

Late Paleogene herpetofaunas from the crossroads between two continents – new amphibian and reptile remains from the Oligocene of southern Balkans and Anatolia

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ABSTRACT

We describe here new amphibian and reptile remains from three Oligocene localities of Turkey. Two of the localities (Kavakdere and Kocayarma) are situated in southeastern Europe and the other one (Kargi 2) in Anatolia, both areas where Oligocene herpetofauna is practically almost unknown. The material consists of albanerpetontids, pelobatid anurans, turtles, crocodylians, lacertids, scinciformatans, anguines, and “tropidophiids”. Albanerpetontids are for the first time identified in southeastern Europe, with the material being reminiscent of the younger species *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976; the material potentially represents the oldest record of that species. Pelobatids, scinciformatans, and “tropidophiids” represent the oldest occurrences of these clades in the northeastern Mediterranean. The anguine genus *Ophisaurus* Daudin, 1803 is identified for the first time in the Paleogene of Eastern Europe. The “tropidophiids” are referred to two genera, *Falseryx* Szyndlar & Rage, 2003 and tentatively also to *Platyspondylia* Rage, 1974, with the latter having been so far exclusively known from western and central Europe. The role of a potential southern dispersal route of taxa among Asia and Europe, involving the area of southern Balkans and Anatolia, similarly to what has been recently demonstrated for mammals, is highlighted also for amphibians and reptiles.

KEY WORDS

Albanerpetonidae,
Anura,
Testudines,
Crocodylia,
Squamata,
Oligocene,
biogeography.

RÉSUMÉ

Herpétofaunes du Paléogène supérieur au carrefour entre deux continents – nouveaux restes d’amphibiens et de reptiles de l’Oligocène des Balkans du Sud et d’Anatolie.

Nous décrivons ici de nouveaux restes d’amphibiens et de reptiles de trois localités oligocènes en Turquie. Deux des localités (Kavakdere et Kocayarma) sont situées dans le Sud-Est de l’Europe et l’autre (Kargi 2) en Anatolie, deux régions où l’herpétofaune Oligocène est pratiquement inconnue. Le matériel se compose d’albanerpétontidés, d’anoures pélobatidés, de tortues, de crocodyliens, de lacertidés, de scinciformatans, d’anguinés et de « tropidophiidés ». Les albanerpétontidés sont pour la première fois identifiés dans le Sud-Est de l’Europe, le matériel rappelant l’espèce plus jeune *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976 ; le matériel représente potentiellement le plus ancien enregistrement de cette espèce. Les pélobatidés, les scinciformatans et les « tropidophiidés » représentent les occurrences les plus anciennes de ces clades au nord-est de la Méditerranée. Le genre d’anguiné *Ophisaurus* Daudin, 1803 est identifié pour la première fois durant le Paléogène en Europe de l’Est. Les « tropidophiidés » se réfèrent à deux genres, *Falseryx* Szyndlar & Rage, 2003 et provisoirement aussi à *Platyspondylia* Rage, 1974, ce dernier étant jusqu’à présent exclusivement connu d’Europe occidentale et centrale. Le rôle d’une voie de dispersion potentielle vers le sud des taxons entre l’Asie et l’Europe, impliquant la région des Balkans méridionaux et de l’Anatolie, de manière similaire à ce qui a été récemment démontré pour les mammifères, est également mis en évidence pour les amphibiens et les reptiles.

MOTS CLÉS
Albanerpetonidae,
Anura,
Testudines,
Crocodylia,
Squamata,
Oligocène,
biogéographie.

INTRODUCTION

The Oligocene represents a major gap in our knowledge of Eurasian herpetofaunas (Rage 2013; Čerňanský *et al.* 2016). In fact, Oligocene herpetofaunas from Europe are less abundant and by far less adequately documented than preceding Eocene and succeeding Miocene ones from the continent. Among Oligocene amphibians and reptiles from Europe, turtles are relatively more adequately known, whereas crocodylians are scarcely documented, with most occurrences being represented by incomplete remains (Szalai 1934; Bergounioux 1935, 1936; de Broin 1977; Schleich & Groessens-Van Dyck 1988; Hervet 2004; Piras & Buscalioni 2006; Böhme 2008). A notable exception to this rule is the fossil “Lagerstätte” locality of Monteviale in Italy, where both turtles and crocodylians are occasionally represented by exceptional and complete specimens (Negri 1892; Pandolfi *et al.* 2017; Macaluso *et al.* 2019). Amphibians and squamates are the least adequately known herpetofaunal elements, as there are only relatively few Oligocene European localities that yielded such remains, all originating from Belgium, France, The United Kingdom, Germany, Italy, and the Czech Republic (Lydekker 1888; Hecht & Hoffstetter 1962; Hoffstetter & Rage 1972; Rage 1974, 1988b, 2013; Böhme *et al.* 1982; Augé 1992, 2005; Roček 1994; Szyndlar 1994; Augé & Rage 1995; Astruc *et al.* 2003; Szyndlar & Rage 2003; Böhme 2008; Szyndlar *et al.* 2008; Augé & Hervet 2009; Augé & Pouit 2012; Čerňanský & Augé 2012, 2013; Vianey-Liaud *et al.* 2014; Rage & Augé 2015; Čerňanský *et al.* 2016, 2017a; Pandolfi *et al.* 2017; Georgalis *et al.* 2021), while they have only recently been described from the eastern parts of the continent, i.e., Romania (Venczel *et al.* 2013; Venczel & Codrea 2018) and the European part of Turkey (Čerňanský *et al.* 2017b). The enigmatic clade of

choristoderans is also present in the Oligocene of France and Germany, represented solely by the genus *Lazarussuchus* Hecht, 1992 (Hecht 1992; Böhme 2008).

The situation is even worse in Asia, where Oligocene herpetofaunas are even more inadequately known than their contemporaries from Europe (Čerňanský 2019; Čerňanský & Augé 2019). Similarly to the case of Europe, Oligocene herpetofaunas from Asia are also less abundant and less well documented than preceding Eocene and succeeding Miocene ones from the continent. Oligocene turtles and crocodylians from Asia are also much better represented, owing to important discoveries across the continent (e.g. Gilmore 1931; Yeh 1963; Chkhikvadze 1973; Claude *et al.* 2007; Hasegawa *et al.* 2007; Böhme *et al.* 2011; Vitek & Danilov 2015; Martin *et al.* 2019). Amphibians and squamates from the Oligocene of Asia are rather scarcely known (Noble 1924; Gilmore 1943; Roček 1982; Böhme 2007; Alifanov 2012; Szyndlar & Hoşgör 2012; Čerňanský 2019; Čerňanský & Augé 2019).

The southern Balkans and Anatolia are geographically situated at the edges of southeastern Europe with southwestern Asia. As such, they are located right at the “crossroads” of various dispersal routes of vertebrates from Asia to Europe (and vice versa). Indeed, the role of Anatolia and southern Balkans for the dispersal of Paleogene Asian taxa to Europe has been recently demonstrated on the basis of mammal finds from the area (e.g. Métais & Sen 2017; Mennecart *et al.* 2018a, 2018b). However, Oligocene herpetofaunas from the southern Balkans have been only barely documented, with our current knowledge confined solely to brief descriptions of fragmentary turtles and crocodylians (Lebküchner 1974; Schleich 1994), and more recently also anguine lizards (Čerňanský *et al.* 2017b). Coeval finds from Anatolia are also poorly known, represented by few remains of amphibians, crocodylians, lizards, and snakes

(Szyndlar & Hoşgör 2012; Čerňanský *et al.* 2017b; Vasilyan *et al.* 2019). This inadequate knowledge substantially hinders our understanding of the evolution, taxonomic composition and diversity, biogeography and origins of the late Paleogene herpetofaunas from the area. In an attempt to alter this situation, we herein describe new amphibian and reptile remains from Kavakdere and Kocayarma, two Oligocene localities in the European part of Turkey, as well as crocodylian and snake remains from the latest Oligocene locality of Kargi 2 in Anatolia. The palaeobiogeography and potential dispersal patterns of Oligocene amphibians and reptiles from Asia to Europe and vice versa is discussed.

MATERIAL AND METHODS

All material described herein is permanently curated at the collections of EUNMH PV. Comparative material of extant amphibians and reptiles was studied in EUNMH PV, HNHN, MDHC, MNCN, NHMUK, NHMW, PIMUZ, PRIF UK, UWŕ, and ZZSiD. Specimens were photographed under a Leica M125 binocular microscope with axially mounted DFC500 camera (LAS software [Leica Application Suite] v.4.1.0 [build 1264]). Several specimens were imaged under a scanning electron microscope (SEM; FEI Inspect F50) at the Slovak Academy of Sciences in Banská Bystrica (Slovakia). Few other specimens were imaged under SEM taken uncoated under low-vacuum conditions using a JEOL JSM-6390LV scanning electron microscope at the Aristotle University of Thessaloniki (Greece).

INSTITUTIONAL ABBREVIATIONS

EUNMH PV	Natural History Museum of Ege University, Izmir;
HNHN	Hungarian Natural History Museum, Budapest;
MDHC	Massimo Delfino Herpetological Collection, University of Torino, Torino;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MP	Mammifères Paleogène (standard level zone);
NHMUK	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Vienna, Austria;
PIMUZ	Palaeontological Institute and Museum, University of Zurich, Zurich;
PRIF UK	Faculty of Natural Sciences, Comenius University, Bratislava;
UWŕ	University of Wrocław, Wrocław;
ZZSiD	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.

GEOLOGICAL AND ECOLOGICAL SETTINGS

The locality of Kavakdere is situated 7 km northwest of the city of Edirne-Keşan, 1.5 km west of Çanakkale-Edirne main road (Fig. 1). The fossiliferous bed is exposed in the west bank of the Kavak valley, 30 m southwest of a water pond. The fossiliferous bed is an about 1 m thick greenish-brownish silt-stone level, rich in gastropod fragments as well as fragmentary remains of large mammals, underlain by a kaolinitised volcanic tuff (Ünay 1989; Mayda 2017). The age of Kavakdere is considered to be at around the boundary between early and

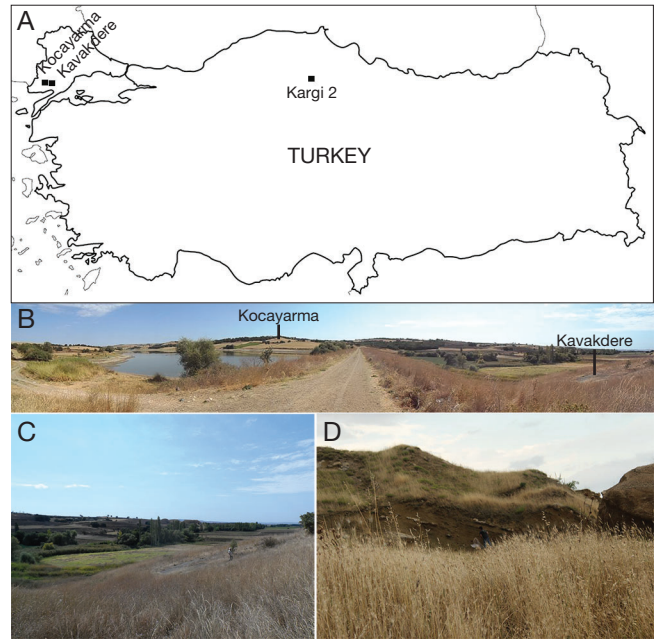


FIG. 1. — **A**, Map of Turkey, showing the localities Kocayarma, Kavakdere, and Kargi 2; **B**, panoramic photograph of the area of the nearby localities of Kavakdere and Kocayarma, showing their precise positions; **C**, photograph of the locality of Kavakdere; **D**, photograph of the locality of Kocayarma.

late Oligocene (MP 25; Rupelian-Chattian boundary). The associated mammal fauna of Kavakdere comprises a diverse assemblage of rodents: the theridomyid *Suevosciurus fraasi* (Major, 1873), the cricetids *Paracricetodon dehmi* Hrubesh, 1957, *Triakymys saratji* Ünay, 1989, *Pseudocricetodon orientalis* (Ünay, 1989), *Pseudocricetodon philippi* Hugueney, 1971, and *Kerosinia variabilis* Ünay, 1989, the eomyid *Eomys* sp., the sciurids *Oligopetes* cf. *lophulus* and *Oligopetes* aff. *obtusius*, the glirids *Glis* aff. *guerbiezi* and *Bransatoglis sjeni* Ünay, 1989, the castorid *Asteneofiber* sp. and an indeterminate ctenodactyloid (Ünay 1989). On the basis of its mammal fauna, the Kavakdere palaeoenvironment represents a forested habitat.

Kocayarma (also known as Kocayarmalar) was situated about 100 m west of the Çanakkale-Edirne main road, 1.4 km to the east of the Kavakdere locality (Fig. 1). The fossiliferous bed is an one meter thick dark greenish-brownish gastropod rich clay, which was overlain by Kocayarma conglomerates. Unfortunately, the original locality and its sampled levels were destroyed due to the construction works carried out around the area in the past years. According to Ünay (1989), Kavakdere is stratigraphically about 120 m below Kocayarma in the same section. The age of Kocayarma is considered to pertain to the late Oligocene (MP 26/27; Chattian). The Kocayarma mammal fauna includes also a rich assemblage of rodents: the pseudosciurid *Suevosciurus ehingensis* Dehm, 1937, the cricetids *Paracricetodon dehmi*, *Pseudocricetodon orientalis*, *P. philippi*, *Lignitella suemengeni*, *Edirnella sinani*, *Eucricetodon* sp., and *Heterocricetodon* cf. *schlosseri*, the eomyids *Eomys fahlbuschi* and *Eomys* sp., the sciurids *Blackia* sp. and *Miopetaurista* sp., and the glirids *Glis guerbiezi* and *Bransatoglis sjeni* (Ünay & Bruijn 1987; Ünay 1989; Freudenthal *et al.* 1994; van de Weerd *et al.* 2018). Contrary to Kavakdere, Kocayarma had yielded also

large mammals; besides the existence of *Elomeryx* Marsh, 1894 (a common Oligocene anthracother), the fauna has also revealed a small palaeochoerid and *Pachycynodon* sp., both representing the oldest suoid and carnivoran respectively from Turkey (Mayda 2017). The presence of eomyids and flying squirrels, which are considered to have been forest dwellers, indicate a wet and forested biotope. The presence of large cricetids and the scarcity of *Eucricetodon* Thaler, 1966 and *Suevosciurus* Dehm, 1937 also supports this scenario (Ünay 1989).

A quick clarification about a previous misconception of the ages of Kavakdere and Kocayarma is needed here: Čerňanský *et al.* (2017b) erroneously stated opposite ages for Kavakdere and Kocayarma. As such, they considered that Kocayarma is older (MP 25), whereas Kavakdere is younger (MP 26/27). We clarify this issue here, firmly stating that Kavakdere is older (MP 25) than Kocayarma (MP 26/27).

The three fossiliferous layers in Kargi lignite mine, which was discovered by Engin Ünay (General Directorate of Mineral Research and Exploration of Turkey [MTA]) in 1994, is situated 6.5 km northeast of the town of Dodurga (Fig. 1). Among these fossiliferous layers, Kargi 2 is considered to be of latest Oligocene (MP 30; latest Chattian) age. The mammal fauna of Kargi 2 comprises of the erinaceids *Galerix saratji* van den Hoek Ostende, 1992 and *Neurogymnurus* sp., the heterosoricid *Dinosorex anatolicus* van den Hoek Ostende, 1995, the soricid *Oligosorex reumeri* van den Hoek Ostende, 2001, the talpids *Desmanodon ziegleri* van den Hoek Ostende, 1997 and *Geotrypus haramiensis* van den Hoek Ostende, 2001, the cricetids *Cricetodon versteegi* de Bruijn, Fahlbusch, Saraç & Ünay, 1993, *Deperetomys anatolicus* de Bruijn, Fahlbusch, Saraç & Ünay, 1993, *Enginia djanpolati* de Bruijn & von Koenigswald, 1994, *Eumyarion* sp., *Melissiodon* sp., *Meteomys alpani* de Bruijn, Ünay, van den Hoek Ostende & Saraç, 1992, *Muhsinia* sp., and *Spanocricetodon sinuosus* Theocharopoulos, 2000, and the zapodid *Heterosminthus firmus* Zazhigin & Lopatin, 2000. The absence of species inhabiting dry environments supports the wet, near-shore conditions at Kargi 2 (van den Hoek Ostende 2001; Kakali 2013).

As for reptile finds, Kocayarma and Kavakdere have previously yielded so far only anguine osteoderms (Čerňanský *et al.* 2017b). From Kargi 2 so far there have been described frogs, crocodylians, and anguine lizards (Čerňanský *et al.* 2017b; Vasilyan *et al.* 2019).

SYSTEMATIC PALAEONTOLOGY

AMPHIBIA Linnaeus, 1758

Family ALBANERPETONTIDAE Fox & Naylor, 1982

Genus *Albanerpeton* Estes & Hoffstetter, 1976

Species *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976

Albanerpeton cf. *inexpectatum*
(Fig. 2)

MATERIAL. — **Turkey.** Kavakdere: a premaxilla (EUNMH PV 14053) and a left dentary (EUNMH PV 14057).

DESCRIPTION

Premaxilla

The premaxilla EUNMH PV 14053 is a robustly constructed, paired element (Fig. 2A, B); the left one is present in the available material (note that Gardner [1999a] reported that small sized premaxillae are paired, whereas larger are fused, suggesting its later fusion during ontogeny). The nasal process is broad, moderately high. The sculpture in the dorsal portion of the process (dorsal boss) exhibits a pustulate irregular ornamentation. Here, the process is slightly laterally constricted due to a presence of a lateral facet for the nasal. The ventrally located labial portion of the nasal process is rather smooth. This portion is pierced by external nutritive foramina (*sensu* Gardner 1999a) of various sizes (in overall, the foramina more or less decrease in size dorsally). The large wedge-shaped facet for maxilla is developed on the labial side of the short maxillary process. The supradental shelf (*sensu* Rage & Augé 2010) is well-developed. The premaxilla bears seven tooth positions. However, only the first four teeth (counted from median plane) are in better condition. The internal portion of the nasal process base is pierced by a suprapalatal pit (*sensu* Gardner 2002). This pit is moderate in size, dorsolaterally bordered by internal strut. The suture with the right premaxilla is well visible in posterior aspect.

Dentary

The left dentary EUNMH PV 14057 is partially preserved (Fig. 2C-E). The otherwise smooth labial surface of the preserved portion is pierced by two labial foramina. In lingual aspect, the high dental crest supports 17 tooth position (12 teeth are still attached plus two anterior ones have preserved their ventral portions). The Meckel's groove is closed, only partly exposed in the posterior section of the dentary. The subdental shelf (*sensu* Rage & Augé 2010) is straight, well medially expanded especially in the anterior section. However, the anterior end of the dentary is broken off and missing. The posterior portion is damaged, but the posterodorsal process (called “unnamed process” by Gardner 2002) is preserved directly behind the tooth row, being short, blunt and low (not distinctly dorsally elevated). The rest of the posterior region is broken off and missing.

Dentition

The tooth implantation is pleurodont. The teeth are conical, not pedicellate. The tooth crowns are smooth and do not contrast with tooth necks. The dentary teeth gradually increase in size anteriorly. The tooth crowns, when are preserved, show some degree of tricuspidity (angulus mesialis and distalis are present). The sizes of inter-dental gaps are roughly half those of the tooth bases. The tooth bases lack resorption pits.

COMMENTS

The morphology of both Kavakdere specimens fits well with albanerpetontids, a clade of middle Jurassic to early Pleistocene extinct lissamphibians, which were chameleon-like ballistic feeders (see Daza *et al.* 2020). They have a mainly documented Laurasian distribution (Gardner 1999a, 1999b, 2002; Venczel & Gardner 2005; Delfino & Sala 2007; Matsumoto & Evans

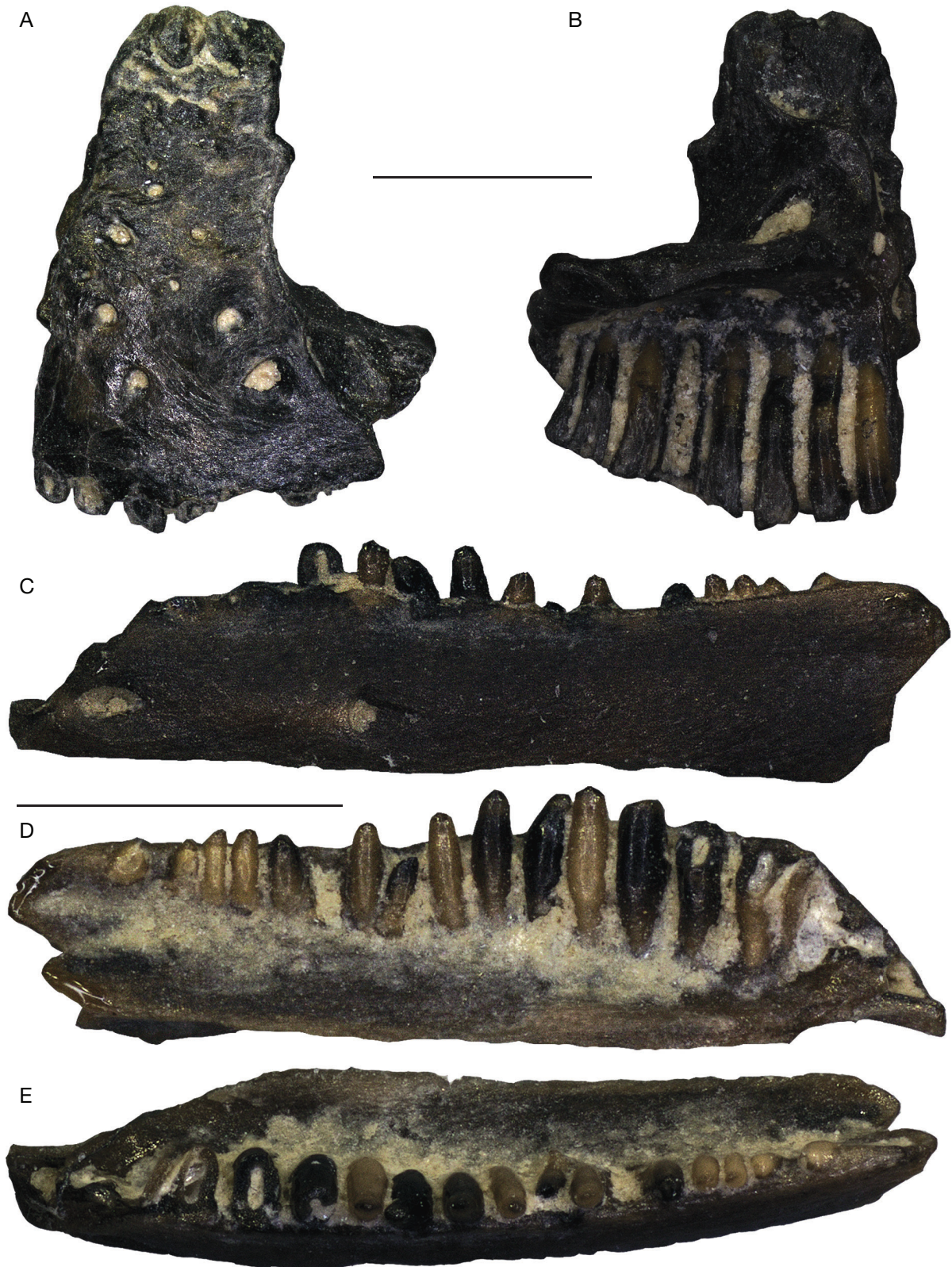


FIG. 2. — *Albanerpeton* cf. *inexpectatum* from Kavakdere: **A, B**, premaxilla EUNMH PV 14053 in labial (**A**) and lingual (**B**) views; **C-E**, left dentary EUNMH PV 14057 in labial (**C**), lingual (**D**), and dorsal (**E**) views. Scale bars: 1 mm.

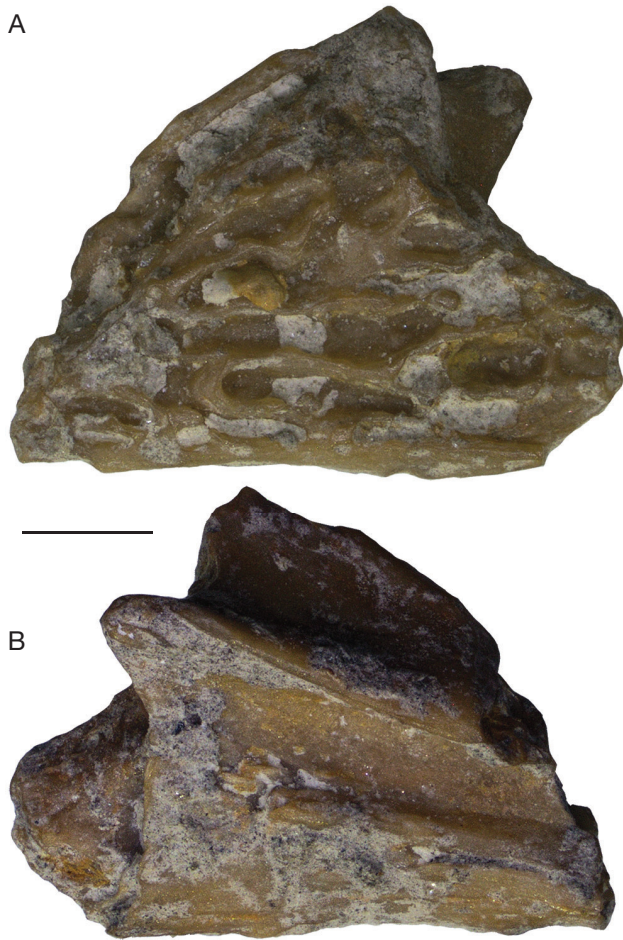


FIG. 3. — ?*Eopelobates* sp. from Kocayarma. Left maxilla EUNMH PV 14065 in labial (A) and lingual (B) views. Scale bar: 1 mm.

2018; Villa *et al.* 2018), although it is noted that they are also reported from Morocco as well (Gardner *et al.* 2003) and finds from the Cretaceous Myanmar amber might also point towards a Gondwanan distribution (see Daza *et al.* 2020). The new material described herein resembles more particularly the genus *Albanerpeton*, found in North America and Europe (however, see Discussion). The Kavakdere material represents the first evidence of this extinct clade in Turkey as well as its easternmost European occurrence.

More precisely, our material shares two diagnostic characters with the type species of the genus, *Albanerpeton inexpectatum* (see Gardner 1999a): 1) a presence of the pustulate ornamentation of the dorsal section of the premaxillary nasal process; and 2) the presence of a small, low posterodorsal process behind the tooth row.

The Pliocene *Albanerpeton pannonicus* Venczel & Gardner, 2005 differs from the new Kavakdere material in, e.g.: 1) nasal process of premaxilla short; 2) short dorsal boss of premaxilla on labial surface occupying about upper one third or less of the nasal process; 3) absence of the posterodorsal process behind the tooth row; and 4) having only weakly heterodont teeth in anterior half of the dentary regarding their size (see Venczel & Gardner 2005; Delfino & Sala 2007).



FIG. 4. — Testudines indet. from Kavakdere: A, shell fragment EUNMH PV 14088a; B, shell fragment EUNMH PV 14088b; C, shell fragment EUNMH PV 14088c; D, shell fragment EUNMH PV 14088d. Scale bar: 25 mm.

ANURA Fischer von Waldheim, 1813
Family PELOBATIDAE Bonaparte, 1850
Genus *Eopelobates* Parker, 1929

?*Eopelobates* sp.
(Fig. 3)

MATERIAL. — **Turkey.** Kocayarma: a fragment of a left maxilla (EUNMH PV 14065).

DESCRIPTION AND COMMENTS

The fragment of a left maxilla (EUNMH PV 14065) is small, with a maximum preserved length of 4.5 mm (Fig. 3). Its external surface is covered by an array of prominent, dense pits and ridges. This prominent sculpturing pattern of the isolated fragmentary maxilla EUNMH PV 14065, consisting of dense pit and ridges, that is integral part of the bone and not a secondary exostosis, is reminiscent of pelobatids (see figures in Roček *et al.* 2014; Blain *et al.* 2016). The pits are rather deep and anteroposteriorly elongated.

Among pelobatids, this sculpturing pattern with dense pits and ridges is more consistent with *Eopelobates*, a genus that has a broad distribution in the late Cretaceous and Paleogene of North America, the Paleogene and Neogene of Europe, and the Paleogene of Central Asia (Roček *et al.* 2014), while it has been recently described also from the earliest Miocene of Anatolia (Syromyatnikova *et al.* 2019a). Such sculpturing pattern is also present in Oligo-Miocene remains attributable to *Pelobates* Wagner, 1830 (Roček *et al.* 2014), however, on the other hand, more recent remains and extant forms of the latter genus are characterized by a rather pustular pattern with numerous isolated tubercles (Venczel 2004; Roček *et al.* 2014).

Anura indet.

MATERIAL. — **Turkey.** Kavakdere: a maxilla (EUNMH PV 14059).

DESCRIPTION AND COMMENTS

The element is rather incomplete, missing its whole posterior portion. In labial view, large portion of its surface is covered by sculpturing pattern, which consists either of elongated ridges or either large pits that penetrate it. Remains of tooth bases are visible on its lingual view. The specimen is too fragmentary to afford any more precise identification and is here treated only as an indeterminate anuran.

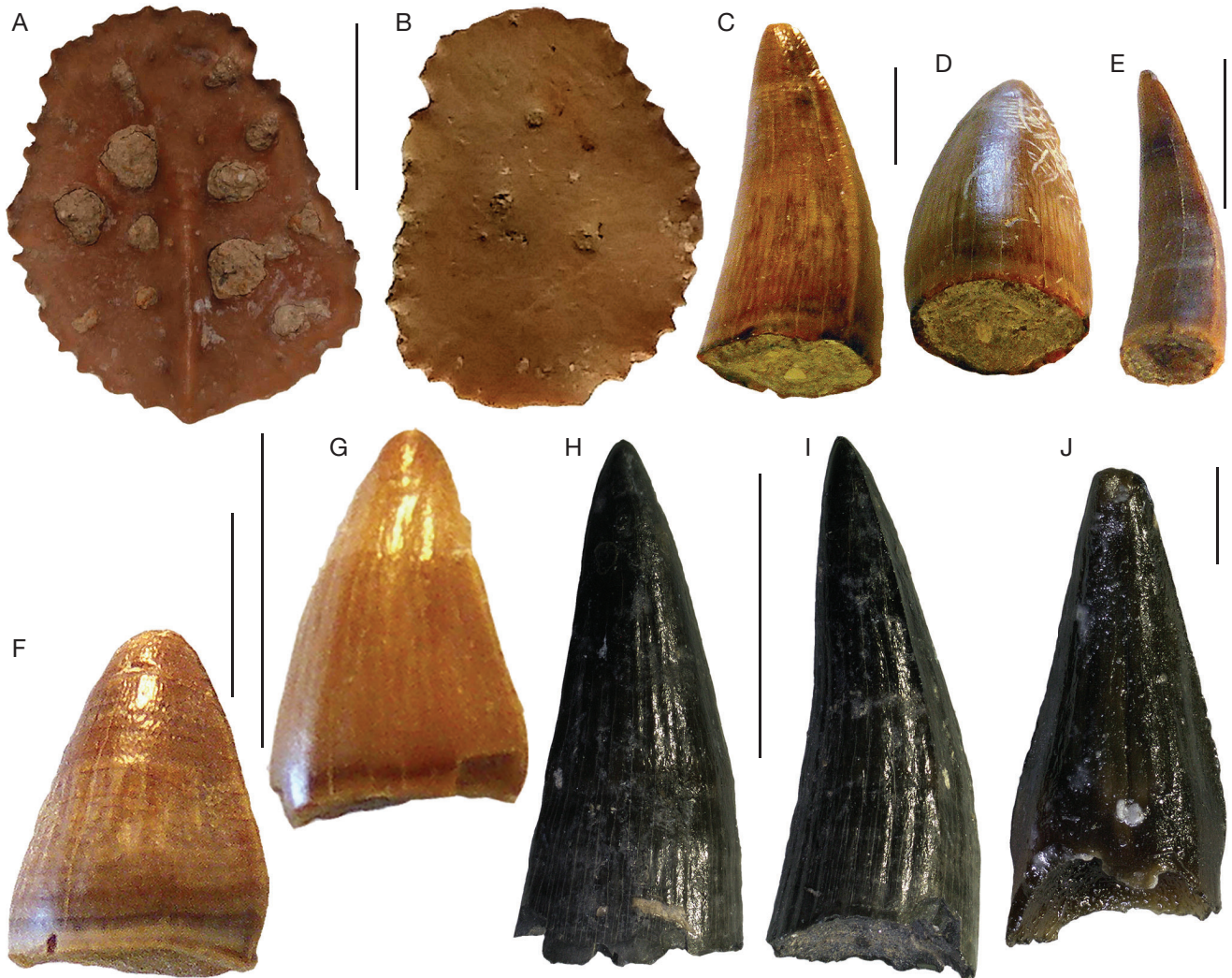


FIG. 5. — **A, B**, *Crocodylia* indet. from Kavakdere: osteoderm EUNMH PV 14073 in dorsal (**A**) and ventral (**B**) views. **C–G**, *Crocodylia* indet. from Kocayarma: **C, D**, tooth EUNMH PV 14087 in lingual (**C**) and ventrolingual (**D**) views; **E**, tooth EUNMH PV 14082 in mesial view; **F**, tooth EUNMH PV 14085 in lingual view; **G**, tooth EUNMH PV 14076 in labial view. **H–J**, *Crocodylia* indet. from Kargi 2: **H, I**, tooth EUNMH PV 14068 in labial (**H**) and mesial (**I**) views; **J**, tooth EUNMH PV 14069 in lingual view. Scale bars: A–I, 5 mm; J, 1 mm.

REPTILIA Laurenti, 1768
TESTUDINES Batsch, 1788

Testudines indet.
(Fig. 4)

MATERIAL. — **Turkey.** Kavakdere: several shell fragments and a limb fragment (EUNMH PV 14088).

DESCRIPTION AND COMMENTS

The material is too fragmentary to permit any kind of a more precise identification with turtles. This is further complicated by the fact that several turtle groups have been identified from the Oligocene of the area, such as testudinoids, chelydrids, and trionychids (Schleich 1994; Georgalis & Joyce 2017). Nevertheless, affinities with the latter group can be readily discarded owing to the absence of the characteristic sculpturing pattern that is present in the shell of that chelonian lineage (Georgalis & Joyce 2017).

CROCODYLIA Gmelin, 1789

Crocodylia indet.
(Fig. 5)

MATERIAL. — **Turkey.** Kavakdere: an osteoderm (EUNMH PV 14073). Kocayarma: 14 isolated teeth (EUNMH PV 14074–EUNMH PV 14087). Kargi 2: two teeth (EUNMH PV 14068 and EUNMH PV 14069).

DESCRIPTION

Osteoderm

The isolated osteoderm EUNMH PV 14073 is relatively large, with a maximum length of 12 mm (Fig. 5A, B). On its external surface, a prominent longitudinal ridge runs throughout large part of its midline. Large pits of irregular size punctuate its external surface, on both sides of the ridge. Small pits are also present on the internal surface of the specimen.

Teeth

All teeth are conical; some of them are relatively robust, while others are more slender (Fig. 5C-J). Their crown varies in pointness, being either pointed or apically blunt. A prominent mesiodistal serration is present in some teeth. These mesiodistal serrations separate the lingual and slightly concave surface from the labial, slightly convex one. Distinct elongated wrinkles are present in most teeth.

COMMENTS

Crocodylian teeth cannot afford a more precise taxonomic assignment (Georgalis *et al.* 2016, 2019a). The same applies for the single isolated osteoderm. On the absence of any diagnostic cranial remains, we therefore have to consider all this material as indeterminate crocodylians. Note also that crocodylian teeth from Kargi 2 have recently been mentioned by Vasilyan *et al.* (2019), however, they have not been figured.

SQUAMATA Oppel, 1811
LACERTIFORMATA Vidal & Hedges, 2005
Family LACERTIDAE Oppel, 1811

Lacertidae indet. (morphotype 1)
(Figs 6; 7)

MATERIAL. — **Turkey.** Kavakdere: a right maxilla (EUNMH PV 14052). Kocayarma: three maxillae (EUNMH PV 14061, EUNMH PV 14064, and EUNMH PV 14066) and a dentary (EUNMH PV 14063).

DESCRIPTION

Maxilla

The description is based on several specimens. Specimen EUNMH PV 14052 represents a fragment of a right maxilla (Fig. 6). It is robustly built. The labial surface of this portion is pierced by two supralabial foramina. The nasal process is broken off, only its base is present. The lingual side bears a broad and massive supradental shelf, which is slightly convex dorsally. Five tooth positions are preserved, where four teeth are still attached (Fig. 6C). The superior alveolar foramen is located at the level of the last posterior preserved tooth. The further posterior portion is damaged and missing in EUNMH PV 14052. This portion is, however, present in the Kocayarma specimen EUNMH PV 14064. In this specimen, the posteroventral process of the maxilla is not stepped, but gradually rises dorsally in anterior direction (Fig. 7D-E). In labial view, a weak ornamentation is present in the dorsalmost region. This section possesses no foramina. The same specimen bears six tooth positions, where all teeth are still attached. The supradental shelf is partly damaged. The posterior lingual region bears an articulation facet for the jugal on its dorsal side.

Dentary

An anterior portion of the right dentary is preserved (EUNMH PV 14063). It is a ventrally arched bone, with a slight medial

curvature at its anterior end (Fig. 7G-I). The otherwise smooth labial surface is pierced by a single series of five labial foramina. Meckel's groove is fully open in lingual view, but rather narrow. It continues to the small rectangular symphysis anteriorly. The subdental shelf is moderately robust in this section and appears to be slightly rounded in cross-section. The dental crest is high, supporting medially 13 tooth positions (four teeth are still attached). The further posterior portion is, however, broken off and missing.

Dentition

Tooth implantation is pleurodont. The teeth are large, robust and closely spaced. They have bicuspid tooth crowns. There is a triangular dominant cusp and a smaller mesial one (note that in EUNMH PV 14052, the posteriormost preserved tooth has a small inconspicuous distal bulge that can be interpreted as incipient additional cusp). The lingual side of the crowns is slightly flattened. The strong distinct striation here is present mainly in EUNMH PV 14052 (Fig. 6C). It possesses around 11 diverged distinct striae which incline mesially and distally in ventral direction. The labial surface is smooth. The tooth necks are slightly enlarged lingually. The tooth bases are covered by sediment, but some of them exhibit large circular resorption pits.

COMMENTS

This lacertid morphotype is characterized by massively built maxillae. The strongly developed striation of the lingual side of the tooth crowns, as present in the Kavakdere specimen EUNMH PV 14052, is not so distinct in other specimens from the nearby slightly younger locality of Kocayarma (although striation is obviously present in the latter material as well). We interpret this difference to be due to preservation reasons and/or possibly individual and ontogenetic variation or even chronostratigraphic variation (considering that the specimens from the two localities are not absolutely contemporary [allotemporal *sensu* Smith & Gauthier 2013]). The tooth morphology resembles that in the extant members of the genus *Timon* Tschudi, 1836, in the following aspects (see Kosma 2004; Čerňanský & Syromyatnikova 2019): 1) teeth are robust; 2) tooth crowns medially flattened; 3) the presence of a distinct striations on the lingual side (the maximum twelve striae is mentioned for *Timon pater* [Lataste, 1880] by Kosma (2004); 4) striae converge apically; 5) bicuspid teeth have been reported for *T. pater* by Kosma (2004), where in some specimens, a tendency to tricuspidity can be observed; and 6) large circular resorption pits at the tooth bases. Moreover, the posteroventral process of maxilla is not stepped, which is also a character present in *Timon* (see Čerňanský & Syromyatnikova 2019).

However, caution is needed here, as the interpretation of such small jaw fragments is always tricky. The similarities in dentition can also be interpreted by convergence due to similar diet preferences. Indeed, robust bicuspid teeth together with the not stepped posteroventral process of maxilla, is also present in the European Paleogene taxon *Plesirolacerta* Hoffstetter, 1942 (Čerňanský & Augé 2013;

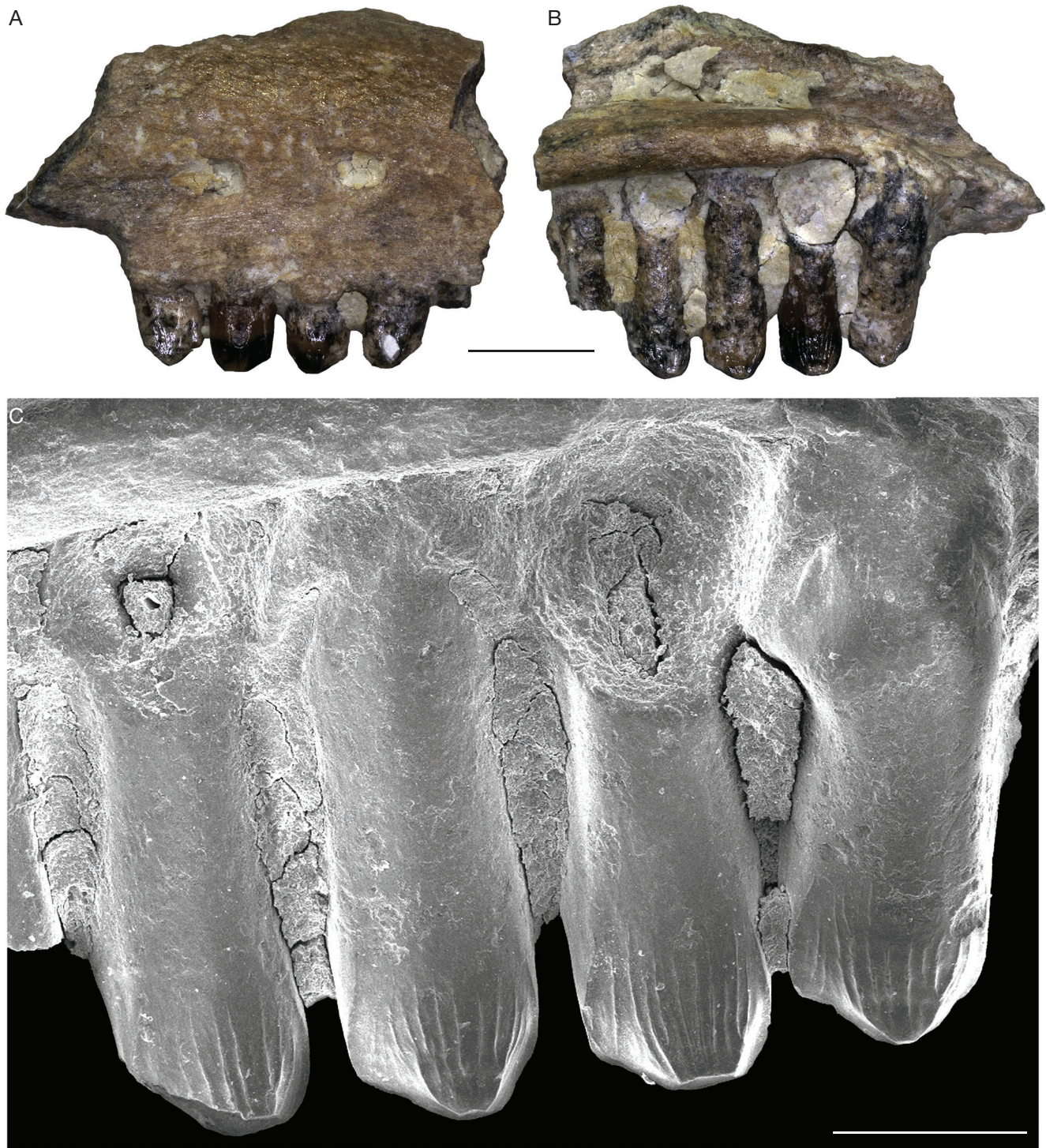


FIG. 6. — Lacertidae indet. (morphotype 1) from Kavakdere. Right maxilla EUNMH PV 14052 in labial (A) and lingual (B) views; C, close up SEM photograph of the same specimen showing the striation of the teeth. Scale bars: A, B, 1 mm; C, 0.5 mm.

Čerňanský *et al.* 2016). This extinct taxon also shares many other characters with the extant *Timon* (see Čerňanský & Syromyatnikova 2019). The dentary of *Plesiolacerta* is characterized by the subdental shelf being rounded in cross-section. This feature is difficult to evaluate in EUNMH PV 14063, because only its anterior portion is preserved. In any case, it appears to be rounded as well. The anterior dentary region

in both *Plesiolacerta* and *Timon* is strongly arched, but this appears to be not so pronounced in EUNMH PV 14063. More complete material is therefore needed to resolve the taxonomy of this Oligocene Turkish lacertid. As such, for now, we decided to allocate this maxilla as Lacertidae indet. (morphotype 1), although some similarities to *Plesiolacerta* and *Timon* are obvious.

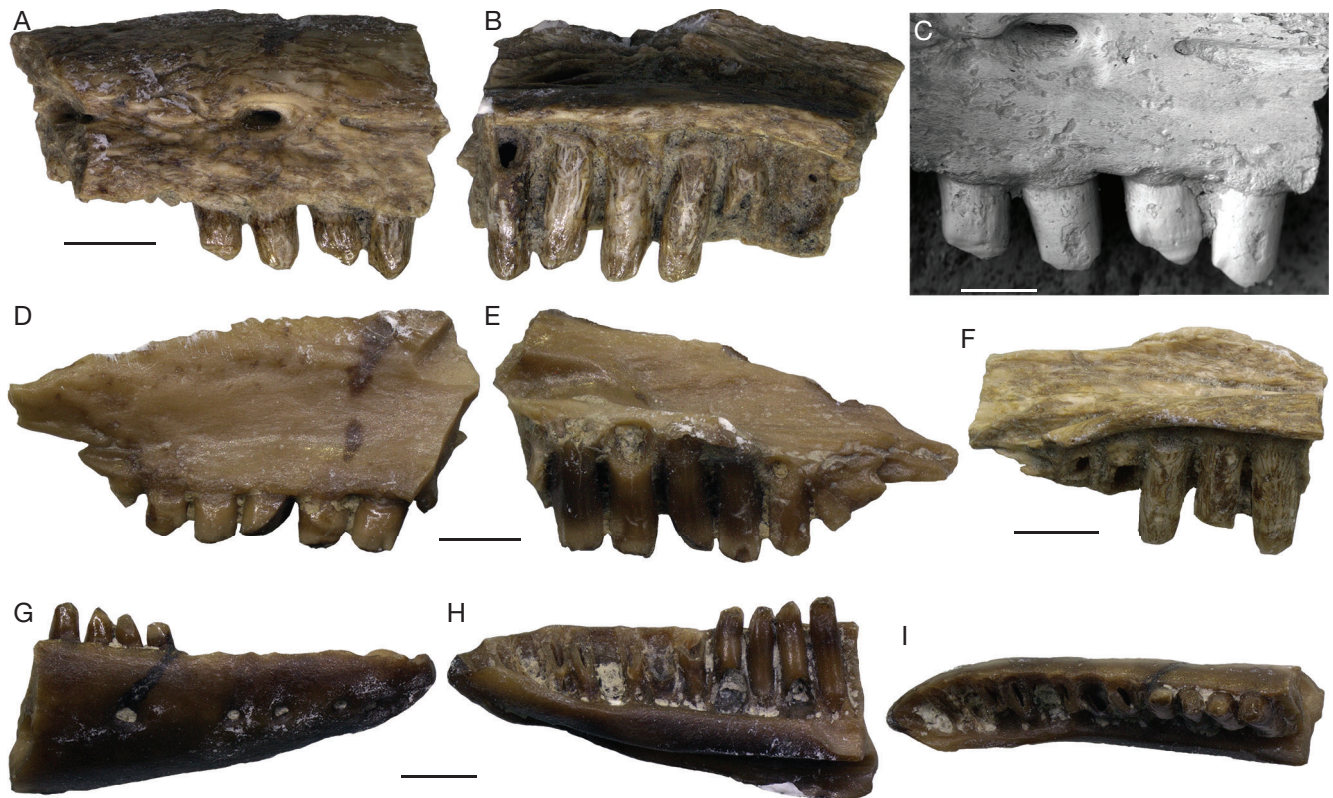


FIG. 7. — Lacertidae indet. (morphotype 1) from Kocayarma: **A–B**, maxilla EUNMH PV 14061 in labial (**A**) and lingual (**B**) views; **C**, close SEM photograph of the teeth of the same specimen; **D, E**, maxilla EUNMH PV 14064 in labial (**D**) and lingual (**E**) views; **F**, maxilla EUNMH PV 14066 in lingual view; **G–I**, Dentary EUNMH PV 14063 in labial (**G**), lingual (**H**), and dorsal (**I**) views. Scale bars: A, B, D–I, 1 mm; C, 0.5 mm.

Lacertidae indet. (morphotype 2) (Fig. 8)

MATERIAL. — **Turkey.** Kavakdere: a premaxilla (EUNMH PV 14055) and a right maxilla (EUNMH PV 14058).

DESCRIPTION

Premaxilla

The premaxilla EUNMH PV 14055 is a small, triradiate element (Fig. 8A, B). Unfortunately, it is only partly preserved; the nasal process is broken off, only its ventral portion is preserved. On its labial side, the ethmoidal foramen is located close to the base of the nasal process. The maxillary process is preserved only on the right side. It is rather long and well developed relative to the size of the premaxilla. The incomplete tooth row bears six tooth positions (two teeth are still attached). But based on the better preserved right side and a position of the central tooth (being the 5th one), the total number of the tooth positions can be estimated as nine. The supradental shelf forms a short incisive process at its mid-region.

Maxilla

Only a small fragment of the posteriormost portion of the right maxilla (EUNMH PV 14058) is preserved (Fig. 8C–E). It bears three tooth position (the last posterior tooth is still attached). The lingual portion is largely damaged. The

posteroventral process of maxilla appears to be not stepped, but gradually rise dorsally in anterior direction. The labial surface of this portion is smooth.

Dentition

The dentition in both specimens is pleurodont. In the premaxilla, the complete tooth is only the central one. It is monocuspid and conical. The crown is well-rounded and blunt. The posteriormost maxillary tooth is rather monocuspid as well, although it should be noted that the mesial portion of the crown is slightly bulged. The labial portion of the crown of this tooth is smooth, whereas its lingual side bears a striation. The tooth base is pierced by a large circular resorption pit.

COMMENTS

It is difficult to associate these lacertid fragmentary specimens from Kavakdere with the above described material of Lacertidae indet. (morphotype 1). The premaxilla EUNMH PV 14055 is small, but it might still represent a juvenile individual. The maxilla EUNMH PV 14058 represents only a small fragment, where the posteriormost tooth is preserved. In the extant species *Timon lepidus* (Daudin, 1802), the posteriormost tooth is smaller than anteriorly located tooth (see Čerňanský & Syromyatnikova 2019: fig. 34). Its tooth crown appears to be monocuspid, although preceding anteriorly located teeth are bicuspid. The same is true for the extinct *Plesirolacerta* (see Čerňanský & Augé

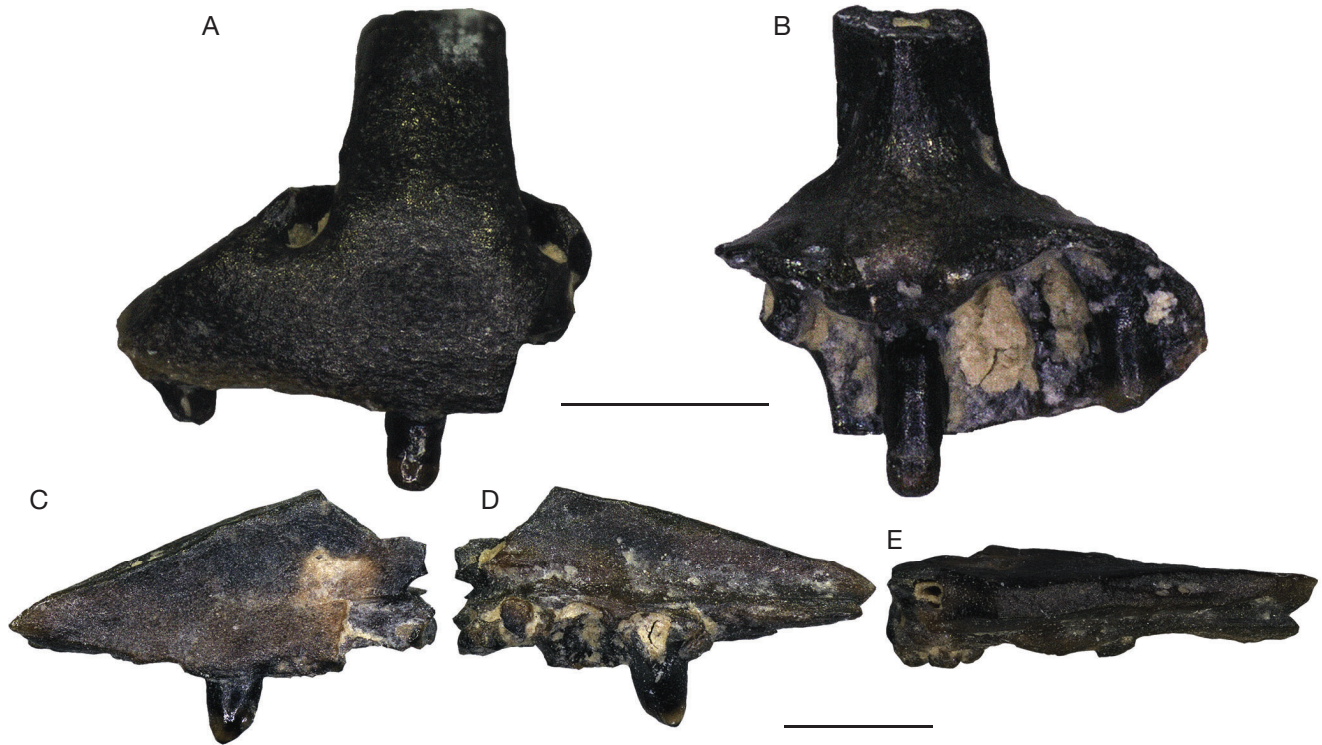


FIG. 8. — *Lacertidae* indet. (morphotype 2) from Kavakdere: **A, B**, premaxilla EUNMH PV 14055 in anterior (**A**) and posterior (**B**) views; **C-E**, right maxilla EUNMH PV 14058 in labial (**C**), lingual (**D**), and dorsal (**E**) views. Scale bars: A, B, 0.5 mm; C-E, 1 mm.

2013: fig. 7). Moreover, the posteroventral process of the Kavakdere maxilla EUNMH PV 14058 appears to be not stepped as well. In conclusion, these two specimens might represent the same taxon as the material described here as *Lacertidae* indet. (morphotype 1), however, there is no strong evidence for it due to a bad preservation and variation of these elements. In that case that it represents the same taxon, it shows another character sharing with extant *Timon* and extinct *Plesirolacerta*: (1) nine premaxillary teeth, although it should be highlighted that this feature is also present in many other lacertids (see Čerňanský & Syromyatniková 2019). Nevertheless, we provisionally treat this material as pertaining to a different morphotype.

SCINCIFORMATA Vidal & Hedges, 2005

Scinciformata indet. (Fig. 9)

MATERIAL. — **Turkey.** Kavakdere: a right dentary (EUNMH PV 14051).

DESCRIPTION

Only a fragment of the right dentary is preserved, representing the anterior region (note that the anterior symphyseal portion is broken off and missing). This specimen possesses five tooth positions, where four teeth are still attached (Fig. 9). Meckel's groove is fully open, but markedly narrow. In contrast, the

subdental shelf is dorsoventrally wide. The dental crest is high, so only the crowns of the teeth exceed it dorsally. The mid-section of the labial surface is pierced by one anteroposteriorly elongate labial foramen.

Dentition

Tooth implantation is pleurodont. The tooth necks are slightly enlarged lingually. The tooth crowns have blunt triangular apices, with their peaks being slightly recurved posterolingually. In lingual view, they possess labial and lingual cusps. The lingual side is bordered by culmen lateralis posterior and anterior and possesses striation formed by apicobasal ridges which are more-or-less parallel to each other. The number of striae ranges from five to seven. The labial aspect of the tooth crowns appears smooth.

COMMENTS

Only a small dentary fragment is preserved, of which allocation is difficult. Transversally bicuspid teeth together with apicobasal striation of their crowns indicate its affinity with members of the group Scinciformata. Among skinks, the fully open Meckel's groove indicates its similarity with members of the clade Scincidae (*sensu* Hedges 2014; Scincinae *sensu* Estes *et al.* 1988; for this character state, see Čerňanský & Syromyatnikova 2021 and literature therein). The dentition bears an overall resemblance with that of members of the genus *Chalcides* Laurenti, 1768 (see Čerňanský *et al.* 2020). However, due to its fragmentary nature, a more precise allocation of this material cannot be made.

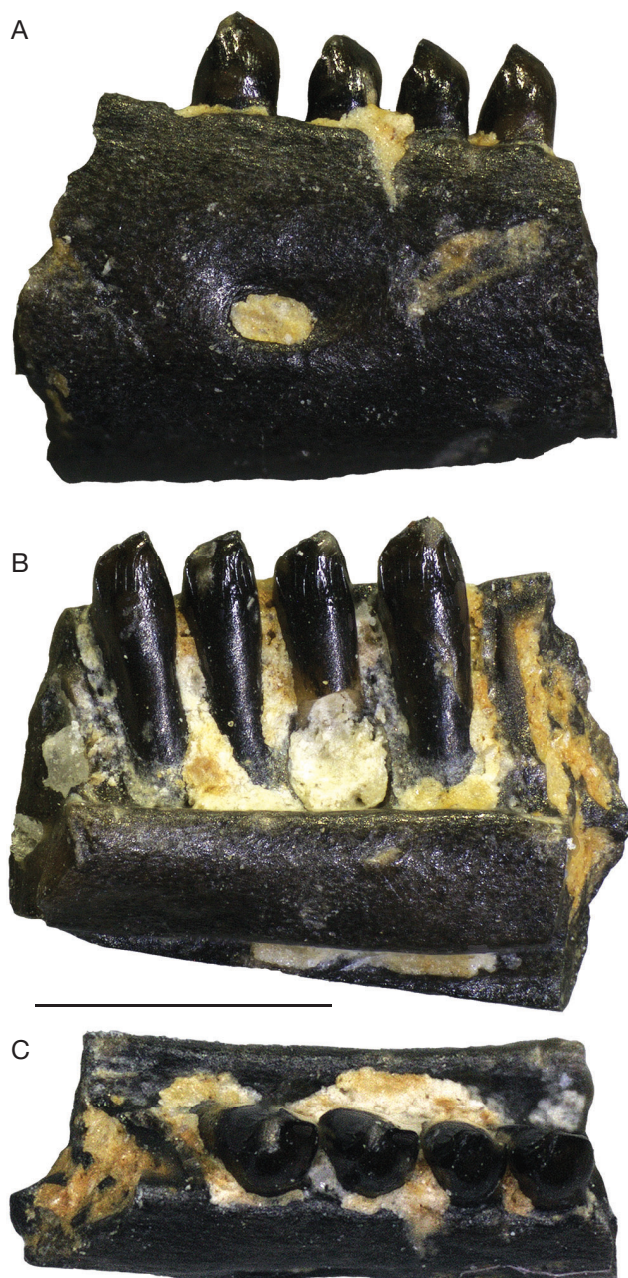


FIG. 9. — Scinciformata indet. from Kavakdere. Right dentary EUNMH PV 14051 in labial (A), lingual (B), and dorsal (C) views. Scale bar: 1 mm.

ANGUIMORPHA Fürbringer, 1900
Family ANGUIDAE Gray, 1825
Subfamily ANGUINAE Gray, 1825
Genus *Ophisaurus* Daudin, 1803

Ophisaurus sp.
(Fig. 10)

MATERIAL. — Turkey. Kavakdere: a presacral vertebra (EUNMH PV 14056).

DESCRIPTION

The vertebra EUNMH PV 14056 is incomplete, missing parts of the neural spine, right prezygapophysis and both postzygapophyses, while its synapophyses and condyle are eroded (Fig. 10). In anterior view (Fig. 10A), the prezygapophyses are dorsally inclined, with their dorsal edges reaching the dorsal floor of the neural canal. The neural canal is triangular and large, with a height larger than that of the cotyle. The cotyle is rather depressed and elongated. In posterior view (Fig. 10B), the neural arch is moderately vaulted. The condyle is rather eroded but it seems that it was originally relatively dorsoventrally depressed. In dorsal view (Fig. 10C), the base of the neural spine crosses most of the midline of the neural arch. The prezygapophyses are directed anterolaterally. The prezygapophyseal articular facets are massive and broad. The interzygapophyseal constriction is well developed. In ventral view (Fig. 10D), the vertebra is longer than wide. The centrum is slightly anteriorly widened. Its ventral surface is almost flattened, though nevertheless, two rather large foramina pierce it at around its anterior level. The lateral margins (subcentral ridges) are slightly concave. There are no signs of precondylar constriction. In lateral view (Fig. 10E), the neural spine is broken and its full height cannot be evaluated; it seems though that it mostly augments in height towards the posterior half of the neural arch. The synapophyses seem to have been well developed but also they are eroded.

COMMENTS

The vertebra can be assigned to *Ophisaurus* on the basis of its concave lateral margins and the height of its neural canal being bigger than the respective one of the cotyle (Čerňanský *et al.* 2019). Osteoderm material from Kavakdere has been recently described as an indeterminate anguine (Čerňanský *et al.* 2017b). It seems probable that this too belongs to *Ophisaurus*, however, the diagnostic utility of osteoderms is far limited for any such generic referral with certainty and we cannot thus exclude the possibility that they pertain to another anguine taxon.

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923

Family “TROPIDOPHIIDAE” Cope, 1894

COMMENT ON THE STATUS OF “TROPIDOPHIIDAE”

Tropidophiids, commonly known as “dwarf boas”, have extant representatives distributed solely in the Neotropics (Wallach *et al.* 2014). Nevertheless, they have a fossil record in the Old World as well, as a number of extinct taxa has been established from the Paleogene and Neogene of Europe (e.g. Rage 1973, 1974, 1988a; Szyndlar & Böhme 1996; Szyndlar & Rage 2003; Szyndlar *et al.* 2008; Rage & Augé 2010), while their remains have been also described from the Paleogene of northern Africa (Augé & Rage 2006; McCartney & Seiffert 2016). Extant tropidophiids have been traditionally lumped into “booids” (e.g. Rage 1984; see Georgalis & Scheyer 2019 for the concept of the informal grouping “Booidea”) and divided

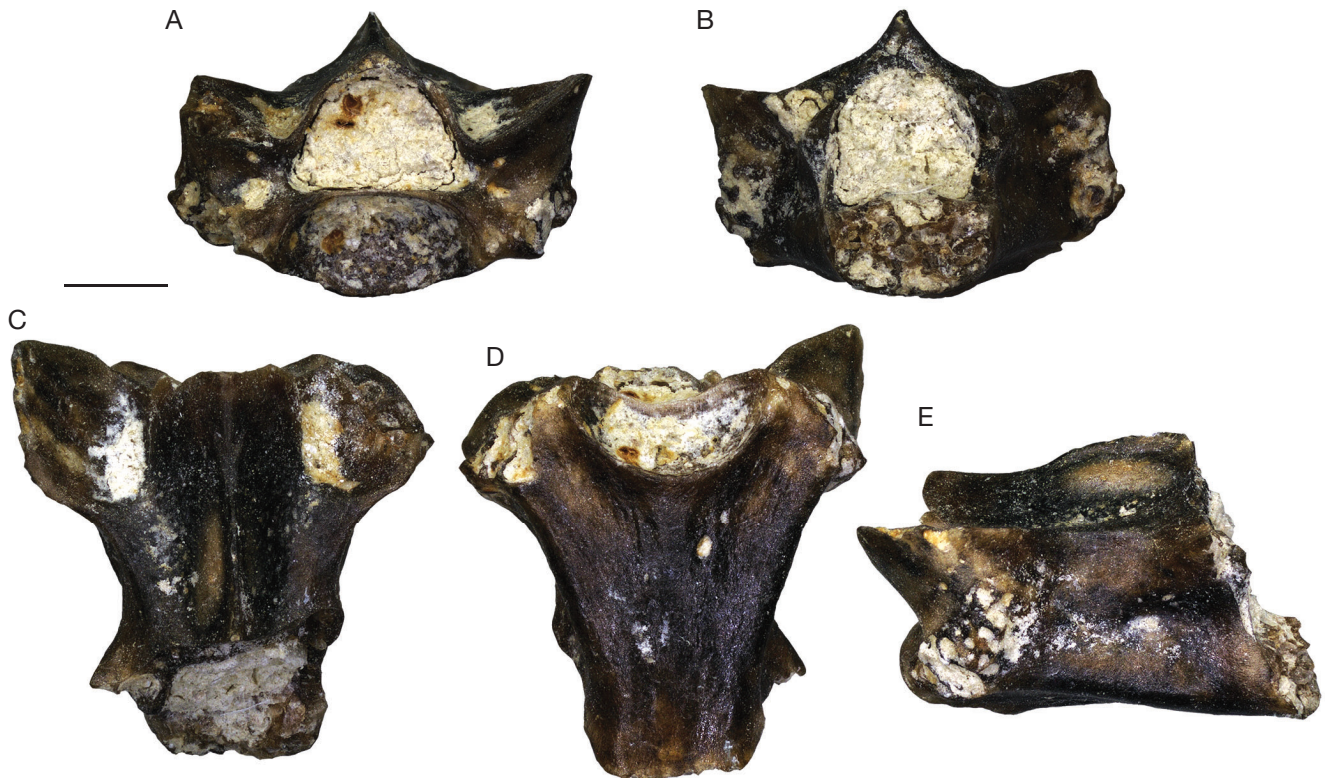


FIG. 10. — *Ophisaurus* sp. from Kavakdere: presacral vertebra EUNMH PV 14056 in anterior (A), posterior (B), dorsal (C), ventral (D), and left lateral (E) views. Scale bar: 1 mm.

into two “subfamilies”, i.e., tropidophiines and ungaliophiines (Szyndlar & Rage 2003). However, in the past few decades they were suggested to represent a paraphyletic assemblage, on the basis of external and musculature morphology (Zaher 1994). This was later further supported by phylogenetic analyses based on molecular data, which recovered tropidophiids (in their traditional sense) as paraphyletic, with tropidophiines (comprising the genera *Tropidophis* Bibron in Ramón de la Sagra 1838-1843, and *Trachyboa* Peters, 1860) nested instead more close to anilioids, while ungaliophiines (comprising the genera *Ungaliophis* Müller, 1880, and *Exiliboa* Bogert, 1968) nested within Booidea (Wilcox *et al.* 2002; Lawson *et al.* 2004; Vidal *et al.* 2007; Wiens *et al.* 2012; Reynolds *et al.* 2014; Streicher & Wiens 2016; Burbrink *et al.* 2020). Such distinction is further corroborated by cranial (Bogert 1968a) and vertebral anatomy (Bogert 1968a, 1968b; Szyndlar & Rage 2003; Smith 2013). Accordingly, such view has met a wide consensus among herpetologists who usually treat these groups as distinct families, tropidophiids and ungaliophiids (e.g. Wallach *et al.* 2014). Ungaliophiines have been subsequently placed as a subfamily of Charinidae (i.e., Ungaliophiinae) (Pyron *et al.* 2014); Burbrink *et al.* (2020) elevated both charinids and ungaliophiids to the family level, but still recovered them as sister groups in their phylogenetic analysis. All these being said, Tropidophiidae in its modern sense is nested close to anilioids and not booids.

On the other hand, in palaeontological literature, fossil Tropidophiidae are still mostly considered as pertaining

to “booids” (e.g. Szyndlar & Rage 2003; Szyndlar *et al.* 2008), i.e., the Constrictores *sensu* Georgalis & Smith (2020). As such, we have to note that with their current family denomination they are automatically considered as close to anilioids and not to Constrictores, even though the latter case may be more likely. Therefore, for the sake of convenience, we use the term “Tropidophiidae” in quotation marks. For a detailed discussion on fossil “tropidophiids”, see Smith & Georgalis (in press).

Among the limited vertebral material from Kargi 2, we here tentatively recognize two distinct “tropidophiid” forms (see below). Although both represented by non overlapping material (i.e., vertebrae not pertaining to the same portion of the column), we tend to treat them as different taxa on the basis of comparison with coeval, more complete taxa from western and central Europe. Nevertheless, such distinction should be considered as provisional, in anticipation of additional vertebral material from Anatolia that may eventually elucidate this taxonomic issue.

Genus *Falseryx* Szyndlar & Rage, 2003

Falseryx sp.
(Fig. 11)

MATERIAL. — Turkey. Kargi 2: a posterior caudal vertebra (EUNMH PV 14071).



FIG. 11. — *Falseryx* sp. from Kargi 2. Posterior caudal vertebra EUNMH PV 14071 in anterior (A), posterior (B), dorsal (C), ventral (D), and right lateral (E) views. Scale bar: 1 mm.

DESCRIPTION

The posterior caudal vertebra EUNMH PV 14071 is almost complete, missing only the distalmost edges of the prezygapophyses and pleurapophyses (Fig. 11). The vertebra is tiny with a centrum length of 2.1 mm and a neural arch width of 1.2 mm. In anterior view (Fig. 11A), the neural spine is high and rather thick; there is a slight dorsal thickening. The zygosphenes are proportionally thin, narrow, and rather arched. The prezygapophyses are much dorsally inclined. The neural canal is almost subcircular. The cotyle is sub-elliptical and slightly laterally compressed. There are no paracotylar foramina. The pleurapophyses are broad and extend ventrolaterally. In posterior view (Fig. 11B), the neural arch is moderately vaulted. The cotyle is rather small, elliptical in shape, and laterally compressed. In dorsal view (Fig. 11C), the prezygapophyses extend much anteriorly, surpassing the level of the zygosphenes. The prezygapophyseal articular facets are narrow and elongated. The base of the neural spine covers almost $\frac{2}{3}$ of the mid-line of the neural arch, commencing well posteriorly from the level of the zygosphenal roof. The postzygapophyses are small and do not extend much laterally. A prominent tubercle-like bump is present on the dorsal sur-

face of each of the postzygapophyses. The interzygapophyseal constriction is shallow. The posterior median notch of the neural arch is moderately deep. In ventral view (Fig. 11D), the vertebra is much elongated and narrow, being at least 1.7 times longer than wide. A haemal keel runs throughout much of the centrum. The postzygapophyseal articular facets are narrow. The condyle is developed on a salient condylar neck. In lateral view (Fig. 11E), the neural spine is high at its anterior edge and gradually diminishes in height posteriorly, reaching its lowest level at its posteriormost edge. The interzygapophyseal ridges are almost straight. The haemal keel is prominent and projects ventrally, with this projection being most prominent at around its mid-level.

COMMENTS

The caudal vertebra EUNMH PV 14071 can be assigned to *Falseryx* on the basis of its small size, elongated centrum, and presence of a haemal keel instead of haemapophyses (Szyndlar & Rage 2003). Moreover, its small size and its elongation, along with the presence of the haemal keel (and not haemapophyses) and pleurapophyses, denote an origination of the vertebra from the posterior caudal region.

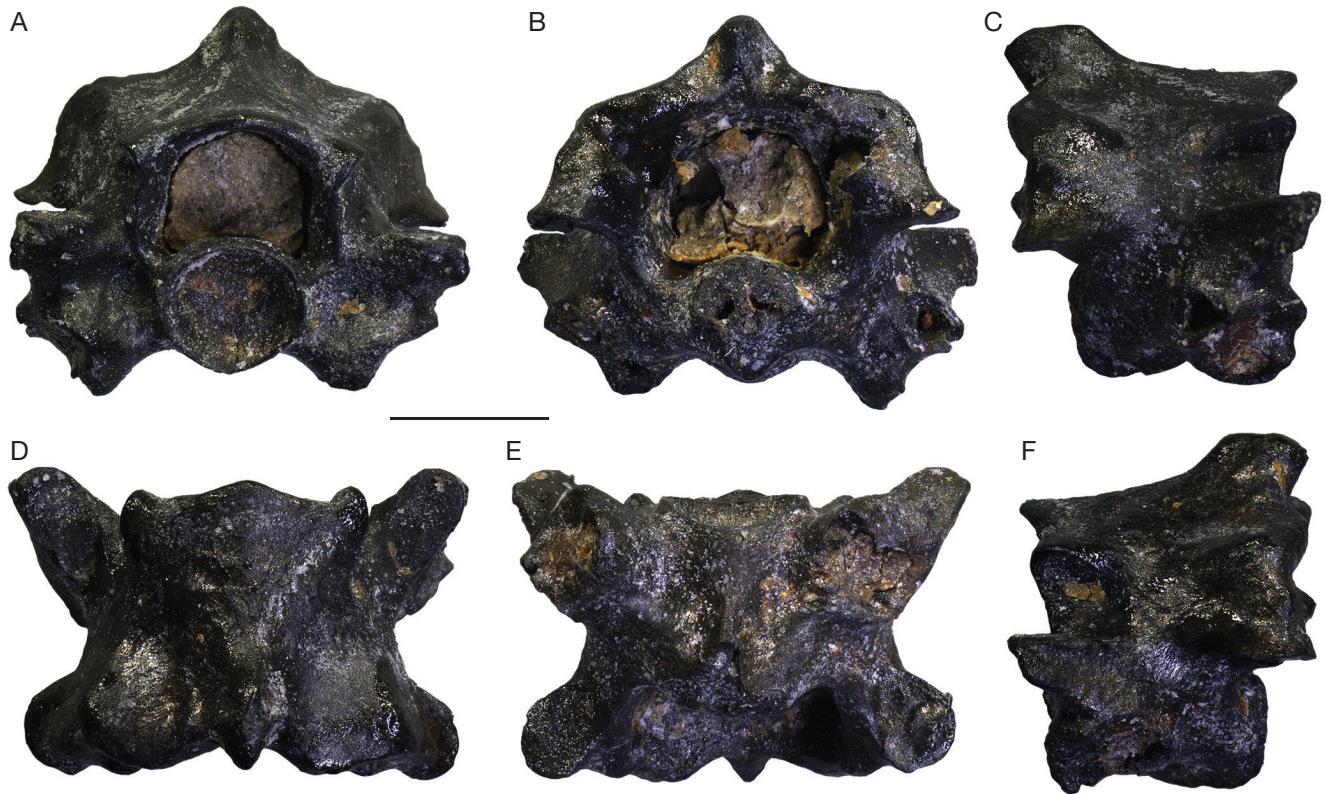


FIG. 12. — cf. *Platyspondylia* sp. from Kargi 2. Cloacal vertebra (EUNMH PV 14070) in anterior (A), posterior (B), right lateral (C), dorsal (D), ventral (E), and left lateral (F) views. Scale bar: 1 mm.

Note that the genus *Rottophis* Szyndlar & Böhme, 1996, from the late Oligocene of Germany, has also caudal vertebrae with haemal keels (instead of paired haemapophyses), with the posteriormost ones having the tips of these keels grooved or slightly bifurcated (Szyndlar & Böhme 1996; Szyndlar *et al.* 2008). The Anatolian specimen lacks this kind of grooves or bifurcation on its haemal keel, therefore we can exclude its referral to *Rottophis*.

Although a generic attribution of this vertebra to *Falseryx* seems relatively favorable, a more precise determination is a difficult task on the basis of such limited material. Nevertheless, it seems that the Kargi 2 *Falseryx* is different from the two named species of the genus, i.e., *Falseryx petersbuchi* Szyndlar & Rage, 2003, from the early Miocene of Germany and Czech Republic (Szyndlar & Rage 2003; Szyndlar *et al.* 2008), and *Falseryx neervelpensis* Szyndlar, Smith & Rage, 2008, from the early Oligocene of Belgium (Szyndlar *et al.* 2008) in terms of the shape of the neural spine and the convexity and thinness of the zygosphenes. Indeed, the height of the neural arch that is an interesting feature. It seems that the Kargi 2 specimen approaches more in morphology the posterior caudal vertebrae of *Falseryx* described recently from the earliest Miocene (MN 1) of Kılçak, near Ankara (Syromyatnikova *et al.* 2019a). We tentatively consider the two Anatolian forms as conspecific, although certainly more vertebrae from Kargi 2 are needed in order to confirm such assumption.

Genus *Platyspondylia* Rage, 1974

cf. *Platyspondylia* sp.
(Fig. 12)

MATERIAL. — **Turkey.** Kargi 2: a cloacal vertebra (EUNMH PV 14070).

DESCRIPTION

The vertebra EUNMH PV 14070 is almost complete but misses most of its lymphapophyses and the posteroventral portion of its centrum (Fig. 12). The vertebra is small, with a neural arch width of 1.9 mm and an approximate centrum length of at least 1.3 mm (the posterior ventral portion of the centrum is damaged). In anterior view (Fig. 12A), the zygosphenes are thin and slightly convex. Its width is larger than that of the cotyle. The neural canal is moderately large and trapezoidal. The prezygapophyses are only slightly dorsally inclined, with their dorsalmost edges slightly exceeding the dorsal level of the cotyle. The cotyle is rather small and almost totally circular. There are no paracotylar foramina. Large and relatively deep paracotylar fossae are located at each side of the cotyle. From the lymphapophyses, only their bases are preserved, but still it can be observed that they were broad and directed ventrolaterally. In posterior view (Fig. 12B), the neural spine is thick and rather short. The neural arch is relatively vaulted and is distinctly upswept

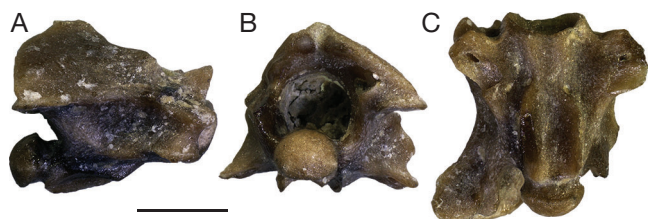


FIG. 13. — “Tropidophiidae” indet. from Kargi 2. Mid-caudal vertebra EUNMH PV 14072 in right lateral (A), posterior (B), and ventral (C) views. Scale bar: 1 mm.

above the zygantrum, with a prominent angle occurring at about mid-length of each postzygapophysis. The condyle is much eroded, though it seems that, similarly to the cotyle, it was rather small and distinctly circular. In dorsal view (Fig. 12D), the base of the neural spine is developed only at the posterior half of the neural arch; its thickness augments gradually towards its posterior direction. The zygosphenes are trilobate, with all three lobes being rather prominent. The interzygapophyseal constriction is deep. The prezygapophyses face anterolaterally. The prezygapophyseal articular facets are slender and elongated. The posterior median notch of the neural arch is shallow. In ventral view (Fig. 12E), the centrum is much wider than long. A thin, salient structure is developed in the (preserved) midline of the centrum that probably corresponds to the remains of a hypapophysis. The postzygapophyseal articular facets are broad and oval. In lateral view (Fig. 12C, F), the vertebra is distinctly higher than long. The neural spine develops only at the posterior portion of the neural arch; it is relatively short and is distinctly posteriorly inclined. The zygosphenal facets are broad. The (probable) hypapophysis slightly projects ventrally.

COMMENTS

The vertebra can be tentatively referred to *Platyspondylia* on the basis of its very tiny size, the distinctly thin zygosphenes, the low neural spine commencing well posteriorly from the level of the zygosphenes and developed mostly at the posterior portion of the neural arch, the deep interzygapophyseal constriction, the very slender prezygapophyses, the tiny and circular cotyle and condyle, the shallow posterior median notch, and not well developed prezygapophyseal accessory processes (see figures in Rage 1974; Szyndlar & Rage 2003; Vianey-Liaud *et al.* 2014). Furthermore, the presence of lymphapophyses, the absence of haemapophyses and the probable presence of a hypapophysis, and the relatively vaulted neural arch, denote that the vertebra originates from the cloacal region (Szyndlar & Rage 2003; Vianey-Liaud *et al.* 2014). In fact, this specimen bears resemblance with the sole other known cloacal vertebra of that genus that has been figured so far, i.e., a referred specimen of *Platyspondylia lepta* Rage, 1974, from the late Oligocene (MP 28) of Pech Desse, Quercy, France (see Szyndlar & Rage 2003: fig. 37i-m), though still it possesses a much more posteriorly inclined neural spine in lateral view and a more vaulted neural arch. As for the probable presence of the hypapophysis, it is known

that several extinct and extant constrictors are known to possess such structure in their anterior cloacal vertebrae, such as *Bavarioboa* and the Neotropical ungaliophiines (Szyndlar & Rage 2003; Smith 2013).

Compared to cloacal vertebrae of *Falseryx*, the Kargi 2 specimen EUNMH PV 14070 is distinct in the vaultness of the neural arch with a distinctive upswept above the zygantrum, the neural spine developing more posteriorly on the neural arch, the broader and anteroposteriorly shorter centrum, and the wider and more prominent zygosphenes (see figures in Szyndlar & Rage 2003; Szyndlar *et al.* 2008; Syromyatnikova *et al.* 2019a). Finally, compared with cloacal vertebrae of *Bavarioboa* Szyndlar & Schleich, 1993, a genus from Western and Central Europe (see figures in Szyndlar & Rage 2003), that has been recently recovered also from Anatolia (Szyndlar & Hoşgör 2012; Syromyatnikova *et al.* 2019a), EUNMH PV 14070 is much smaller, has no paracotylar foramina, and neural spine commencing well posteriorly on the neural arch (see figures in Szyndlar & Rage 2003).

Taking the above notices in consideration, we choose to treat EUNMH PV 14070 as pertaining to a second “tropidophiid” taxon, with more close probable affinities with *Platyspondylia* than *Falseryx*. Whether it truly belongs to the otherwise western and central European genus *Platyspondylia* or represents a totally novel taxon, is a question that certainly requires more material recovered from the Anatolian Oligocene.

“Tropidophiidae” indet. (Fig. 13)

MATERIAL. — Turkey. Kargi 2: A mid-caudal vertebra (EUNMH PV 14072).

DESCRIPTION

The vertebra EUNMH PV 14072 is rather incomplete, missing large part of both prezygapophyses, the left postzygapophysis, and the dorsalmost portion of the neural spine (Fig. 13). It is tiny, with a centrum length of 2.0 mm and a neural arch width of 1.6 mm. The neural spine is developed only at the posterior half of the neural arch. The neural arch is vaulted. The haemapophyses develop around the mid-portion of the centrum, they are almost parallel to each other in ventral view and extend rather ventrally in posterior view. The cotyle and condyle are small. The pleurapophyses are broad and extend ventrolaterally. The postzygapophyseal articular facets are massive.

COMMENTS

This vertebra could pertain to one of the two above described “tropidophiids”. Note that *Platyspondylia* was so far considered to have haemapophyses throughout the caudal region (Rage 1974; Szyndlar & Rage 2003), however, it is now known that haemapophyses are absent in the anterior caudal vertebrae but present in mid- and posterior caudal ones of this taxon (Vianey-Liaud *et al.* 2014).

Squamata indet.

MATERIAL. — **Turkey.** Kocayarma: two caudal vertebrae (EUNMH PV 14062 and EUNMH PV 14067).

DISCUSSION

The scarce knowledge of Oligocene herpetofaunas of Eurasia hinders significantly our understanding of major climatic events and faunal turnovers that took place during the Paleogene, such as the “Grande Coupure” extinction event in the Eocene-Oligocene boundary (e.g. Rage & Roček 2003; Rage 2013). A number of such faunal turnovers are linked directly with dispersal events of vertebrate taxa from Asia to Europe and vice versa (e.g. Godinot & Lapparent de Broin 2003; Rage & Roček 2003; Szyndlar & Rage 2003; Rage 2013; Čerňanský & Augé 2019). As far as it regards herpetofaunal studies, it has been variously suggested that several lineages of amphibians and reptiles dispersed from Asia to Europe during the Oligocene following a relatively northern route, i.e., north of the Paratethys Sea and eventually leading to central and western Europe. According to such a scenario, up to the Oligocene, the Turgai Strait formed a marine barrier between Europe and Asia, but the subsequent emergence of land in that area (the so called Mazury-Mazowse continental bridge; early Oligocene) provided direct terrestrial connection between the two continents. This pattern of dispersals has been repeatedly suggested for frogs (Rage & Roček 2003), turtles (Godinot & Lapparent de Broin 2003), lizards (Augé & Smith 2009), and colubrid snakes (Ivanov 2001). In fact, this scenario of a northern route dispersal of Asian immigrant taxa has already been suggested since more than a century (Stehlin 1909) and remains still the most well known and intensively studied, especially for mammals. Nevertheless, recent studies based on mammal finds from both Balkans and Anatolia suggested that an array of Asian vertebrate lineages dispersed to Europe during the Paleogene from an alternative, southern route, i.e., via Anatolia and the southern Balkan Peninsula and from there to central and western Europe (Métais & Sen 2017; Mennecart *et al.* 2018a, 2018b). Such a dispersal, at least from the Balkans to central Europe seems to have taken place slightly later than the above discussed northern route (i.e., around 31 Ma versus around 33 Ma; see Mennecart *et al.* 2018b). Interestingly, it has also been recently demonstrated, again on the basis of mammal finds, that during the Eocene, the area of central Anatolia was an island environment (the “Pontide terrane”) possessing a remarkable diversity of peculiar and endemic forms, all of which became ultimately extinct during the Oligocene when the loss of the insular status of the area permitted the arrival of several other mammal lineages from both Europe and Asia (see Métais *et al.* 2018). Nevertheless, given the absence of adequate Oligocene amphibian and reptile remains from the area of Anatolia and the southern Balkans, such southern dispersal route for the herpetofauna as well and any relevant biogeographic patterns have remained obscure.

The new material from the Oligocene of southern Balkans and Anatolia described herein demonstrates that certain taxa, otherwise present in central and/or western Europe, were present also in that area. Such taxonomic referrals provide evidence for a broader geographic expansion of these lineages across the western Palaearctic.

The material of *Albanerpeton* cf. *inexpectatum* from the early-late Oligocene of Kavakdere represents the first evidence of the extinct clade of albanerpetontids in Turkey. In fact, *Albanerpeton* has a stratigraphically and biogeographically interesting distribution. The type species of the genus, *Albanerpeton inexpectatum*, is known from the middle Miocene of France (Estes & Hoffstetter 1976; Gardner 1999a). The geologically youngest species are reported from the Miocene and Pliocene of France (Estes & Hoffstetter 1976; Estes 1981; Gardner 1999a; Rage & Hossini 2000), Austria (Sanchíz 1998), Germany (Böhme 2010), Czech Republic (Čerňanský 2010), and Hungary (Venczel & Gardner 2005), with early Pleistocene material from Italy representing the youngest known occurrence of the clade globally (Delfino & Sala 2007; Villa *et al.* 2018). However, some species of *Albanerpeton* range from the early Cretaceous to the Paleocene of North America (Estes 1981; Fox & Naylor 1982; Gardner 1999a, 1999b, 1999c, 2000), while indeterminate remains attributable to the genus are known also from the Cretaceous of Europe (Grigorescu *et al.* 1999). It should be noted that the Cretaceous species currently referred to *Albanerpeton* certainly require a taxonomic revision (in this regard, restriction of the genus *Albanerpeton* solely to post-Cretaceous species is not excluded). The new material described herein demonstrates an even wider European distribution of *Albanerpeton* during the Paleogene and also represents the easternmost record of the genus from the whole continent. Moreover, if indeed conspecific with *A. inexpectatum*, then it is potentially the oldest record of the species from Oligocene deposits (previously from Oligocene deposits, this species was reported only from the younger, German Oberleichtersbach locality [MP 30] by Böhme [2008] based on fragmentary dentary).

Frogs are poorly represented in the new Turkish Oligocene material. Pelobatids are already known in Turkey in different Miocene localities (Paicheler *et al.* 1978; Rückert-Ülkümen *et al.* 2002; Syromyatnikova *et al.* 2019a; Vasilyan *et al.* 2019). The probable referral of the Kocayarma material to *Eopelobates* extends the geographic distribution of that genus, as it represents the first known record from southern Balkans. This further augments the rather broad distribution of *Eopelobates* in the Palaearctic, being so far known from the Paleogene and Neogene of Europe, the Paleogene of central Asia (Roček *et al.* 2014) and the earliest Neogene of southwestern Asia (Syromyatnikova *et al.* 2019a). Furthermore, its stratigraphic distribution in Turkey is extended back to the Oligocene, as *Eopelobates* is known from Anatolia based on recently described material from the earliest Miocene of Kilçak near Ankara (Syromyatnikova *et al.* 2019a). If correct, the Kocayarma record, along with the Kilçak occurrence, denote that *Eopelobates* was a shared faunal element in both southern Balkans and Anatolia during the Oligocene and earliest Miocene.

The material of crocodylians and turtles is fragmentary, not permitting any kind of precise taxonomic determination that could perhaps elucidate some biogeographic patterns for these two groups. Nevertheless, especially for the crocodylians, the new material originating from these three Turkish localities further add to the so far poorly known record of that group from the area (Schleich 1994; Sen *et al.* 2011; Syromyatnikova *et al.* 2019a; Vasilyan *et al.* 2019).

Lizards, in our collection, are known only from the two European localities Kocayarma and Kavakdere. They are represented by two morphotypes of lacertids, a scinciformatan, and the anguine *Ophisaurus*. The material referred to Lacertidae morphotype 1 potentially hints for the presence of a *Plesiolacerta*-like (or *Timon*-like) form. If indeed a related or congeneric form to *Plesiolacerta*, the new remains would add another shared genus that was distributed in both western and eastern parts of Europe during the Oligocene (note that *Timon* is present in the extant herpetofauna of the area; see Sindaco & Jeremčenko 2008). However, the fragmentary nature of the new Turkish lacertids does not allow a precise taxonomic allocation and any definite palaeobiogeographical conclusions. Caution is therefore needed until new and more complete Oligocene lacertid material is eventually recovered from the area. As for the second lacertid morphotype, it is as yet unclear if it represents a distinct taxon or simply some kind of intraspecific variation with regard to Lacertidae morphotype 1. It is further not certain if the scinciformatan from Kavakdere represents a scincid (*sensu* Hedges 2014), though its preserved anatomy indicates that this is most plausible. The scincid *Chalcides*, with which it shares some resemblance, is broadly distributed in Turkey, though still this range is in southern Anatolia, far away from the European locality of Kavakdere. The identification of *Ophisaurus* in Kavakdere marks the sole known occurrence of this genus in the Oligocene of eastern Europe. The new find along with the recent identification of *Ophisaurus* in the Oligocene of Anatolia (Čerňanský *et al.* 2017b) provide further support for a relatively broad distribution of the genus in the late Paleogene of the eastern Mediterranean, a distribution that would reach its peak in the area during the Miocene (Georgalis *et al.* 2017, 2019a, 2019b) and the genus becoming ultimately extinct from the area during the latest Miocene/earliest Pliocene boundary (locality of Maramena, northern Greece; Georgalis *et al.* 2019b). The genus *Ophisaurus* is currently present in the extant herpetofauna of southeastern Asia (Čerňanský *et al.* 2019).

Snakes, in our new material, are solely represented in the Anatolian locality of Kargi 2. The only three available vertebrae suggest a referral to “tropidophiids”, a clade that is widespread in the Paleogene and Neogene of western and central Europe (Szyndlar & Rage 2003; Szyndlar *et al.* 2008; Rage & Augé 2010) and has recently been identified also from the earliest Miocene of Anatolia (Syromyatnikova *et al.* 2019a). The Kargi 2 material suggests the probable presence of two “tropidophiid” taxa: one pertaining to *Falseryx* plus another form, reminiscent of the western and central European genus *Platyspondylia*. The record of *Falseryx* extends

the stratigraphic distribution of that genus in Anatolia back to the Oligocene, while as for the latter form, if indeed *Platyspondylia*, then it represents a significant geographic extension, as the genus was so far totally unknown from Asia. Notably, it has been suggested that *Falseryx* and related Oligocene European “tropidophiids” are of Asian origin, with their ancestors dispersing to Europe and subsequently product this moderately diverse “tropidophiid” assemblage (Szyndlar & Böhme 1996; Szyndlar *et al.* 2008); however, it was so far not possible to determine this scenario with certainty. Nevertheless, the new Oligocene “tropidophiid” material from Anatolia described herein, in addition to the recently described earliest Miocene material from Kılçak (Syromyatnikova *et al.* 2019a) could provide some support to this scenario as they confirm that “tropidophiids” were present in both Europe and (at least) southwestern Asia. However, it cannot be excluded that the opposite dispersal route (i.e., Europe to Asia via Anatolia) was followed by *Falseryx* and *Platyspondylia*.

The new Oligocene amphibian and reptile remains from the European localities of Kavakdere and Kocayarma and the Asian locality of Kargi 2, are certainly not adequate for claiming with certainty any kind of south dispersal route(s). Nevertheless, they provide significant geographic and stratigraphic expansions of certain western and central European lineages in both southeastern Europe and southwestern Asia, especially for the case of albanerpetontids, squamates, and perhaps anurans.

The new material from Kavakdere, Kocayarma, and Kargi 2, further adds to the poorly known fossil record of amphibians and reptiles from Turkey (Malik & Nafiz 1933; Lebküchner 1974; Rage & Sen 1976; Schleich 1994; Rückert-Ülkümen *et al.* 2002; Staesche *et al.* 2007; Sen *et al.* 2011, 2017; Szyndlar & Hoşgör 2012; Čerňanský *et al.* 2017b; Georgalis *et al.* 2018, 2020; Syromyatnikova *et al.* 2019a, 2019b; Vasilyan *et al.* 2019).

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