of the teeth is fully congruent with that of generalized
365 crocodylians, but does not allow a more precise identification, since in most cases crocodylian
366 teeth are not diagnostic. These are, however, congruent with the morphology of the
367 *Crocodylus* teeth from the late Miocene of Italy (Delfino et al., 2007). Not much can be said
368 about the phalanges, except for the fact that they show standard crocodylian morphology.
369 They are referred to the same taxon as the teeth. The Plakias specimens constitute the first

370 fossils of crocodylians described from Greece, as also one of the last occurrences of this
371 group in the European continent (Table 1).

372

373 SQUAMATA Oppel, 1811

374 AMPHISBAENIA Gray, 1844

375 *Amphisbaenia* indet.

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

377 **Description:** The specimen is a rather small, procoelous vertebra, with a centrum length of
378 only 1.2 mm (Fig. 6). A slight degree of deformation is recognizable in anterior view. The
379 centrum is dorsoventrally compressed and has a flattened ventral surface and subparallel
380 lateral margins. A massive and rounded synapophysis is visible on the right side of the
381 vertebra. In dorsal view, the neural arch is constricted in the middle. Its dorsal surface is
382 flattened and the neural spine is lacking, as well as the zygosphene. Only the right
383 prezygapophysis is preserved: it is roughly sub-elliptical and tilted dorsally about 30°. The
384 prezygapophyseal process is rather short. Neither the posterior end of the neural arch nor the
385 postzygapophyses are preserved.

386 **Remarks:** The specimen can be attributed to *Amphisbaenia* on the basis of the combination
387 of the following characters: small size, dorsoventrally compressed centrum with a flattened
388 ventral surface and roughly parallel lateral margins, short and robust prezygapophyses,
389 massive and rounded synapophyses, absence of zygosphene, and a dorsally flattened neural
390 arch lacking a neural spine (Estes, 1983; Delfino, 2003). *Amphisbaenians* are present in the
391 extant herpetofauna of Greece, with *Blanus* occurring in the Dodecanese Islands (see below in
392 Biogeography), but they were totally absent in the fossil record of the country. As such, the
393 specimen described herein represents the first known fossil *amphisbaenian* from Greece. Its
394 affinities with *Blanidae*, which are the only extant *amphisbaenians* inhabiting Europe, cannot

395 be tested on the basis of the vertebral morphology: isolated vertebrae of *Amphisbaenia* do not
396 show significant diagnostic features that would allow for a more precise identification (Estes,
397 1983). The sole other known fossil amphisbaenian from the Aegean region has been
398 recovered from the Pliocene of Çalta, Turkey (Rage and Sen, 1976). The Çalta amphisbaenian
399 is represented by three vertebrae, none of which was figured or described in detail. As a
400 matter of fact, no further comparison between these specimens can be made.

401 Interestingly also, the vertebra UU PL 733 represents the sole non-snake squamate
402 from Plakias, as other lizards are conspicuously absent. We consider that this absence is due to
403 taphonomic or collection biases and does not reflect the actual lizard palaeodiversity of
404 Plakias.

405

406 SERPENTES Linnaeus, 1758

407 COLUBROIDEA Opperl, 1811

408 ?NATRICINAE Bonaparte, 1838 (sensu Szyndlar, 1991b)

409 ?Natricinae indet.

410 **Referred specimen:** UU PL 734, a single preloacal vertebra.

411 **Description:** The vertebra is fragmentary, with the prezygapophyses, part of the cotyle and
412 part of the neural spine being eroded (Fig. 7). The vertebra is procoelous, relatively large and
413 proportionally elongate, with a centrum length of 5.5 mm. The prezygapophyseal processes
414 are not clearly visible, due to the fact that the anterior portion of the vertebra is not well
415 preserved. The cotyle is rather incomplete but appears to be relatively rounded. Only part of
416 the zygosphenes is preserved. The condyle is spherical and rather robust, and protrudes
417 significantly from the posterior part of the vertebra. The roof of the zygantrum is visible and
418 appears to be relatively thick. The neural canal is rather large, almost equal in size to the
419 condyle. Synapophyses are divided in diapophyses and parapophyses. The neural spine is

420 broken. The hypapophysis was probably present, however, this cannot be evaluated with
421 certainty. In ventral view, a subcentral foramen is also visible at mid centrum length of the
422 vertebra.

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

433

434 **5. Discussion**

435 *5.1 Palaeoecology of Plakias*

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

445 *Planorbis* and *Brotia* (de Bruijn et al., 2012), which further suggest the presence of a river or
446 lake system.

447 The new amphibian and reptile finds from Plakias allow us to draw further
448 conclusions regarding the palaeoecology of this locality. The presence of an alytid frog
449 implies wet habitats, which is the common environment for the extant members of the group
450 (Vitt and Caldwell, 2014). All extant Crocodylia are known to be water dwellers, inhabiting
451 river systems, lakes, and even venture into the open sea (Steel, 1973; Britton et al., 2012). The
452 fragmentary nature of the Cretan crocodylian does not allow us to make a proper specific or
453 generic identification, but as the teeth from Plakias bear strong resemblance with certain
454 Neogene finds from the Mediterranean that are assigned to Crocodyloidea or Alligatoroidea,
455 we can infer a similar lifestyle. All extant pan-trionychids are known to be strictly aquatic,
456 and a similar or identical life strategy has been proposed for all fossil taxa of this group as
457 well (Vitek and Joyce, 2015 and references therein). The presence of a geoemydid further
458 indicates the presence of lake and river systems (Busack and Ernst, 1980). The amphisbaenian
459 vertebra is fragmentary and cannot be assigned to the specific level. However, the vast
460 majority of amphisbaenians are fossorial (Kearney, 2003) and as such, a similar, burrowing
461 lifestyle is also proposed for the Cretan representative of this clade. Additionally, the presence
462 of a natricine snake adds a further aquatic or semi-aquatic taxon to the locality (Vitt and
463 Caldwell, 2014).

464

465 *5.2 Biogeography*

466 At least until the late Serravallian (middle Miocene), Crete was located at the southern
467 part of Aegäis, the continental area that united modern Greece with Anatolia, but it was most
468 probably already isolated as an island by the Tortonian (late Miocene), after the opening of
469 the Proto-Aegean Sea (Dermitzakis and Papanikolaou, 1981; Poulakakis et al., 2005). The

470 suggested age of the Plakias fauna as early Tortonian (de Bruijn et al., 2012) coincides with
471 the breakup of the southern Aegean landmass and the early formation of Crete as an island
472 (Poulakakis et al., 2005: fig. 4). As such, we cannot determine with certainty whether Plakias
473 hosted a truly continental fauna or an insular fauna at least partly deriving from the former
474 continental assemblages. However, even if the fauna was an insular one, it should have strong
475 biogeographic affinities with coeval mainland Aegæis faunas.

476 The micromammal fauna of Plakias bears strong affinities with coeval ones from
477 Central Europe (de Bruijn et al., 2012). The amphibian and reptile fossils described herein
478 provide additional information about the palaeobiogeography of this part of southeastern
479 Europe, as Miocene herpetofaunas are not well documented in that region (Georgalis et al.,
480 2013; Georgalis and Kear, 2013).

481 The presence of an alytid frog in the late Miocene of Crete is not of biogeographic
482 importance, as this group was widespread throughout Europe during that time interval and has
483 been also found from several other Neogene localities from Greece (Rage and Roček, 2003).
484 All other fossil amphibians from Crete are of Quaternary age (Caloi et al., 1986; Sanchiz,
485 1998).

486 The two distinct turtle taxa recovered from Plakias represent the oldest turtles from
487 Crete, as also the oldest occurrences of Geoemydidae and Pan-Trionychidae from Greece up
488 to date. Turtles, in general, were considered up to now to be absent from Neogene localities of
489 Crete, with their only remains known from Pleistocene and Holocene sediments (Bachmayer
490 et al., 1975; Kotsakis, 1977; Brinkerink, 1996; Chesi et al., 2007; Georgalis and Kear, 2013).
491 Although Brinkerink (1996: p. 208) noted that no turtles are known from pre-Pleistocene sites
492 from Crete, he pointed out the potential of the site of Plakias. The presence of pan-trionychids
493 in the early late Miocene of Greece represents the oldest record and the second only
494 occurrence of this group from the country, which was otherwise only known from the

495 Pliocene of northern Greece (Vlachos et al., 2015a). Pan-trionychids are widespread
496 throughout Europe during the Neogene (Hummel, 1932; Młynarski, 1976; Danilov, 2005;
497 Karl, 1999), however, their alpha taxonomy has not been settled with certainty, mostly
498 because of the homoplastic characters that are observed in their morphology (Vitek and Joyce,
499 2015). Curiously also, Miocene pan-trionychids were totally absent until now from Greece,
500 despite the wealth of fossil localities of that age in the country and extensive sampling
501 (Georgalis and Kear, 2013). The new specimens from Plakias could probably indicate that
502 this absence was not genuine and that pan-trionychids will be subsequently found in other
503 Greek Miocene localities. This is further supported by the presence of pan-trionychids in the
504 Miocene of Bulgaria (Pamouktchiev et al., 1998; Georgalis and Kear, 2013) and Anatolia
505 (Staesche et al., 2007). Affinities of the new Cretan pan-trionychid with the Bulgarian and
506 Anatolian forms cannot be established due to the fragmentary nature of the new specimens.
507 Other, relatively geographically close Miocene pan-trionychids are also known from Cyprus
508 (Hadjisterkotis et al., 2000), Egypt (Lapparent de Broin, 2000), Italy and Malta (Kotsakis,
509 1985). The Plakias geoemydid adds to the Miocene diversity of this group in southeastern
510 Europe. Additionally, this pre-Messinian occurrence of *Mauremys* further corroborates the
511 suggestion of Chesi et al. (2009) for warm and wet conditions during that period in southern
512 Mediterranean Europe.

513 Crocodylians are conspicuous elements in several Miocene faunas across European
514 localities (among others, Ginsburg and Bulot, 1997; Kotsakis et al., 2004; Delfino et al., 2007;
515 Delfino and Rook, 2008; Martin, 2010; Martin and Gross, 2011; Delfino and Rossi, 2013).
516 However, they are relatively scarce by the late Miocene and were apparently absent from
517 southeastern Europe and Anatolia (Böhme, 2003; Sen et al., 2011). The youngest up to date
518 published records of crocodylians from Europe are known from the latest Miocene of Italy
519 (Table 1), as supposed occurrences from the late Miocene and Pliocene of Spain and Portugal

520 have not been accompanied by descriptions or figures, and are here considered anecdotal
521 (Delfino et al., 2007). The taxon *Diplocynodon levantinum* from Bulgaria, was initially
522 thought to be of Pliocene age (Huene and Nikoloff, 1963), whereas it was later treated
523 questionably as late Miocene (Delfino and Rossi, 2013), but its type locality is now believed
524 to pertain most probably to the middle Miocene (Sen et al., 2011). With the exception of the
525 slender snouted forms attributed to *Tomistoma* (Capellini, 1890; Vianna and Moraes, 1945),
526 several late Miocene occurrences are considered to be members of *Crocodylus* or at least cf.
527 *Crocodylus* (Delfino et al., 2007; Delfino and Rook, 2008; Delfino and Rossi, 2013) that
528 possibly dispersed from Africa, well before the so-called Messinian Salinity Crisis (Delfino et
529 al., 2007). Interestingly also, Gargano and Scontrone, that yielded *Crocodylus* remains, were
530 palaeoislands during the latest Miocene; we can thus speculate that the Cretan crocodylian
531 could also belong to the same lineage and had originated through a similar dispersal route
532 from Africa. Whatever the case, the isolated teeth from Plakias represent the first crocodylians
533 from Greece to be formally described and one of only few late Miocene occurrences of this
534 group in Europe.

535 Our knowledge of squamate biogeography during the Miocene of Europe is hindered
536 by the lack of consensus surrounding the taxonomy and phylogenetic relationships of its
537 representatives. This is especially true for the southeastern European localities, from where
538 only few specimens have been recovered, most of which originating from classic, well known
539 mammal-bearing sites (Gaudry, 1862-67; Weithofer, 1888; Richter, 1995; Georgalis et al.,
540 2016b). The presence of a natricine in the late Miocene of Plakias adds to the already known
541 diversity of this widespread snake group (Szyndlar, 1991b), and in fact, represents one of the
542 southernmost fossil occurrences of colubroids in Europe. Whether the Plakias snake bears
543 close affinities with other Neogene natricines from southeastern Europe (e.g. the natricine
544 from Maramena described by Szyndlar [1995]) cannot be tested due to the fragmentary nature

545 of the single known specimen. Furthermore, the Plakias natricine represents the sole Neogene
546 record of snakes from Crete, as all other fossil occurrences from the island are confined to
547 Pleistocene and Holocene sediments (Holman, 1998). Amphisbaenians are well known from
548 several Miocene European localities, but almost only from the western and central parts of the
549 continent (Roček, 1984; Bolet et al., 2014; Čerňanský et al., 2015), whereas they have never
550 been described from the Balkan Peninsula and eastern Europe in general (Delfino, 2003), with
551 the single exception of a blandid from the middle Miocene of Tauț, Romania (Venczel and
552 Știucă, 2008). After the end of the Miocene, the distribution of amphisbaenians in Europe
553 became gradually restricted to its Mediterranean margins, becoming extinct from most
554 regions after the Pleistocene and surviving today only in the Iberian Peninsula and few Greek
555 Islands (Delfino, 1997; Delfino and Bailon, 2000). Amphisbaenians are represented in the
556 Greek extant herpetofauna solely by the species *Blanus strauchi* (Bedriaga, 1884), which is
557 distributed in the islands of Samos, Fournoi, Leros, Kos, Symi, Rhodes and Kastellorizon
558 (Valakos et al., 2008). *Blanus* occurs also in the adjacent Anatolia, represented by *B. strauchi*
559 and two additional, recently described or revalidated species: *Blanus alexandri* Sindaco,
560 Kornilios, Sacchi and Lymberakis, 2014, and *Blanus aporus* Werner, 1898. The Anatolian
561 fossil record of amphisbaenians is also poor, consisting of only a single record from the
562 Pliocene of Çalta (Rage and Sen, 1976; Delfino, 1997). Whether or not the Plakias specimen
563 represents a species of *Blanus*, cannot be evaluated on the basis of vertebral characters. It is,
564 however, probable that the Plakias amphisbaenian belongs indeed to *Blanus*, as members of
565 this genus have a wide Miocene distribution in western and Central Europe (Bolet et al.,
566 2014; Čerňanský et al., 2015) and the disjunct extant restricted distribution in the western and
567 eastern edges of the continent has been in fact interpreted as relics of an once continuous
568 range in southern Europe (Alexander, 1966; Delfino, 2003), a situation that has also been
569 observed for other squamate groups, such as erylid and elapid snakes (Szyndlar, 1991a, b;

570 Rage, 2013). In fact, Greece and in general the southern Balkans have been suggested as
571 acting as a refugium for multiple squamate groups, such as scolecophidians, erylids, the large
572 anguid *Pseudopus* and the so called “Oriental Vipers” (Delfino, 2003), which all have their
573 sole extant European populations only in that region (Sindaco and Jeremčenko, 2008).
574 However, an alternative hypothesis of the Plakias amphisbaenian sharing affinities with
575 African ones should also be taken into consideration, due to the geographical proximity of
576 Crete to Africa and the unexpected but now well known marine dispersal capabilities of these
577 squamates (Kearney, 2003; Longrich et al., 2015), but such hypothesis is severely hindered by
578 the poor fossil record of African squamates (Rage, 2003; Delfino et al., 2004). Pending the
579 discovery of more complete material from Plakias that could ideally comprise cranial
580 elements that bear diagnostic features, no further biogeographic correlations of the Cretan
581 amphisbaenian with European, Anatolian or African taxa can be made with certainty.

582

583 **6. Conclusions**

584 The herpetofauna of Plakias described in this paper includes the oldest amphibians and
585 reptiles from the Island of Crete and represents one of the southernmost fossil herpetofaunas
586 of Europe. The alytid frog presented herein adds to the known record of this group from the
587 Miocene of southern Europe. The crocodylians are the first such described faunal elements
588 from the country and represent one of the youngest occurrences of this group in Europe.
589 Turtles include two distinct taxa: a geoemydid and a pan-trionychid, both representing the
590 oldest occurrences of these groups from Greece. The single colubroid snake specimen adds
591 further to the published record of Miocene snakes from Greece, whereas the amphisbaenian
592 vertebra from Plakias represents the first described fossil of this group from the country,
593 suggesting that amphisbaenians had a continuous range in the northern Mediterranean area.
594 The herpetofauna of Plakias is shown to be diverse. Overall, it further adds to our knowledge

595 of the Miocene herpetofaunas of southeastern Europe, a region in which amphibian and
596 reptile fossils are still not adequately known.

597

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616

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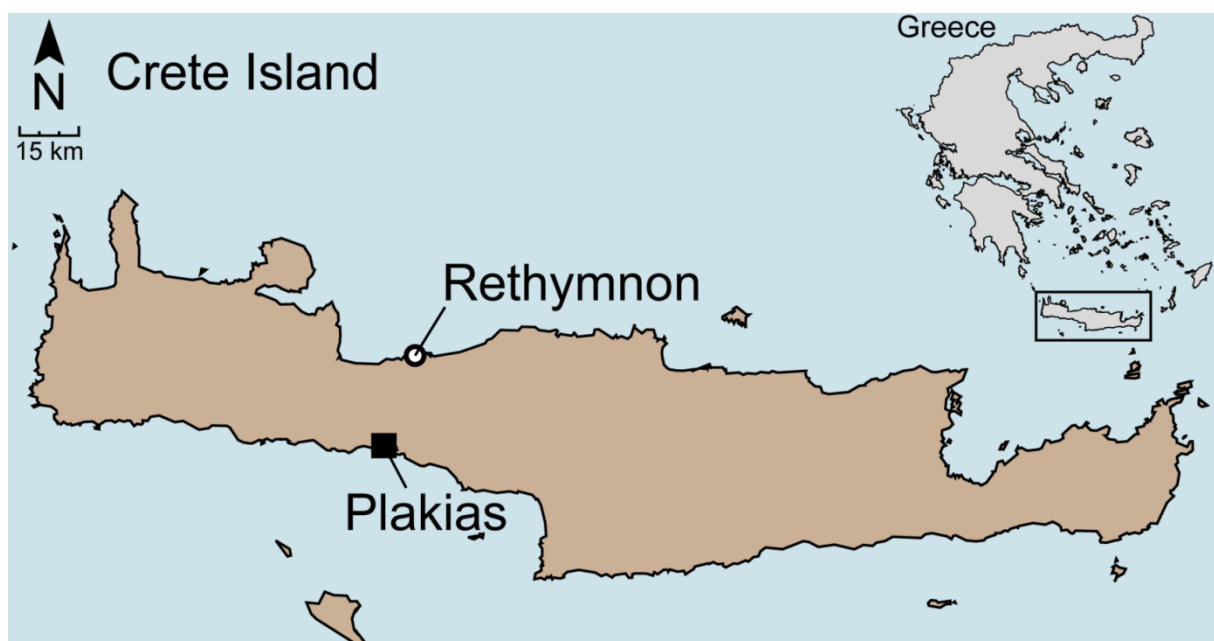
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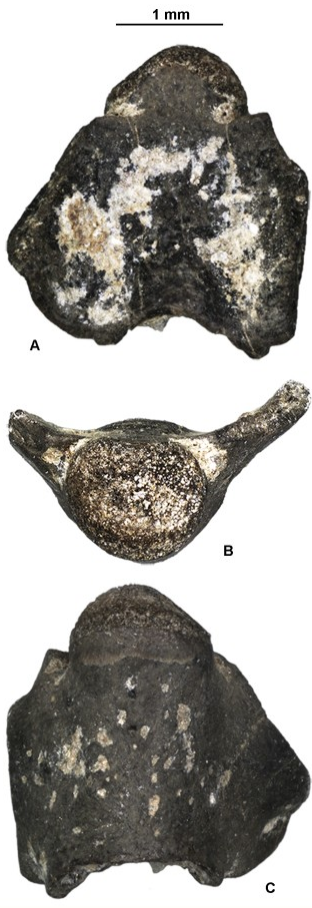
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950 **Figure captions**



951

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

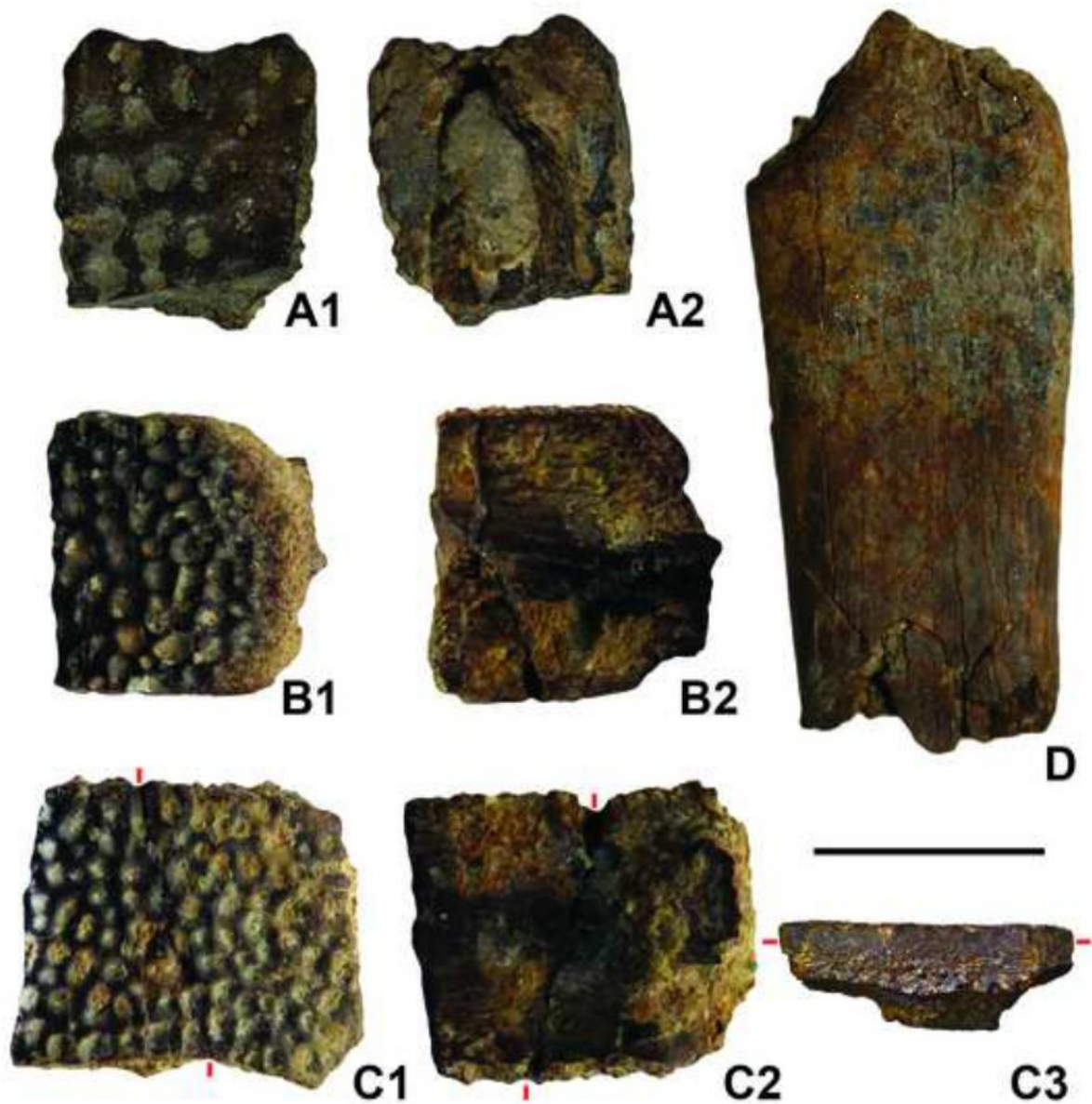


953

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

956

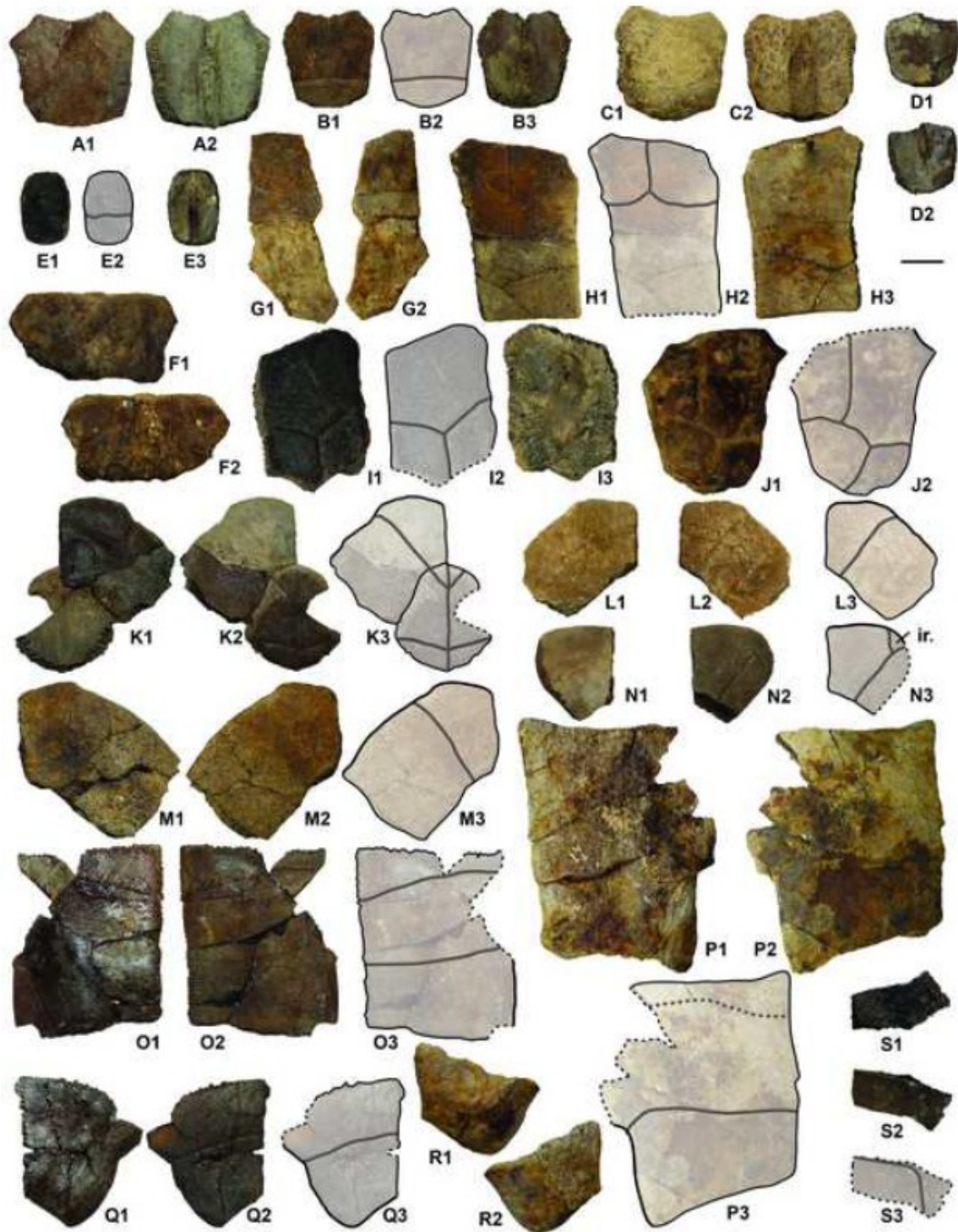
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959

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

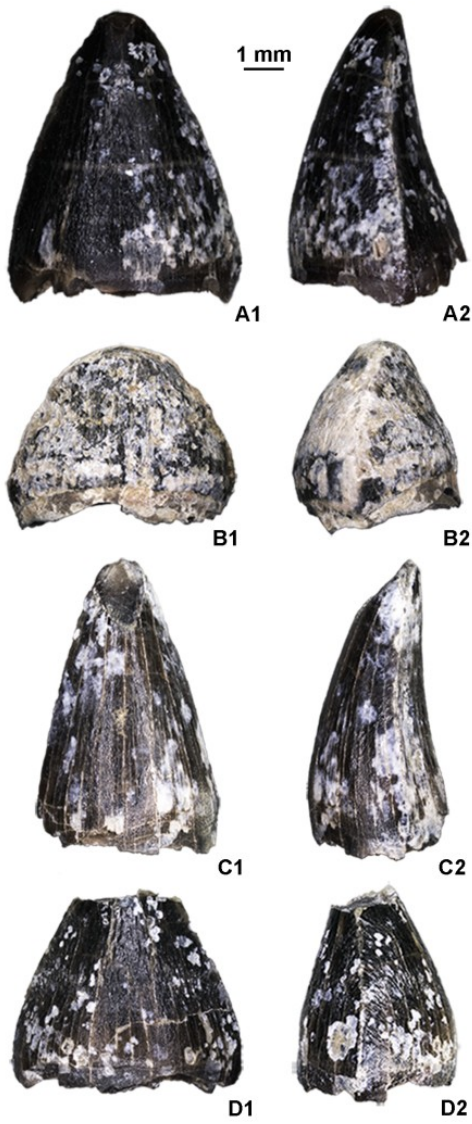


964

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

969 views.E, NHMC 21.7.3.1651, neural in (E1) dorsal, (E2) drawing of the dorsal and (E3)
970 visceral views. F, NHMC 21.7.3.1649, neural fragment in (F1) dorsal (F3) visceral views. G,
971 NHMC 21.7.3.1640, two successive costals in (G1) dorsal and (G2) visceral views.H, NHMC
972 21.7.3.1638, costal in (H1) dorsal, (H2) drawing of the dorsal and (H3) visceral views. I,
973 NHMC 21.7.3.1639, costal fragment in (I1) dorsal, (I2) drawing of the dorsal and (I3) visceral
974 views. J, NHMC 21.7.3.1641, peripheral in (J1) dorsal and (J2) drawing of the dorsal views.
975 K, NHMC 21.7.3.1618, right epiplastron and entoplastron in (K1) visceral, (K2) ventral and
976 (K3) drawing of the ventral views. L, NHMC 21.7.3.1637, left epiplastron in (L1) visceral,
977 (L2) ventral and (L3) drawing of the ventral views. M, NHMC 21.7.3.1635, right epiplastron
978 in (M1) visceral, (M2) ventral and (M3) drawing of the ventral views. N, NHMC 21.7.3.1632,
979 left epiplastron fragment in (N1) visceral, (N2) ventral and (N3) drawing of the ventral views.
980 O, NHMC 21.7.3.1620, left hypoplastron in (O1) visceral, (O2) ventral and (O3) drawing of
981 the ventral views. P, NHMC 21.7.3.1643, right hypoplastron in (P1) visceral, (P2) ventral and
982 (P3) drawing of the ventral views. Q, NHMC 21.7.3.1619, right xiphiplastron in (Q1)
983 visceral, (Q2) ventral and (Q3) drawing of the ventral views. R, NHMC 21.7.3.1642 right
984 xiphiplastron fragment in (R1) visceral and (R2) ventral views. S, UU PL 705, possible
985 hyoplastron fragment in (S1) visceral, (S2) ventral and (S3) drawing of the ventral views.
986 Abbreviation: ir, irregular scute growth.

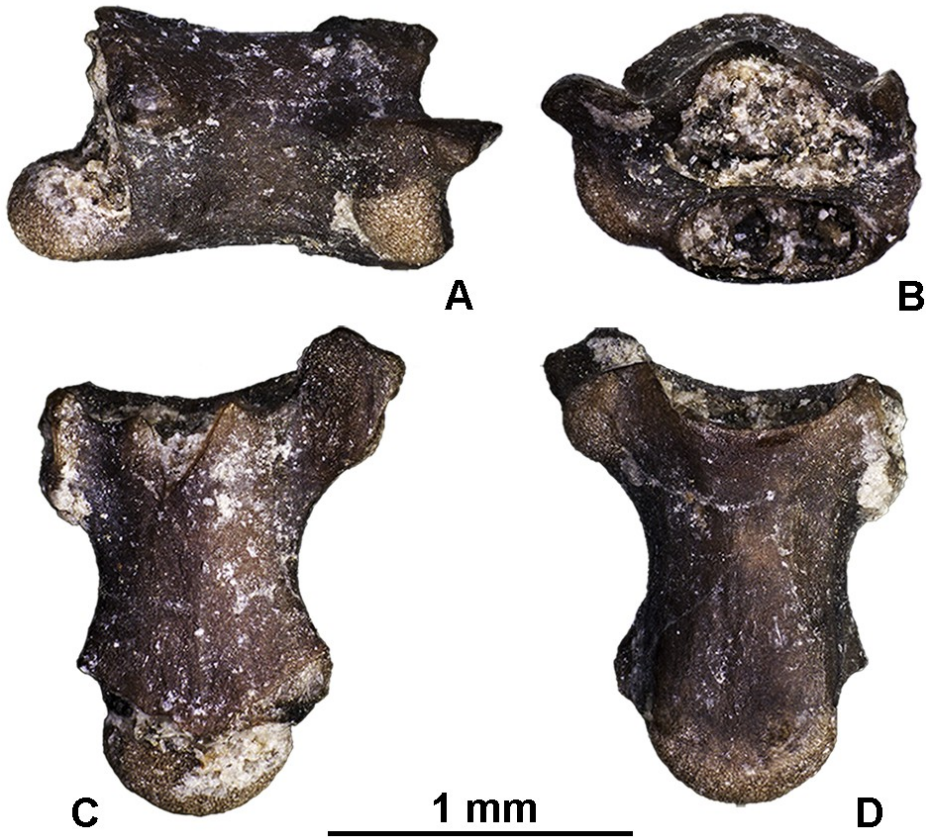
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989 **Fig. 5.** Crocodylia from the earliest late Miocene of Plakias. A, UU PL 706, isolated tooth in
 990 labial (A1) and mesial (A2) views. B, UU PL 707, isolated tooth in labial (B1) and mesial
 991 (B2) views. C, UU PL 708, isolated tooth in labial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

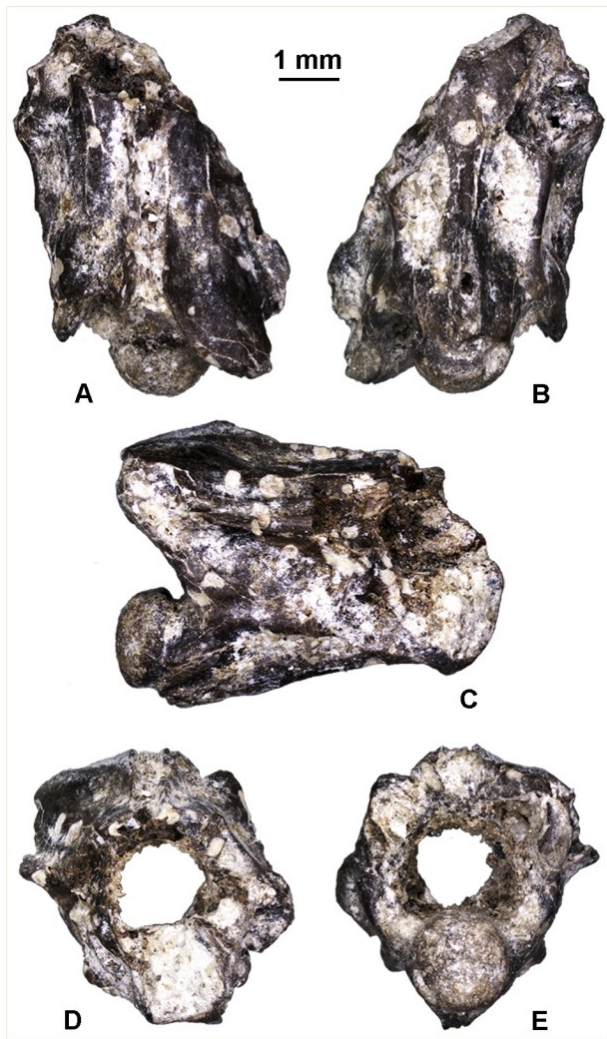
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995 **Fig. 6.** Amphisbaenia from the earliest late Miocene of Plakias. UU PL 733, presacral

996 vertebra in right lateral (A), dorsal (B), ventral (C) and anterior (D) views.



997

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

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1001

1002

1003 **Table 1**

1004 The youngest occurrences of crocodylians in Europe.

Taxon	Age	Locality	Reference
<i>Crocodylus</i> 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
<i>Tomistoma calaritanus</i>	Tortonian–Messinian	Is Mirrionis, Sardinia, Italy	Capellini, 1890
Crocodylia indet.	late Tortonian	Fiume Santo, Sardinia, Italy	Abbazzi et al., 2008
cf. <i>Crocodylus</i> sp. (type of <i>Crocodylus bambolii</i>)	Tortonian	Montabamboli- Casteani-Ribolla, Tuscany, Italy	Delfino and Rook, 2008
<i>Tomistoma</i> cf. <i>lusitanica</i>	Tortonian	Olhos de Agua, Algarve, Portugal	Vianna and Moraes, 1945
Crocodylia indet. (<i>Diplocynodon</i> sp.)	Tortonian	Soblay, Ain, France	Ménouret and Mein, 2008
Crocodylia indet.	early Tortonian	Plakias, Crete, Greece	this paper
cf. <i>Crocodylus</i> sp.	early Tortonian	Scontrone, Abruzzo, Italy	Rustioni et al., 1993; Delfino and Rossi, 2013

