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Poor but classic: The squamate fauna from the late Miocene of Pikermi, near Athens, Greece

Pauvre mais classique : la faune squamate du Miocène supérieur de Pikermi, près d'Athènes, Grèce

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ABSTRACT

I here describe new fossil remains of lizards and snakes from the late Miocene of Pikermi, near Athens, Greece. This classical locality, known since at least the middle of the 19th century, has yielded over the decades abundant mammal fossils, whereas squamate remains have been confined to early discoveries of *Varanus* remains during the 19th century. The first specimen among these varanid fossils, a large vertebra described by Albert Gaudry during the 1860s, represents also one of the earliest discoveries of a fossil monitor lizard worldwide. Nevertheless, this historically important specimen has only been briefly described and its so far only available images were the original lithographs and subsequent sketches of two only of its views. I here describe this specimen in detail and provide photographs of all its standard views. The additional squamate remains from the Pikermi area are fragmentary. Nevertheless, they document the presence in Pikermi of other lizard groups, such as lacertids and probable anguines, while snakes are described for the first time. Among the snake fossils, probable erycines and colubrids are identified; if indeed an erycine, this would be the oldest occurrence of that group in the Eastern Mediterranean, thus extending back its stratigraphic range in the area by several million years.

RÉSUMÉ

Je décris ici de nouveaux restes fossiles de lézards et de serpents du Miocène supérieur de Pikermi, près d'Athènes, en Grèce. Cette localité classique, connue depuis la première moitié du XIX^e siècle au moins, a fourni sur des décennies, d'abondants fossiles de mammifères, tandis que les restes de squamates sont limités aux découvertes précoces de restes de *Varanus* au XIX^e siècle. Le premier spécimen parmi ces varanidés fossiles, à savoir une grande vertèbre décrite par Albert Gaudry au cours des années 1860, représente aussi l'une des découvertes les plus précoces de par le monde d'un lézard fossile monitor. Néanmoins, ce spécimen historiquement important n'a été que brièvement décrit et, jusqu'à présent, les seules représentations que l'on en ait sont des lithographies originelles et des schémas de

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deux de ces dernières. Je décris ici ce spécimen en détail et j'en fournis des photographies de toutes les vues standard. Les restes de squamate additionnels, de la région de Pikermi, sont fragmentaires. Cependant, ils documentent la présence, à Pikermi, d'autres groupes de lézards, tels des lacertidés et des anguilles probables, tandis que des serpents y sont décrits pour la première fois. Parmi les serpents fossiles, des erycinés et colubridés sont identifiés; s'il s'agit bien d'un eryciné, ce serait la plus ancienne occurrence de ce groupe dans la Méditerranée orientale, ce qui reculerait sa fourchette stratigraphique dans la région de plusieurs millions d'années.

1. Introduction

Pikermi is a fossil locality, situated only few kilometres away from Athens, with its age considered to pertain to the late Miocene (Tortonian) (Koufos, 2006). The locality has been known at least since the first decades of the 19th century and was the focus of several different publications (Gaudry, 1855, 1860, 1861a, 1861b; Gaudry and Lartet, 1856; Roth and Wagner, 1854; Wagner, 1848). The spectacular fossil finds of Pikermi provided the locality with an immense reputation as one of the most classical and famous fossil Neogene localities across the world, surpassing in significance other classical Miocene localities such as Samos and Maragheh (Abel, 1912; Woodward, 1901). The abundance of the fossil material attracted researchers from various countries, resulting in a dispersion of specimens in a large number of museums and institutions across the globe. Most of the early studies dealt exclusively with mammal finds, and a mammalian focus has been maintained in almost all works dealing with the Pikermi fauna ever since (Roussiakis, 2002 and Theodorou et al., 2010 and references therein). Pikermi has become a standard reference point for all coeval Turolian localities across the Old World and the term Pikermian fauna has been applied to encompass a large region in the late Miocene of the Eastern Mediterranean, characterized by similar, savannah-like ecosystems and several shared mammal taxa (Bernor et al., 1996; Böhme et al., 2017; Koufos, 2006; Kostopoulos, 2009).

Whereas mammals in Pikermi are represented by a huge amount of fossil specimens, reptiles are known from relatively limited material, despite the early date of publication of such remains (Gaudry, 1862a, 1862b, 1862–1867; Weithofer, 1888). Among reptiles, turtles are definitely the most numerous, being represented by at least two testudinid taxa, the small *Testudo marmorum* Gaudry, 1862b, and a giant tortoise (Bachmayer, 1967; Bachmayer and Symeonidis, 1970; Gaudry, 1862a, 1862b, 1862–1867; Georgalis and Kear, 2013; Vlachos et al., 2019). A purported crocodylian fragment from Pikermi, mentioned by Abel (1912) cannot be verified, as it was not accompanied by any kind of description or figure. As for squamates, they have been so far known from Pikermi exclusively from limited material pertaining to the genus *Varanus* (Gaudry, 1862a, 1862b, 1862–1867; Villa et al., 2018; Weithofer, 1988). Interestingly, the first recovered specimen among this *Varanus* material, a large dorsal vertebra described by the prominent French palaeontologist Albert Gaudry (1862a, 1862b, 1862–1867) represents one of the first known fossil records of monitor lizards globally. Nevertheless, this important specimen has never been properly figured or described in detail. I provide photographs of this specimen for the first time and thoroughly discuss the rather complicated taxonomic history of Pikermi varanids. In addition, I describe new material of lizards and snakes from the Pikermi area, thus documenting for the first time the presence of non-*Varanus* squamates in this classical locality.

2. Materials and methods

The large dorsal vertebra of *Varanus* described by Gaudry (1862a, 1862b, 1862–1867) is permanently curated at the collections of MNHN, under the collection number MNHN.F.PIK 3715 (not "MNHN Pikermi 31" as stated by Villa et al. (2018)). The rest of the herein described material of lizards and snakes from Pikermi is permanently curated at the collections of UU. Comparative material of multiple skeletons of extant lizards and snakes was studied at the collections of HNHM, MDHC, MNCN, MNHN, NHMW, NMP, PRIF UK, and ZZSiD.

Abbreviations: AMPG, Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Athens, Greece; IPU, WInstitut für Paläontologie, University of Vienna, Vienna, Austria; Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine; MDHC, Massimo Delfino Herpetological Collection, University of Torino, Torino, Italy; MN, Mammifères Neogène (standard level zone); MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum national d'histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMP, Národní Muzeum Praha, Prague, Czech Republic; PRIF UK, Faculty of Natural Sciences, Comenius University, Bratislava, Slovakia; UU, Department of Earth Sciences, University of Utrecht, The Netherlands; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

3. Geological settings

The geological settings of Pikermi have been extensively described in the literature over the past 150 years, and so there is no need to repeat it in detail. Thorough information can be found in Roussiakis (2002), Theodorou et al.

(2010), and Böhme et al. (2017). What appears to be of importance is that the specimens described in the early excavations of the 19th and early 20th centuries apparently originate from a mix of two or three different levels within the locality of Pikermi, whose age differs by tens or even hundreds of thousands of years (Roussiakis, 2002; Theodorou et al., 2010). New fossil sites have recently been identified in the area of the Pikermi locality, namely the Chomateri (or Chomateres or Kisdari) and the PV1 (i.e., Pikermi-Valley 1) (Bachmayer et al., 1982; Theodorou et al., 2010). Chomateri is situated around 2 km east of the classical site of Pikermi (Konidaris and Roussiakis, 2019). The classical sites of Pikermi are generally attributed to the MN 12 stage of the late Miocene (Koufos, 2006), but for the "new" sites in the area, a more conservative approach of MN 11–MN 13 has been suggested (Theodorou et al., 2010). In any case, all sites of Pikermi pertain to the Pikermi Formation (Konidaris and Roussiakis, 2019). In particular for the Chomateri Member of the Pikermi Formation, this is considered to date between 7.17 and 7.11 Ma (Böhme et al., 2017; Konidaris and Roussiakis, 2019). Note that the now confirmed late Miocene age of Pikermi contrasts with previous works that took the locality to be Pliocene, especially in the 19th century (Fejérváry, 1918, 1935; Lydekker, 1886), but also even more recently (Estes, 1983; Molnar, 2004; Rage and Sen, 1976). Detailed information about the palaeoenvironments and the palaeoecology of the Pikermi area is provided by Böhme et al. (2017), who suggested the presence of a savannah landscape with woodlands.

The *Varanus* vertebra originally described by Gaudry (1862a, 1862b, 1862–1867) originates from one of the classical excavations and lacks precise stratigraphic data. The UU specimens originate from Chomateri, some eight and ten meters above the level with large mammals, and were collected during two field seasons, by H. de Bruijn and R. Rumke in 1973 and H. de Bruijn in 1974 (Hans de Bruijn, pers. comm., March 2019).

4. Taxonomic history of the Pikermi monitor lizards

Gaudry (1862a, 1862b) was the first to describe a varanid fossil specimen from Pikermi, a large trunk vertebra (MNHN.F.PIK 3715), without, however, providing any illustration of the material. The same author first figured it in his large, classical full treatise of the Pikermi fauna, where he provided a lithograph of the vertebra, though only in ventral and lateral views (Gaudry, 1862–1867:pl. 60.2–3). Interestingly, these actions of Gaudry (1862a, 1862b, 1862–1867) comprise one of the first descriptions of a varanid fossil specimen worldwide: it precedes the Paleogene varanid *Saniwa* Leidy, 1870, from North America (Leidy, 1870) and, in fact, it is surpassed only by the iconic gigantic "Megalania" *Varanus priscus* (Owen, 1859) from the Quaternary of Australia (Owen, 1859). With the limited available material at hand, Gaudry (1862a, 1862b, 1862–1867) could not make a more precise determination of the material and, with a brief description, he rejected affinities with crocodylians and snakes and only referred to it as "Reptile du groupe des Varans" (Gaudry, 1862a, 1862b, 1862–1867), though in his list of taxa from Pikermi he tentatively referred it to the genus?*Varanus* (Gaudry, 1862–1867:323). The large size of the Pikermi varanid was already highlighted by Gaudry (1862a, 1862b, 1862–1867), who suggested an estimated length of around 1.5 m, an estimation that was more or less subsequently followed in the literature (e.g., "between four and five feet" of Lydekker, 1886:236), or even exceeded (six feet of Dunn, 1927). Cranial material of monitor lizards was soon later recovered from Pikermi: Weithofer (1888) established his new species, *Varanus marathonensis*, on the basis of two cranial specimens from that locality, a left portion of a skull, including the maxilla (currently specimen IPUW 1888-001-001) and a single left supraorbital (currently probably lost). *V. marathonensis* was the first named species of a varanid from Europe, taking into consideration that *Palaeovaranus cayluxi* Zittel (1887–1890) from the Eocene of the Phosphorites du Quercy, France, is now considered to pertain to another lizard clade, Palaeovaranidae (Hoffstetter, 1943; Georgalis, 2017). A few years later, Nopcsa (1908) established a second varanid species from Pikermi, *Varanus atticus*, this time on the basis of the large trunk vertebra MNHN.F.PIK 3715, originally described by Gaudry (1862a, 1862b, 1862–1867). Curiously, Nopcsa (1908) did not mention at all Weithofer's (1888) work or *V. marathonensis* that had been previously described from Pikermi. Nevertheless, Nopcsa (1908:47) admitted that he in fact named this species in order to render the specimen more "accessible" in the palaeontological community, as he attested that for a large amount of fossil lizards, the species epithet means nothing more than a number that makes it easier to find the piece in question ("Da bei einer überaus großen Anzahl fossiler Lacerten der spezifische Name nichts anderes bedeutet als ein Zeichen resp. eine Nummer, wodurch das betreffende Stück leichter aufzufinden ist, so möchte ich Gaudrys Varanus mit den Speziesnamen atticus bezeichnen.") In any case, the name *V. atticus* did not stand the test of time, as soon after Fejérváry (1918) placed it into the synonymy of *V. marathonensis*, a synonymizing that has since been subsequently followed by most workers (Estes, 1983; Georgalis et al., 2018; Kuhn, 1939, 1963; Molnar, 2004; Rage and Sen, 1976; Villa et al., 2018). Fejérváry (1918) provided further descriptions and comments on Gaudry's (1862a, 1862b, 1862–1867) and Weithofer's (1888) material, whereas he provided new, pen drawings of the specimens after their original publications (Fejérváry, 1918:figs. 7–8). The same author further referred additional cranial and postcranial varanid remains from the Neogene of Hungary to the same species (Fejérváry, 1918). Later he highlighted again the significance of *V. marathonensis* by calling it "the first well known and generically safely identifiable Varanian remains" (Fejérváry, 1935:72). The overall resemblance of the morphology of the maxilla of *V. marathonensis* with that of the extant *Varanus griseus* (Daudin, 1803b) has been highlighted in the literature since several decades (Dunn, 1927). Subsequent authors even proposed close relationships between the two taxa (Levshakova, 1986; Stanner, 2004) and *V. marathonensis* was even considered as the oldest member of the subgenus *Psammosaurus* Fitzinger, 1826, to which *V. griseus* pertains (Levshakova, 1986). Rage and Sen (1976) described new varanid vertebral material from the Pliocene of Çalta, Turkey, which they referred to *V. marathonensis*, highlighting the most important vertebral features of this species in comparison with other extinct varanids. Estes (1983) provided a new diagnosis of *V. marathonensis* but this was exclusively based on vertebral characters. Molnar (2004) erroneously stated that new varanid finds had since been recovered from Pikermi and that they were attributable to *V. marathonensis*. This is, however, not the case, and apparently Molnar (2004) misread Estes (1983) who had simply anticipated more varanid finds from Pikermi. Conrad et al. (2012) described a new varanid taxon, *Varanus amnhophilis*, from the late Miocene of Samos, and erroneously stated that the holotype of *V. marathonensis* was Gaudry's (1862a, 1862b, 1862–1867) vertebra and not Weithofer's (1888) type skull elements, considering the latter as simply referred material. In doing so, Conrad et al. (2012) included the type skull material of *V. marathonensis* in their phylogenetic analysis, simply as *Varanus* cf. *marathonensis*. Georgalis et al. (2017b) treated *V. marathonensis* as a valid taxon and noted resemblance of the youngest European varanid material from the Pleistocene of Tourkobounia 5, near Athens, with that species on the basis of a clearly developed medial lamina on the maxilla. Georgalis et al. (2018) briefly discussed the Pikermi varanids and provided for the first time a formal collection number for Gaudry's vertebra (MNHN.F.PIK 3715). Finally, Villa et al. (2018) redescribed the type material of *V. marathonensis*, selected the syntype skull IPUW 1888-001-001 as the lectotype, and described articulated caudal vertebrae from Pikermi, as well as new material from the late Miocene of Samos and the middle and late Miocene of Spain, expanding significantly the geographic and stratigraphic distribution of this monitor lizard species. On the basis of the new finds, these authors synonymized *V. amnhophilis* with *V. marathonensis* and conducted a rather complete phylogenetic analysis combining both anatomical characters and molecular data (modifying Conrad et al. (2012) matrix), demonstrating Asian affinities for that species (Villa et al., 2018).

As it is evident, the Gaudry's varanid vertebra MNHN.F.PIK 3715 is a historically rather important specimen. However, so far there existed only the original lithograph of Gaudry (1862–1867), which depicted it only in two views (an image that has been also reproduced in subsequent literature), as well as its brief descriptions of Gaudry (1862a, 1862b, 1862–1867) and Fejérváry (1918). Here I provide photographs of this vertebra for the first time, figuring it in all standard views, accompanied by a detailed description of the specimen. In addition, a tiny caudal vertebra from Pikermi is further tentatively referred to *Varanus*, while another, large vertebral fragment may represent a cervical vertebra of the same genus.

5. Systematic palaeontology

SQUAMATA Oppel, 1811
LACERTIDAE Oppel, 1811
Lacertidae indet.
Fig. 1

Material. A right dentary (UU PK 1001); a left dentary (UU PK 1002); a fragment of a tooth bearing bone (UU PK 1004); an isolated tooth (UU PK 1012).

Description. UU PK 1001 is an incomplete, small-sized portion of a right dentary with a portion of the splenial articulated to it (Fig. 1A–B). It bears six teeth, of which only one is relatively complete, whereas the rest of them are much damaged and fragmentary. The complete tooth is bicuspid, possessing a distinct accessory cusp on the mesial side of the main one. The labial surface of the specimen is relatively smooth, but a rather large, deep, and elongated foramen is present at around its mid-length. The splenial anterior inferior alveolar foramen is visible below the subdental shelf. UU PK 1002 is a small, incomplete and fragmentary anterior portion of a left dentary (Fig. 1C–E). It preserves three more or less complete, heterodont teeth, but remains of at least four additional teeth and tooth positions are visible. The teeth are cylindrical and slender; they are monocuspid or slightly bicuspid, with an incipient accessory cusp, at least present in the best preserved tooth. All preserved teeth protrude well above the labial wall of the dentary (jaw parapet of Estes, 1983). The symphyseal region is preserved. The subdental shelf is rather eroded and its thickness and full length cannot fully be evaluated. The same applies to Meckel's groove. In labial view, the dentary surface is relatively smooth, although at least two large and rather deep foramina pierce its surface near its ventral level. As for other tooth bearing elements, not a lot can be said about UU PK 1004 (Fig. 1F–G). Three well preserved teeth are present, being cylindrical, slender, and bicuspid, with the accessory cusp being most prominent in the third tooth in the row, though this may well be due to some kind of erosion of the other two teeth. There are striae on the mesial surface of the crown of all teeth. In labial view, there is a slight outward bulge of the jaw parapet. Dentition is pleurodont in all three specimens. The isolated tooth UU PK 1012 is poorly preserved (Fig. 1H); it is slender and bicuspid.

Comments. These specimens can be assigned to Lacertidae on the basis of their heterodont dentition and the overall shape of teeth, often with bicuspid teeth situated at least in posterior positions. Such taxonomic allocation is also supported by a general geographic and stratigraphic rationale. As is the case with all other fossil lacertids known from the Greek area, a more precise determination to the species or even genus level, is currently impossible (Georgalis et al., 2017a, 2019; Villa et al., 2017).

ANGUIMORPHA Fürbringer, 1900
ANGUIDAE Gray, 1825
ANGUINAE Gray, 1825
?Anguinae indet.
Fig. 2

Material. A caudal vertebra (UU PK 1013; Fig. 2).

Description. The caudal vertebra UU PK 1013 is rather fragmentary, preserving only its anterior portion, while the transverse processes are damaged, the prezygapophyses (especially the left one) are rather eroded, and the neural spine is missing (Fig. 2). The transverse processes are directed anterolaterally and are almost horizontal. There is a foramen at the base of each transverse process. The prezygapophyses are relatively large and they face dorsolaterally in anterior view. The cotyle is large and dorsoventrally

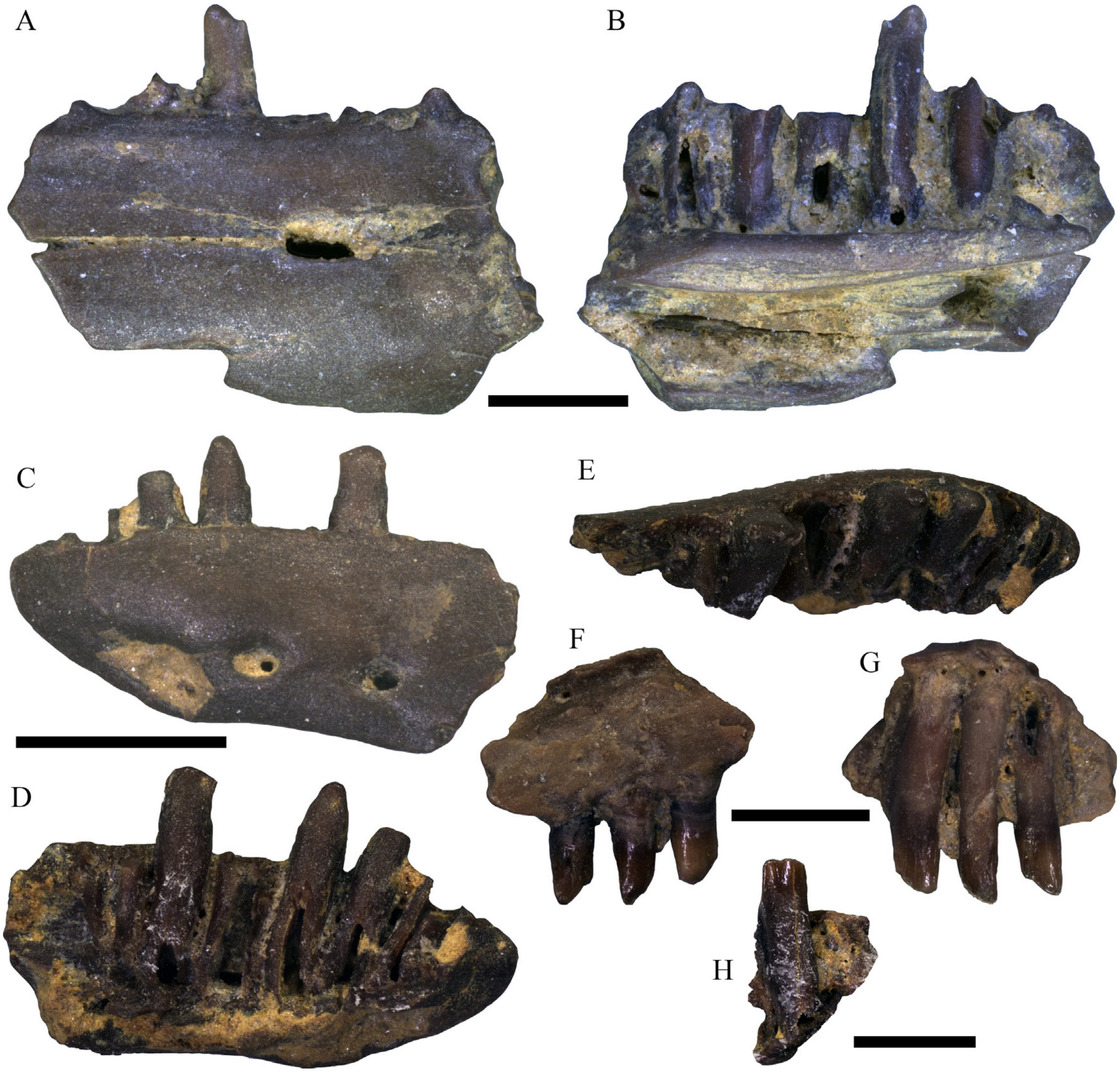

Fig. 1. Lacertidae indet. from Pikermi (Chomateri). A and B. Right dentary (UU PK 1001) in labial (A) and medial (B) views. C and E. Left dentary (UU PK 1002) in labial (C), medial (D), and dorsal (E) views. F and G. Fragment of a tooth bearing bone (UU PK 1004) in labial (F) and medial (G) views. H. Isolated tooth (UU PK 1012). Scale bars = 1 mm.

Fig. 1. Lacertidae indet. De Pikermi (Chomateri). A et B. Dentaire droit UU PK 1001) en vues labiale (A) et médiale (B). C–E. Dentaire gauche (UUPK 1002) en vues labiale (C), médiale (D) et dorsale (E). F et G. Fragment d'os portant une dent (UU PK 1004) en vues labiale (F) et médiale (G). H. Dent isolée (UU PK 1012). Barres d'échelle = 1 mm.

Fig. 2. ?Anguinae indet. from Pikermi (Chomateri). Caudal vertebra UU PK 1013 in anterior (A), dorsal (B), and ventral (C) views. Scale bar = 1 mm.

Fig. 2. ?Anguinae indet. de Pikermi (Chomateri). Vertèbre caudale UU PK 1013 en vue antérieure (A), dorsale (B) et ventrale (C). Barre d'échelle = 1 mm.

Fig. 3. *Varanus* sp. from Pikermi. The trunk vertebra MNHN.F.PIK 3715. A–F. Photographs of the specimen. G–H. Lithograph of the specimen modified from the original by Gaudry (1862–1867:pl. 60:2–3). (I) The original label accompanying the specimen, with the script "Saurien du groupe des Varans. Pikermi. m. Gaudry". Specimen figured in dorsal (A), ventral (B, G), anterior (C), posterior (D), right lateral (E, H), and left lateral (F) views. Note that the original lithograph of Gaudry (1862–1867) figured the specimen only in two views, which also appear to be reverse images of the actual photographs, a case that is a common fact for 19th century's lithographs. Scale bar = 5 mm.

Fig. 3. *Varanus* sp. de Pikermi. La vertèbre de tronc MNHN. PIK 3715. A–F. Photographie du spécimen. G–H. Lithographie du spécimen modifiée à partir de l'original de Gaudry (1962–1867: pl. 60:2–3). Le label original accompagnant le spécimen, avec la mention « Saurien du groupe des Varans. Pikermi. M. Gaudry. » Spécimen figurant en vues dorsale (A), ventrale (B), antérieure (C), postérieure (D), latérale droite (E, H) et latérale gauche (F). À noter que la lithographie originale de Gaudry (1862–1867) représente le spécimen selon seulement deux vues, qui alors apparaissent comme les images inverses des photographies actuelles, cas fréquent pour les lithographies du XIX^{e} siècle. Barre d'échelle = 5 mm.

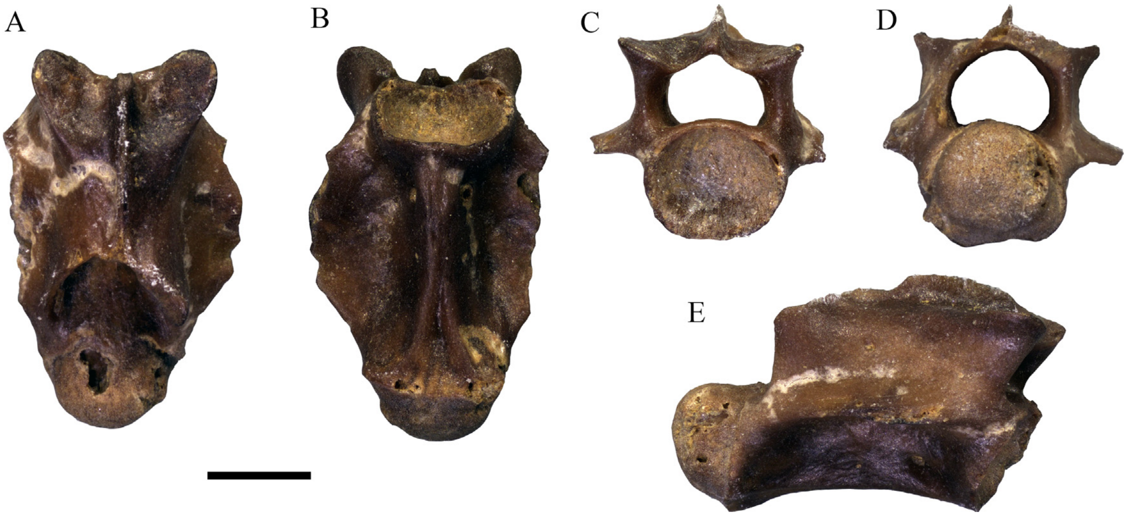

Fig. 4. ?*Varanus* sp. from Pikermi (Chomateri). Caudal vertebra UU PK 1011 in dorsal (A), ventral (B), anterior (C), posterior (D), and right lateral (E) views. Scale bar = 1 mm.

Fig. 4. ? *Varanus* sp. de Pikermi (Chomateri). Vertèbre caudale UU PK 1011 en vues dorsale (A), ventrale (B), antérieure (C), postérieure (D) et latérale droite (E). Barre d'échelle = 1 mm.

depressed. An autotomy plane is observed at around the level of the transverse processes.

Comments. The overall morphology of the caudal vertebra UU PK 1013 resembles both anguines and varanids. Nevertheless, the presence of an autotomy plane in the vertebra hints towards a taxonomic allocation to anguine lizards (Arnold, 1984; Bateman and Fleming, 2009). This is further concordant with the presence of a foramen at the base of each transverse process, as well as the overall morphology of the specimen that is reminiscent of anguine caudal vertebrae. However, on the total absence of the posterior portion of the Pikermi vertebra that would enable to observe the shape of the haemapophyses, I only tentatively assign this specimen to anguines.

PLATYNOTA Duméril and Bibron, 1835
VARANIDAE Gray, 1827 (sensu Estes et al., 1988)
VARANUS Merrem, 1820
Type species. *Lacerta varia* White, 1790.
Varanus sp.
Figs. 3–4

Material. A trunk vertebra (MNHN.F.PIK 3715; Fig. 3) and (tentatively) also a caudal vertebra (UU PK 1011; Fig. 4).

Description. MNHN.F.PIK 3715 is a large and robust vertebra, missing most of its neural spine, part of the left prezygapophysis, and most of the postzygapophyses, while its left synapophysis is eroded and part of the ventral surface of the cotyle is damaged (Fig. 3). The vertebra is procoelous. In dorsal view (Fig. 3A), the prezygapophyses extend anterolaterally, projecting anteriorly well beyond the level of the cotyle. The prezygapophyseal facets are relatively large and oval. A pars tectiformis is present in the anterior portion of the neural arch. No pseudozygosphene (sensu Hoffstetter, 1969) is present. Distinct fibrous striae are present on the surface of the vertebra. In ventral view (Fig. 3B, G), the centrum is almost triangular in shape. The surface of the centrum is relatively smooth, with few ridges occasionally present throughout it. A precondylar constriction is present and is prominent, separating the condyle from the centrum. As is common with varanid vertebrae, the cotyle faces anteroventrally and so its inner surface and even its dorsal level are largely visible from this view as well. The synapophyses extend laterally. In anterior view (Fig. 3C), the vertebra seems rather dorsoventrally compressed. The cotyle is rather large, dorsoventrally depressed, and highly elliptical in shape. The prezygapophyseal facets (only the right one is well preserved) are clearly dorsally inclined, extending well above the dorsal level of the neural canal. The neural canal is rather small and is dorsally arched and ventrally flattened. In posterior view (Fig. 3D), the condyle is rather large and much dorsoventrally depressed. The posterior portion of the neural arch is highly damaged so the extent and exact shape of the postzygapophyses cannot be evaluated. There is no preudozygantrum (sensu Hoffstetter, 1969). The neural canal is small and is almost triangular in shape. In lateral view (Fig. 3E–F, H), the centrum is almost straight and becomes only slightly convex ventrally, just before the ventral edges of the cotyle and the condyle. The neural arch gradually increases in height posteriorly. The neural spine is broken and its height cannot be evaluated, although, judging from the preserved portion, it seems that it was gradually ascending posteriorly and that its base was developed across most of the midline of the posterior length of the neural arch. The synapophyses are massive.

UU PK 1011 is a much incomplete caudal vertebra, missing most of the neural spine, the posterior portion of the neural arch, part of the transverse processes, and most of the haemapophyses (Fig. 4). The vertebra is procoelous, rather small (centrum length only 2.9 mm), and rather elongated. The centrum is rather dorsally arched in lateral view. Lateral foramina are present. The cotyle faces anteroventrally and so its whole surface and even its dorsal margin are fully visible in the ventral view of the vertebra. There is no “pseudozygosphene” or “pseudozygantrum” (sensu Hoffstetter, 1969). The anterior surface of the neural arch in dorsal view possesses a triangular and deeply recessed area situated between the neural spine and each of the prezygapophyses. The prezygapophyses are dorsally inclined and project anteriorly beyond the dorsal edge of the cotyle. The prezygapophyseal articular facets are broad and oval-shaped. The transverse processes extend laterally and only slightly ventrally in anterior view, but their full size and extent cannot be evaluated as they are broken. The neural canal is large. The cotyle is large and slightly elliptical. The condyle is large and almost circular. Subcentral foramina are present. There is no visible autotomic fracture plane. The pedicels for articulation with the chevron bones are broken and only in the left one, there is a tiny preserved portion of its base. Two prominent ridges are present on the ventral surface of the centrum, commencing anteriorly at the ventral lip of the cotyle and terminating posteriorly at the pedicels for the haemapophyses (i.e., chevron bones), prior to the level of the condyle. The two ridges are curved and approach one another closely at mid-length on the centrum.

Comments. The vertebra MNHN.F.PIK 3715 can be referred to Varanidae on the basis of the presence of a well-developed pars tectiformis on its neural arch, the overall morphology of the ventral surface of the centrum that is widened anteriorly and convex ventrally in cross section, and the shape of the condyle that is strongly depressed, with its articular surface facing mainly dorsally (Georgalis et al., 2018; Rage and Bailon, 2005). MNHN.F.PIK 3715 can be further assigned to the genus *Varanus* on the basis of the prominent precondylar constriction, the presence of striae on the neural arch, and the much anteroventrally facing cotyle (Bailon and Rage, 1994; Delfino et al., 2013; Georgalis et al., 2018; Smith et al., 2008). Such generic placement is also fully supported by a biogeographic and stratigraphic rationale, considering that *Varanus* is the sole known genus of varanids in the Neogene and Quaternary of Europe; the sole other known Cenozoic genus of monitor lizards from the continent, *Saniwa*, had become extinct already by the Eocene (Delfino et al., 2013; Rage, 2013; Georgalis et al., 2017b, 2018, 2019). The specimen can be considered to originate from the presacral region of the trunk on the basis of its absolute large size and the total absence of structures that are present on lizard sacral and caudal vertebrae, such as transverse processes and haemapophyses. Furthermore, the absence of a hypapophysis from the ventral surface of the centrum denotes that the vertebra does not originate from the anterior trunk region. Taking these into account, it can be safely deduced that MNHN.F.PIK 3715 originates from around the mid-portion of the trunk region, an assumption further supported by the lack of strong dorsoventral elongation of the synapophyses (in the anterior trunk these are highly elongate due to the shape of the ribs, while close to the sacrum they are basically circular).

With regard to the vertebra UU PK 1011, this tiny specimen is more puzzling and can only tentatively be referred to Varanidae and *Varanus* on the basis of its overall shape, the presence of a pars tectiformis on the anterior portion of the neural arch, the much anteroventrally facing cotyle, the haemapophyses being articulated on two pedicels which are located far anteriorly on the centrum, and the absence of an autotomic septum. UU PK 1011 can be identified as a caudal vertebra on the basis of the articulation of haemapophyses (i.e., chevron bones) and transverse processes. The large size difference between the rather tiny caudal vertebra UU PK 1011 and the large trunk vertebra MNHN.F.PIK 3715 described above, but also with the caudal vertebrae from Pikermi recently described by Villa et al. (2018) is indeed contrasting and could probably be

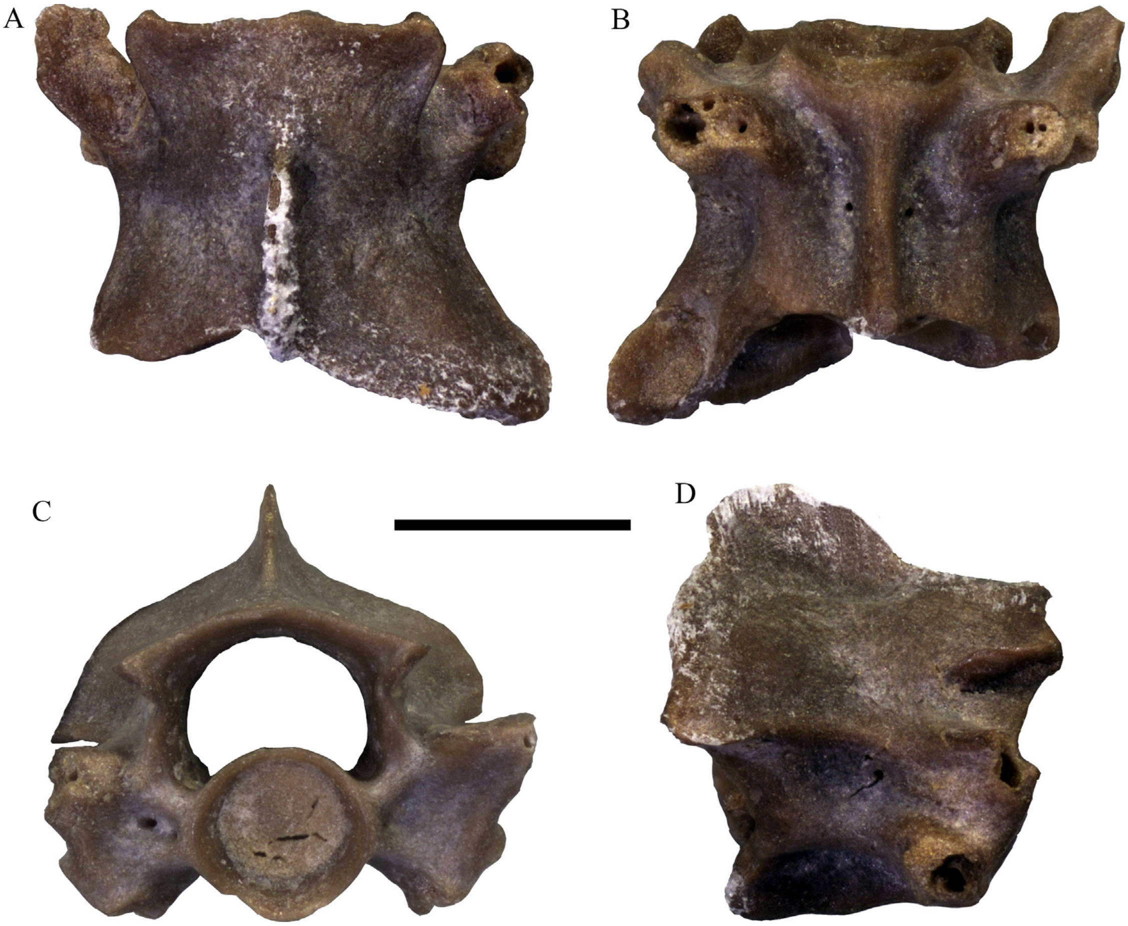

Fig. 5. ?Erycinae indet. from Pikermi (Chomateri). Trunk vertebra UU PK 1010 in dorsal (A), ventral (B), anterior (C), and right lateral (D) views. Scale bar = 1 mm.

Fig. 5. ?Ercynae indet. de Pikermi (Chomateri). Vertèbre de tronc UU PK 1010 en vues dorsale (A), ventrale (B), antérieure (C) et latérale droite (D). Barre d'échelle = 1 mm.

attributed either to an origination of the vertebra from a rather posteriormost caudal region or a much early ontogenetic stage of this specimen or perhaps a combination of both these cases. Posterior caudal vertebrae of varanids can be rather small (e.g., Villa et al., 2018:fig. 13), but still they are larger than UU PK 1011. Another difference among UU PK 1011 and other described fossil varanids (including the Pikermi large caudal vertebrae described by Villa et al. [2018]) is that in the new specimen the two prominent ridges in the ventral surface of the centrum are not parallel but are rather curved, closely approaching one another at mid-length on the centrum, whereas in most caudal vertebrae of varanids these are relatively straight and parallel (e.g., Augé and Guével, 2018; Villa et al., 2018). Nevertheless, there are cases in the literature that fossil varanid caudal vertebrae possess such curved and not parallel ridges, such as specimens from the late Pliocene of Kotlovina "middle/upper layer", Russia (Ratnikov, 2002:fig. 27). Moreover, the lateral expansions of the centrum are proportionally larger in UU PK 1011 in comparison with other published fossil varanid caudal vertebrae (e.g., Černanský et al., 2019:fig. 6G; Ivanov et al., 2018: fig. 6S), though there are still in the literature cases of caudal vertebrae with broad and large lateral expansions (e.g., Holmes et al., 2010: fig. 5H). All these observations render this referral of UU PK 1011 to varanids as tentative. It has to be noted that this specimen bears a general resemblance with the above described probable anguine caudal vertebra UU PK 1013, however, the former specimen lacks an autotomy plane. Furthermore, such an alternative taxonomic assignment of UU PK 1011 to anguines, which would fit more in terms of size and bear also relative resemblance to varanid caudal vertebrae, seems to be excluded, as the former are characterized by haemapophyses fused to the centrum (Georgalis et al., 2018; Smith and Gauthier, 2013).

As was discussed above in detail, MNHN.F.PIK 3715 is one of the first described fossil remains of monitor lizards and has a rather long taxonomic history. Its distinctiveness as a species of its own, as was suggested by Nopcsa (1908) who established *Varanus atticus* upon this material, cannot be supported on the basis of our current knowledge of vertebral anatomy and intraspecific variability of varanid lizards (Delfino et al., 2013; Georgalis et al., 2018; Ivanov et al., 2018; Villa et al., 2018). As it has been repeatedly suggested, conspecific affinities of this vertebra with the cranial-based species *V. marathonensis* are indeed highly probable, considering that they were found in the same locality and all are indicative of large size; furthermore, the caudal vertebrae of *V. marathonensis* from Pikermi described recently by Villa et al. (2018), resemble in certain aspects MNHN.F.PIK 3715, and the same applies for the trunk vertebrae of the same species recovered from Spanish localities (Villa et al., 2018). On the other hand, the high diversity observed among sympatric extant varanid species in areas such as Australia (e.g., D'Amore et al., 2018; Pianka et al., 2004), implies that high diversity of these lizards could also have existed in the Neogene of Europe. Accordingly, although conspecificity of the vertebra MNHN.F.PIK 3715 with *V. marathonensis* appears to be the most probable case, with no overlapping material this specimen can only be currently identified as *Varanus* sp. As such, *V. atticus* is a nomen dubium.

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
BOIDAE Gray, 1825
ERYCINAE Bonaparte, 1831
?Erycinae indet.
Fig. 5

Material. A trunk vertebra (UU PK 1010; Fig. 5).

Description. The vertebra is small and incomplete, missing part of the right prezygapophysis, part of the left postzygapophysis, the dorsal part of the neural spine, and the condyle (Fig. 5). In dorsal view (Fig. 5A), the zygosphene possesses a distinct median and two lateral lobes. The prezygapophyses extend anterolaterally, whereas anteriorly they surpass the level of the zygosphene. The prezygapophyseal articular facets (only the left one is even partially preserved) are elongated and relatively thin. The neural spine is thin and its base commences well behind the zygosphene. The postzygapophyses extend laterally. In ventral view (Fig. 5B), the centrum is wide. A prominent haemal keel runs along the midline. Two relatively large subcentral foramina are present, at around mid-length on the centrum, one at each side of the haemal keel. The postzygapophyseal articular facets are relatively large and oval-shaped. The paradiapophyses are eroded, but still it can be observed that they were not clearly divided into diapophyses and parapophyses. In anterior view (Fig. 5C), the zygosphene is rather thin and convex. The width of the zygosphene is much greater than that of the cotyle. The neural spine appears to be moderately high and the neural canal is large. The prezygapophyses are situated entirely dorsal to the cotyle. The cotyle is almost totally circular. One tiny paracotylar foramen is found on the left side of the cotyle, whereas from its right side, two paracotylar foramina are present, one of which is quite large and rather deep. The paradiapophyses extend slightly beyond the ventral level of the cotyle and are separated from it by deep lymphatic grooves. In posterior view, the neural arch is moderately vaulted. The condyle is not preserved. In lateral view (Fig. 5D), the vertebra appears to be taller than long. The neural spine is inclined posteriorly; it is damaged though and its shape and full extent cannot be evaluated. Lateral foramina are present below the level of the interzygapophyseal constriction. The subcentral ridges are convex.

Comments. The vertebra UU PK 1010 can be referred to "booid" snakes on the basis of its wide and short centrum, with the centrum length shorter than the neural arch width, the reduced prezygapophyseal accessory processes, and paradiapophyses not or only weakly divided into diapophyseal and parapophyseal portions (Georgalis and Scheyer, 2019; Rage, 1984; Szyndlar, 1991a; Szyndlar and Rage, 2003). However, "booids" usually lack paracotylar foramina (Kluge, 1991; Smith, 2013), but there are, nevertheless, certain forms that possess them, such as the Oligo-Miocene *Bavarioboa* Szyndlar and Schleich, 1993, and rarely also the extant *Eunectes* Wagler, 1830 (Hsiou and Albino, 2009; Szyndlar and Schleich, 1993; Szyndlar and Rage, 2003). On the other hand, it has to be noted that colubrids, which most usually possess paracotylar foramina, have also occasionally short centra during early ontogenetic stages (e.g., Szyndlar, 1984), but still, UU PK 1010 is too short to attest any colubrid affinities. An assignment to *Bavarioboa*, although would sound relatively consistent with a biogeographic rationale, does not seem so probable due to the rather small size (for "booid" standards) of the Pikermi vertebra. In fact, among "booids", such small size could be observed in erycines and ungaliophiines. However, the latter group is present only in Tropical America and have never been found with certainty in the European fossil record - whether the several supposed "tropidophiids" from the European Paleogene and early Neogene (e.g., Szyndlar and Rage, 2003) have potential affinities with ungaliophiines, requires a revision of the fossil forms. It seems that UU PK 1010 can be tentatively assigned to Erycinae, on the basis of its rather small size, although a fully secure determination would be only available if there were caudal vertebrae in the fossil sample, as the latter elements possess characteristic complex apophyses that are diagnostic for erycines (Hoffstetter and Rage, 1972; Rage, 1984; Szyndlar and Rage, 2003). On the basis of its overall shape and size, it could pertain to the extant genus *Eryx* Daudin, 1803a, and this could be further supported by a general biogeographic and stratigraphic rationale, as the genus is now present in the area and has been recovered from Pliocene and Quaternary localities in Greece and Anatolia (Rage and Sen, 1976; Szyndlar, 1991a). Nevertheless, the Pikermi specimen differs from the extant *Eryx jaculus* (Linnaeus, 1758), which still occurs in modern Greek herpetofauna, by its differently-shaped zygosphene, more circular cotyle, the prominent paracotylar foramina, and its more vaulted neural arch. *Eryx primitivus* Szyndlar and Schleich, 1994, from the Pliocene of Spain is known exclusively from caudal vertebrae, so it cannot be compared with the Greek form. The Pikermi vertebra can be further differentiated from the other two erycine genera that occur in the Neogene of Europe, i.e., *Albaneryx* Hoffstetter and Rage, 1972, and *Bransateryx* Hoffstetter and Rage, 1972, by certain aspects, such as its much thinner and convex zygosphene in anterior view and the shape and the inclination of the prezygapophyses. Note that a supposed erycine taxon of a third genus, *Ogmophis europaeus* Szyndlar in Młynarski et al., 1982, from the middle Miocene of Poland (Młynarski et al., 1982), was later reinterpreted to be instead an indeterminate “colubrine” (Szyndlar, 1991a). Paracotylar foramina that are present and distinct in the Pikermi vertebra appear to be usually absent or at least rather rare in erycines (Hoffstetter and Rage, 1972; Rage, 1984; Szyndlar, 1991a; Szyndlar and Schleich, 1994; pers. observ.). However, they have still been, even though rarely, identified in the fossil record, e.g., in a referred caudal vertebra (IZANU 22-1090) of *Albaneryx volynicus* Zerova, 1989, from the Miocene of Ukraine (see Zerova, 1989:fig. 8), the paratype anterior caudal vertebra of *Bransateryx vireti* Hoffstetter and Rage, 1972, from the late Oligocene of France (see Hoffstetter and Rage, 1972: fig. 7D), referred caudal vertebrae of *Bransateryx vireti* from the early Oligocene of Germany (see Szyndlar, 1994: fig. 3), and caudal vertebrae of an indeterminate species of *Eryx* from the middle Miocene of Hungary (see Venczel and Hír, 2015: fig. 9), whereas as far as it concerns the precloacal region, paracotylar foramina have been observed in an indeterminate erycine from the late Miocene (MN 11) of Baccinello V0, Italy (see Cirilli et al., 2016:fig. 4P). Indeed, the latter Italian specimen resembles at a certain point the Pikermi one, sharing, besides the distinct paracotylar foramina, also a similar, rather thin and convex zygosphene in anterior view and a relatively vaulted neural arch. In any case, the presence or absence of paracotylar foramina in “booids” can indeed be variable and the taxonomic utility of this character has been questioned (see Rage, 2001, for a discussion). I consider that the preservation of the single known vertebra does not permit a more precise determination and select to tentatively refer this specimen as?Erycinae indet., although a potential allocation to some other tiny “booid” lineage cannot be excluded with certainty.

The absence of haemapophyses, pleurapophyses, lymphapophyses, and any of the “bizarre” structures that characterize the caudal vertebrae of erycines, along with its absolute size, denote that the vertebra UU PK 1010 originates from the precloacal region. Furthermore, the absence of a hypapophysis and of a wide haemal keel preclude an identification of the specimen as an anterior trunk (i.e., cervical) and posterior trunk vertebra respectively. On the basis of its relatively sharp haemal keel, the relative vaulted neural arch, and the deep lymphatic grooves around the haemal keel separating the paradiapophyses from the cotyle, I would conclude that this vertebra originates from somewhere from the mid-trunk or posterior mid-trunk region of the vertebral column.

CAENOPHIDIA Hoffstetter, 1939
COLUBRIDAE Oppel, 1811 (sensu Rage, 1984)
Colubridae indet.
Fig. 6

Material. Three caudal vertebrae (UU PK 1007–UU PK 1009; Fig. 6).

Description and comments. All three vertebrae are incomplete (Fig. 6). UU PK 1007 lacks most of the right haemapophysis, most of the cotyle and the zygosphene, and a large portion of the prezygapophyses (Fig. 6A–C). Its neural arch is moderately vaulted in posterior view. The pleurapophyses extend ventrolaterally in anterior view. A distinct posterior median notch of the neural spine is present in dorsal view. The neural canal is rather large. The condyle is elliptical.

UU PIK 1008 lacks the zygosphene, part of the cotyle, part of the right pleurapophysis, a great portion of both prezygapophyses, most of the neural spine, the left postzygapophysis, while both haemapophyses are broken off close to their bases. The centrum is much elongated. A large subcentral foramen pierces the centrum on the anterior right side of the right haemapophysis. The condyle is relatively small. The subcentral ridges are convex in lateral view.

UU PK 1009 lacks most of the neural spine, whereas both haemapophyses are broken off close to their bases (Fig. 6D–F). The vertebra is elongated. The zygosphene possesses a distinct median and two lateral lobes in dorsal view. The prezygapophyses are directed more anteriorly than laterally, with the prezygapophyseal articular facets being relatively small and elongated. The neural spine is thin in dorsal view, with its base commencing well behind the zygosphene. The interzygapophyseal ridges are almost straight in lateral view. Large lateral foramina are present. The pleurapophyses extend ventrolaterally. Large subcentral foramina are present on both sides of the haemapophyses. The postzygapophyseal articular facets are oval-shaped.

All three vertebrae can be referred to Colubridae on the basis of their elongated centrum and their much lightly built structure (Georgalis et al., 2017a; Rage, 1984; Szyndlar, 1991a). All three vertebrae can be identified as caudal vertebrae on the basis of the presence of pleurapophyses and haemapophyses. The third of them (i.e., UU PK 1009) is most probably a posterior caudal vertebra. Caudal vertebrae of colubrids usually do not permit a more precise taxonomic determination, considering that the main distinguishment of the colubrid “subgroups” “colubrines” and natricines is principally conducted via the presence or not of a hypapophysis in the mid- and posterior trunk vertebrae (Georgalis et al., 2017a; Rage, 1984; Szyndlar, 1984, 1991a, 1991b). As such, all three specimens can only be identified as indeterminate colubrids, however, how many species they represent is unknown.

Squamata indet.
Fig. 7

Material. A trunk vertebra (UU PK 1006; Fig. 7); a tooth bearing bone (UU PK 1003).

Description and comments. UU PK 1006 is by far the largest squamate remain from the Chomateri site. It is a rather fragmentary and incomplete vertebra, missing most of the dorsal and anterior parts (Fig. 7). There are remains of what appears to have been either a hypapophysis or an articular surface for an intercentrum. The condyle is rather large, being slightly elliptical in posterior view. A small subcentral foramen is present at around the mid-height of the ventral surface of the vertebral centrum. A proper taxonomic allocation of this specimen is hindered by the fact that it cannot be recognized whether that structure in its ventral surface is what remains from a hypapophysis or an articular surface for an intercentrum. If this structure

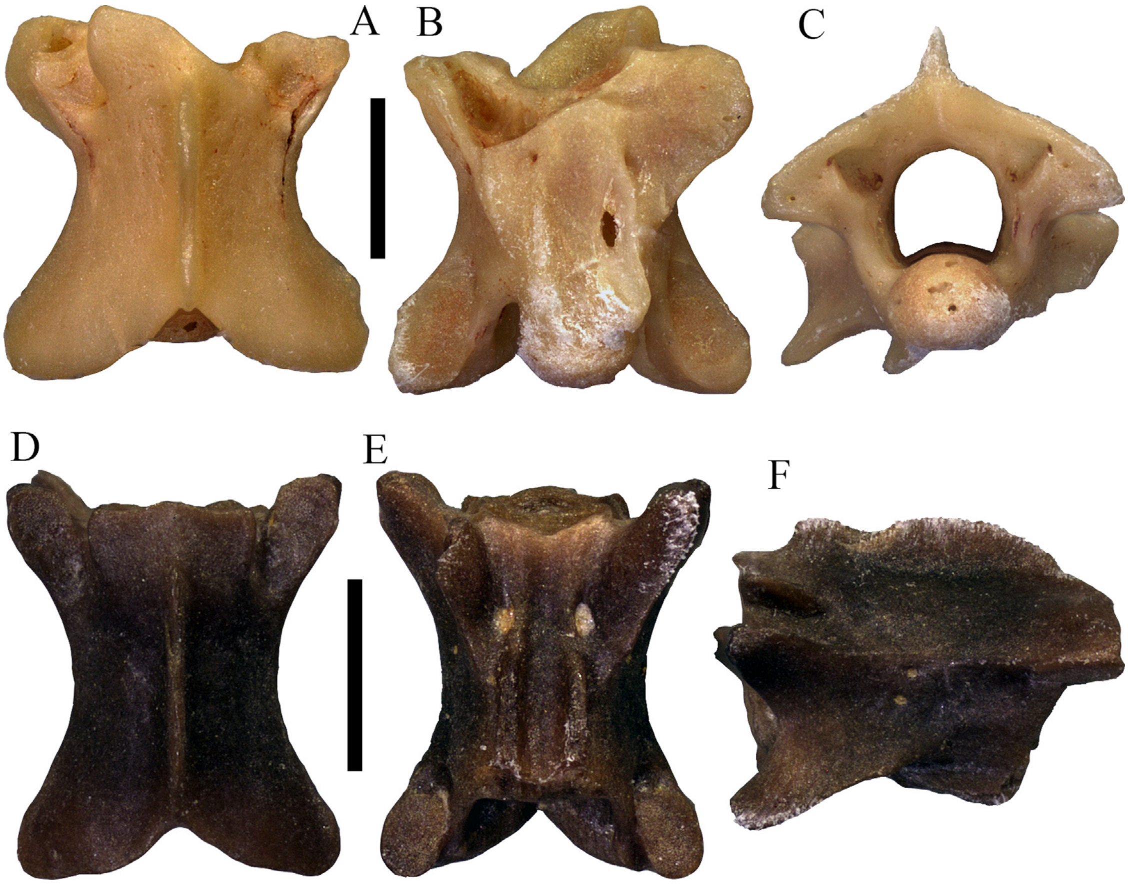

Fig. 6. Colubridae indet. from Pikermi (Chomateri). A–C. Caudal vertebra UU PK 1007 in dorsal (A), ventral (B), and posterior (C) views. D–F. Caudal vertebra UU PK 1009 in dorsal (D), ventral (E), and left lateral (F) views. Scale bars = 1 mm.

Fig. 6. Colubridae indet. de Pikermi (Chomateri). (A–C) Vertèbre caudale UU PK 1007 en vues dorsale (A), ventrale (B) et postérieure (C). (D–F) Vertèbre caudale UU PK 1009 en vues dorsale (D), ventrale (E) et latérale gauche (F). Barres d'échelle = 1 mm.

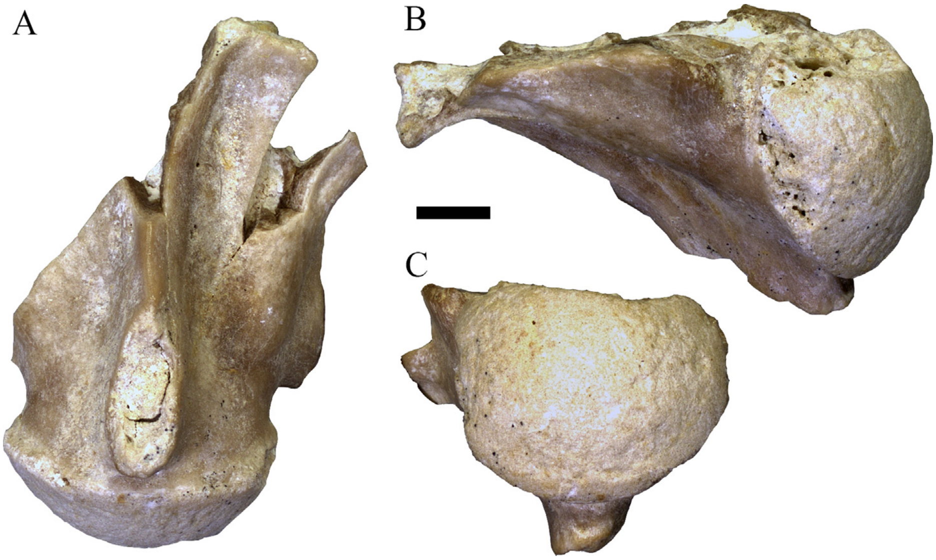

Fig. 7. Indeterminate squamate from Pikermi (Chomateri). Trunk vertebra UU PK 1006 in ventral (A), left lateral (B), and posterior (C) views.

Fig. 7. Squamate indéterminé de Pikermi (Chomateri). Vertèbre de tronc UU PK 1006 en vues ventrale (A), latérale gauche (B) et postérieure (C).

is a hypapophysis, such element is characteristic of the majority of natricines, elapids, and viperids, whereas "colubrines" and psammophiids also possess this structure in their anterior trunk (i.e., cervical) vertebrae (Georgalis et al., 2016a, 2016b, 2017a, 2018, 2019, in press; Holman, 2000; Ikeda, 2007; Ivanov, 2000; Rage, 1984; Smith, 2013; Szyndlar, 1984, 1988, 1991a, 1991b, 2005; Szyndlar and Rage, 1999). In that case, this specimen could pertain to some large indeterminate caenophidian. If, however, this structure represents a remnant of an articular surface for an intercentrum, this would hint for an identification of this specimen as a cervical vertebra of *Varanus*, a taxonomic allocation that is further supported by its large size and the distinct precondylar constriction.

The tooth bearing bone is incomplete, bearing five partially preserved or fragmentary teeth. One interesting feature is the rather different orientation of the three first teeth, the crown of which is directed rather anteriorly, whereas the rest have their crowns facing posteriorly. The teeth are pleurodont. A rather large foramen pierces the labial surface of the bone, which is otherwise almost totally smooth. Not a lot can be said about this specimen, other than it represents an indeterminate lizard, most probably a lacertid.

6. Discussion

Although known since the 1860's, the squamates from the classical locality of Pikermi have been rather scarce and their whole taxonomic spectrum was confined to the genus *Varanus* (Gaudry, 1862a, 1862b, 1862–1867; Villa et al., 2018; Weithofer, 1888). Nevertheless, this scarce but important varanid material formed the basis of the establishment of two species of fossil monitor lizards, *V. marathonensis* and *V. atticus* (Nopcsa, 1908; Weithofer, 1888). The former especially has played a pivotal role into our understanding of the evolution, systematics, and palaeobiogeography of the genus *Varanus* in Europe (Delfino et al., 2013; Estes, 1983; Fejérváry, 1918, 1935; Georgalis et al., 2017b, 2018; Ivanov et al., 2018; Molnar, 2004; Villa et al., 2018). Moreover, the holotype of *V. atticus*, i.e., Gaudry's famous vertebra MNHN.F.PIK 3715, was the first varanid fossil ever discovered in Europe and the second one worldwide and is thus of historical importance; the detailed description and photographs are provided for the first time and will enable more direct comparisons with other varanid vertebral finds. Nevertheless, this isolated find does not afford any direct comparison with the cranial-based sympatric *V. marathonensis*, as there is no overlapping material. However, it remains highly likely that the two forms are indeed synonyms, as it has been already variously suggested (Estes, 1983; Fejérváry, 1918, 1935; Georgalis et al., 2018; Molnar, 2004; Rage and Sen, 1976; Villa et al., 2018), an hypothesis supported also by the overall large size and the recovery of abundant cranial and vertebral material of *V. marathonensis* from the Miocene of Spain (Villa et al., 2018). Pending, however, the recovery of articulated and/or associated cranial material in the ongoing excavations of Pikermi, I prefer to be more reluctant and treat MNHN.F.PIK 3715 as pertaining to an indeterminate large *Varanus*.

The description of additional squamate remains from the Pikermi area enriches the palaeobiodiversity of this classical locality, with new lizard groups (i.e., lacertids and probable anguines) and snakes documented for the first time. Note that a find of "a small undetermined snake" from Pikermi that was previously simply mentioned by Woodward (1901:485), without any kind of figure or description or even the nature of the material, cannot be verified and I was further unable to locate such specimen in the collections of either AMPG or NHMUK. Unfortunately, the scarceness and fragmentary nature of the lizard and snake finds does not permit precise taxonomic determinations. Nevertheless, the new squamate records from Pikermi provide novel biogeographic occurrences for the respective groups. An interesting shared feature of almost all the new squamate remains from Pikermi is their extremely small size, probably denoting some collection biases or taphonomical factors. Lacertids are currently a dominant and rather species-rich reptile group in Europe, being highly diverse in the Greek mainland and islands (Arnold et al., 2007). The current identification of (at least one species of) lacertids in the Pikermi fossil assemblage expands the geographic distribution of Neogene lacertids in Greece, where they were so far previously known by indeterminate remains exclusively from the early Miocene (?MN 3) of Lapsarna, Lesvos Island (Vasileiadou et al., 2017), the early Miocene (MN 4) of Aliveri, Euboea Island (Georgalis et al., 2019), the early Miocene (MN 4) of Karydia, eastern Macedonia and Thrace (Georgalis et al., 2019), the late Miocene (MN 13) of Ano Metochi, Central Macedonia (Georgalis et al., 2017a), and the late Miocene/early Pliocene (MN 13/14) of Maramena, Central Macedonia (Georgalis et al., in press; Richter, 1995). Anguines are among the most abundant fossil squamates from the Neogene of Greece, being already known from the early Miocene of Aliveri and Karydia (Georgalis et al., 2019), the late Miocene of Ravin de la Pluie, central Macedonia (Georgalis et al., 2018), Ano Metochi (Georgalis et al., 2017a), and the latest Miocene/earliest Pliocene of Maramena (Georgalis et al., in press; Richter, 1995), while the group has a prevailing presence in the extant herpetofauna of the country. Erycine snakes are currently represented in the Greek extant herpetofauna by the Javelin Sand Boa, *Eryx jaculus*. The description of a potential fossil erycine from Pikermi is of importance as it represents the oldest record of these snakes not only from Greece but from the whole eastern Mediterranean basin, where so far the oldest records were from the Pliocene of Rhodes Island and Central Anatolia (Rage and Sen, 1976; Szyndlar, 1991a). In Greece specifically, fossil erycines had been described from the early Pliocene of Maritsa, Rhodes Island (Szyndlar, 1991a), the middle Pleistocene of Latomi, Chios Island (Schneider, 1975), and the (indeterminate) late Quaternary of Pili B, Kos Island (Szyndlar, 1991a), whereas a mention (without a figure or description) about an occurrence from the early Pliocene of Spilia-4, central Macedonia also exists (Szyndlar, 1991a). The rest of the snakes do not afford a lot of room for taxonomic conclusions; nevertheless, the geographic and stratigraphic distribution of fossil colubrids in Greece, the dominant and most species-rich extant serpent clade in Europe, is now expanded with these fragmentary colubrid caudal vertebrae from Pikermi.

7. Conclusions

The squamate fauna from the late Miocene of the Pikermi area, near Athens, Greece, is described. One of the described specimens, a large dorsal varanid vertebra, recovered from the classical site of Pikermi during the 19th century, represents the first discovery of a varanid fossil from Europe. Despite its importance, this specimen, originally described by Gaudry (1862a, 1862b, 1862–1867) has been only inadequately figured in the literature by lithographs and sketches, and these still only depict the specimen in ventral and lateral views. I herein provided photographs of this specimen for the first time, documenting all views, followed by a detailed description. Furthermore, I described additional squamate remains from the site of Chomateri in the Pikermi area. This new material denotes the presence in Pikermi of lacertids, probable anguines, potential erycines, and colubrids, whereas also other indeterminate squamates supplement the herpetofauna of the locality. Although the new material is relatively fragmentary and of low diversity, it nevertheless documents for the first time the presence of squamates other than *Varanus* and increases our knowledge of the herpetofauna of this classical locality and the Pikermian biome.

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