

# Giant rhinoceros *Paraceratherium* and other vertebrates from Oligocene and middle Miocene deposits of the Kağızman-Tuzluca Basin, Eastern Turkey

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**Abstract** A recent fieldwork in the Kağızman-Tuzluca Basin in northeastern Turkey led us to the discovery of three vertebrate localities which yielded some limb bones of the giant rhino *Paraceratherium*, a crocodile tooth, and some small mammals, respectively. These discoveries allowed, for the first time to date some parts of the sedimentary units of this basin. This study also shows that the dispersal area of *Paraceratherium* is wider than it was known before. Eastern Turkey has several Cenozoic sedimentary basins formed during the collision of the Arabian and Eurasian plates. They are poorly documented for vertebrate paleontology. Consequently, the timing of tectonic activities, which led to the formation of the East Anatolian accretionary complex, is not constrained enough with a solid chronological framework. This study provides the first biostratigraphic evidences for the infill under the control of the compressive tectonic regime, which built the East Anatolian Plateau.

**Keywords** Cricetidae · Erinaceidae · *Paraceratherium* · Oligocene · Miocene · Turkey

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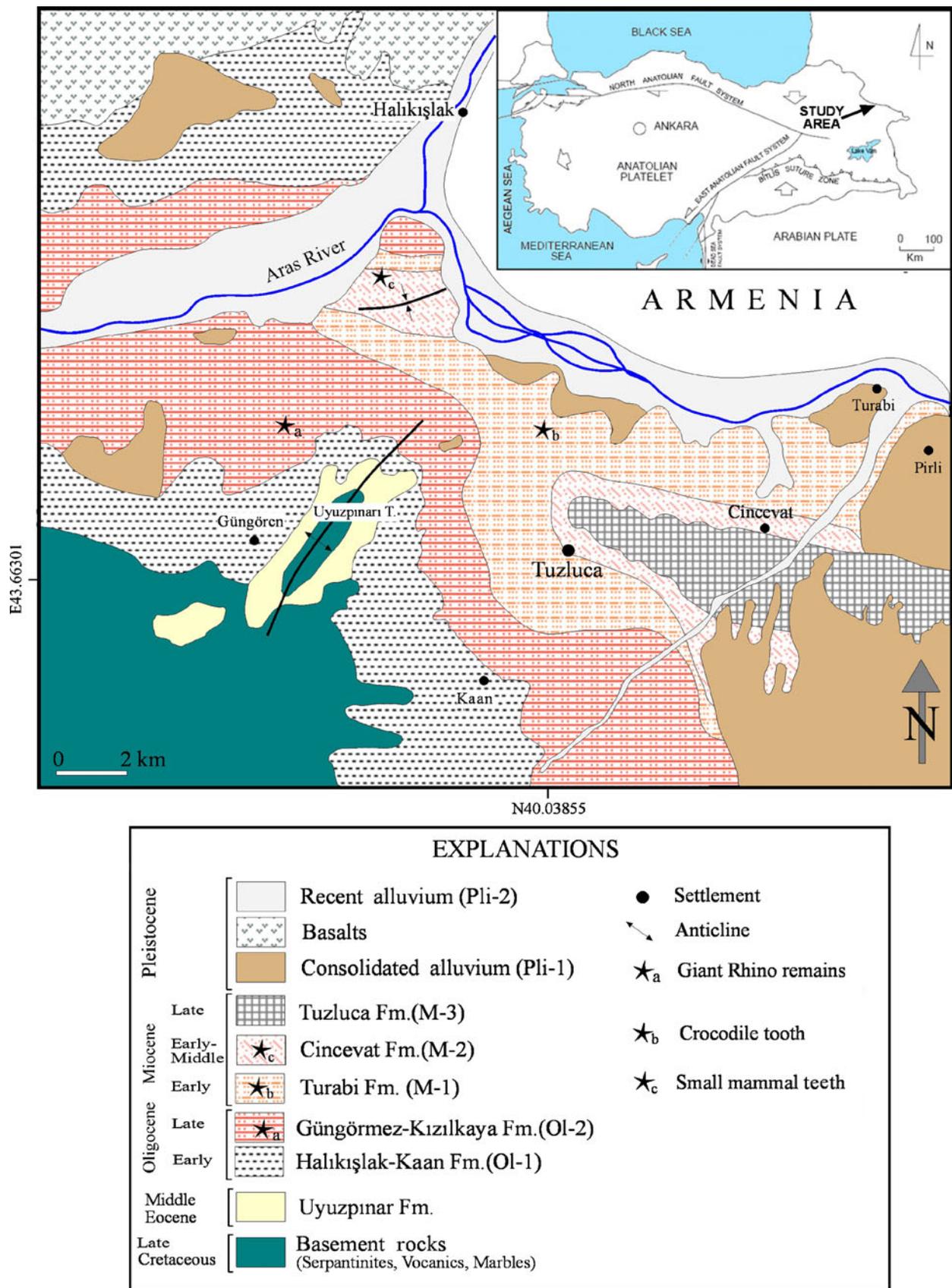
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## Introduction

Eastern Turkey is an almost total Terra incognita for vertebrate paleontology, except for eight localities in the Elazığ, Muş, and Pasinler basins, of which Ünay and de Bruijn (1998) reported Pliocene rodent fossils, and a locality in the Posof-Ahalsikhe Basin at the Turkish-Georgian border yielded a rich Late Eocene/Early Oligocene small mammalian fauna (De Bruijn et al. 2003). Otherwise, the age of the Cenozoic terrestrial sedimentary deposits are given by their relative position with respect to marine deposits, few pollen data, or they are dated as “undifferentiated Neogene”. In fact, Cenozoic terrestrial deposits formed in compressional intermountane or pull-apart basins cover about half of Eastern Turkey, the sedimentary infill of which is potentially suitable for preservation of vertebrate fossils (Şengör et al. 1985, 2008). In addition, most of these basins are in part underlain and in part filled with thick sedimentary sequences spanning in age from late Cretaceous up to the Pleistocene (Koçyiğit et al. 2001; Şengör et al. 2008). The age of terrestrial deposits is poorly constrained by some mollusk and pollen data (Sancay et al. 2006), and consequently the filling history of these basins and their related tectonic context are often debated because of the lack of reliable age data. A better knowledge of the depositional chronology of these basins will in turn contribute to the timing of related tectonic events in the region.

The study area is situated in NE Turkey, near the Armenian border, in the intramountane, i.e. compressional Kağızman-Tuzluca Basin (Fig. 1), which continues into Armenia south of Yerevan as Aras/Araxes or Hoktemberian Basin, filled with lagoonal marine to continental/lacustrine and alluvial deposits broadly dated (similar to their Turkish



**Fig. 1** Geological map of the Kağızman-Tuzluca Basin in the region of Tuzluca, and the location of vertebrate fossil sites

counterparts) as Early–Middle Miocene covered by much later alluvium of Quaternary age (Balian 1969) or as Late Oligocene to Late Miocene by Gabrielyan (1964). Eastern Turkey, also known in the geological literature as the East Anatolian High Plateau forming the northeastern part of the broader Turkish-Iranian High Plateau (Şengör et al. 2008), has many Cenozoic sedimentary basins formed under diverse strain regimes, ranging from shortening to transpressional and transtensional dictated by the local vagaries of the broadly north–south shortening and east–west extension generated by the collision of the Arabian and Eurasian plates. Some of these basins are as large as several hundred square kilometres (e.g. Elazığ, Muş and Van Gölü basins), whereas others, situated farther to the north, are much smaller (e.g. Tercan, Askale, Pasinler and Kağızman-Tuzluca basins). For the Kağızman-Tuzluca Basin, Yılmaz and Şener (1984, Fig. 12) and Şaroğlu and Yılmaz (1986, Fig. 10) published some sketch stratigraphic columns and attributed a Pliocene age to the Cenozoic terrestrial deposits. As we will see below, the terrestrial deposits in the Kağızman-Tuzluca Basin have instead a time-range covering the Oligocene–Miocene interval, closer to the dating from its easterly continuation in Armenia.

In May 2010, our team aimed to establish a chronological framework for the Cenozoic deposits outcropping in the Tuzluca area of the Kağızman-Tuzluca Basin. Our search of vertebrate fossils led us to the discovery of some vertebrate remains in three formations. These fossils are characteristic enough to date some stratigraphic units of this basin, and are also well interesting for the knowledge of several vertebrate groups.

As described below, the sedimentary units of the Tuzluca area yielded some remains of a crocodile, an insectivore, two rodents and two rhinoceroses. For the last group, we collected four bones of a giant rhino, referable to *Paraceratherium*. *Paraceratherium* is for Cenozoic land mammals what the largest dinosaurs are for the Mesozoic world. Indeed, *Paraceratherium* is recognized as being among the largest land mammals that ever lived on Earth (Fortelius and Kappelman 1993). This genus and its relatives, grouped in the indricotheriine Hyracodontidae, are well-known from the Oligocene of Asia (China, Mongolia, Kazakhstan, and Pakistan), but scarcely in western Asia and southeastern Europe (Georgia, Turkey, Bulgaria and Romania; e.g. Antoine et al. 2008). Their dispersal history may be correlated with the paleogeographic evolution of the Alpine-Himalayan belt, in particular in the Middle East, and the environmental conditions, which prevailed during the Oligocene.

This paper aims to provide a comprehensive stratigraphy of the Kağızman-Tuzluca Basin in the Tuzluca area, and to describe the vertebrate remains collected from three stratigraphic units, for their identification and their biostrati-

graphic and paleobiogeographic significance and input. In addition, the discovery of the giant rhino *Paraceratherium* in the Kağızman-Tuzluca Basin questions the environmental context and paleobiogeographic relations of this area during the Late Paleogene and Early Neogene times.

## Geological setting

The study area is within the Eastern Turkish High Plateau lying east of the intersection point of the North and East Anatolian faults at Karlıova (see Şengör et al. 1985, 2008) where folds, thrust and strike-slip faults, and large-scale extensional fractures related to a shortening regime have been developing as a result of continent–continent collision during the Neotectonic episode (Şengör and Yılmaz 1981). Simultaneously with the shortening phase, structural basins developed such as intermountane and pull-apart basins. The Kağızman-Tuzluca Basin, which is interpreted as a ramp (Şengör et al. 1985) or pull-apart basin (Şaroğlu and Yılmaz 1986; Varol et al. 2009), is also accompanied by intense volcanism, which started during the Late Miocene. Our mapping (Fig. 1) has shown that the basin has suffered shortening and it is thus most likely to be an intermountane ramp valley (half-ramp?) basin. Its orientation is also incompatible with a pull-apart origin. The sub-active Holocene volcanic centers, such as Ararat (Ağrı) Mountain, have been controlled by active faults within the pull-apart basin structures (Şaroğlu and Yılmaz 1986; Yılmaz et al. 1998; Karakhanian et al. 2002). The Kağızman-Tuzluca Basin occupies a narrow area (40 km long and 10–15 km wide), which is crossed by the Aras River and continues into Armenia as the Araxes or Hoktemberian Basin (Balian 1969). It is bordered by the Cretaceous ophiolitic basement rocks of the Kağızman Complex to the south and the Late Miocene–Pliocene mafic volcanic rocks of the Kars Plateau to the north and west.

Detailed mapping of the Cenozoic deposits in the eastern part of this basin allowed the recognition of five successive sedimentary units (Varol et al. 2009). The Cenozoic infill starts with the marine deposits of the Kaan Formation (Fig. 2), which crop out in a limited area in the southwestern margin of the basin. They mainly consist of foraminifera bearing sandy limestones, rich in nummulites, dominated by *Nummulites fichteli* MICHELOTI, 1841, indicating an Early Oligocene age, more precisely the Rupelian SB 21–22 zones (Sirel, oral communication).

This marine unit is overlain by the Güngörmez Formation with a local unconformity. The Güngörmez Formation shows a complex depositional character, represented by vertical and lateral transitions of fluvial and deltaic deposits (Fig. 3a, b).

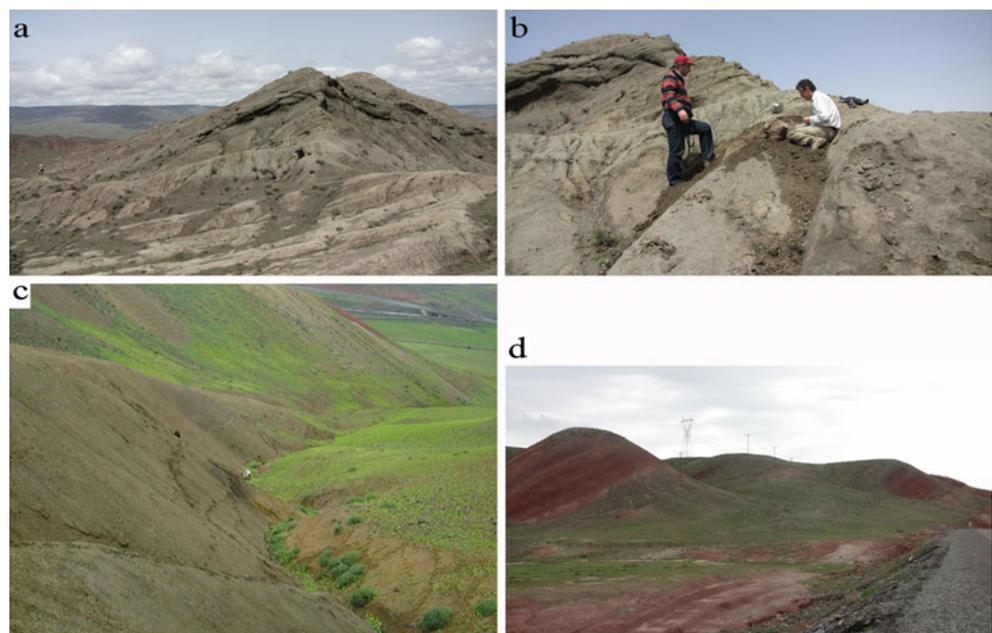
**Fig. 2** Cenozoic stratigraphy of the Kağızman-Tuzluca Basin in the Tuzluca region

SYSTEM	EPOCH	STRATIGRAPHIC UNITS		ENVIRONMENT	
		SE	NW		
CENOZOIC	PLEISTOCENE		RECENT ALLUVIUM	Fluvial	
			VOLCANICS	Volcanic	
			CONSOLIDATED ALLUVIUM	Fluvial	
	MIOCENE	LATE		TUZLUCA	Saline Pan
		MIDDLE		CINCEVAT	Fluvial
		EARLY		TURABI	Shallow Lake
	OLIGOCENE	LATE		GÜNGÖRMEZ	Fluvial - Delta
				KIZILKAYA	
				HALIKIŞLAK	
		EARLY		KAAN	Siliciclastic - Carbonate Shore
			UNKNOWN		
	MIDDLE		UYUZPINAR	Carbonate Platform	
MESOZOIC	CRETACEOUS	LATE		Basement	

Some layers within the deltaic deposits are rich in pollen and spores. They were dated as late Oligocene, based on the presence of the following taxa (determinations of Z. Batu): Spores: *Magnastriatites howardi*, *Baculatisporites* sp.; Pol-

len: *Pityosporites* sp., Compositae (Tubuliflorae type), Umbelliferae, Gramineae, *Subtriporipollenites simplex*, *Polyporipollenites undulosus*, Sparganiaceae, *Tricolpopollenites* sp.; Fungal Spores: *Anatolinites dongyngensis*, *Inapertis-*

**Fig. 3** Landscapes of the fossiliferous outcrops in the Tuzluca area (Kağızman-Tuzluca Basin). **a** Güngörmez Formation at the *Peracerasatherium* locality seen from the east; the fossiliferous spot is at the mid height of the section. **b** The fossil locality. **c** The crocodile bearing locality (dark horizon) in the Turabi Formation. **d** The small mammal locality (top of the hill) in the Cincevat Formation, seen from the southwest



*porites* sp. and *Dicellaesporites* sp. The fluvial deposits occur as meandering river, channel-fill and flood plain (overbank) facies. The remains of the giant rhinoceros, described here below, have been found in the channel margin deposits, mainly composed of sands ranging from very fine to coarse grained (Fig. 5).

The fluvial deposits grade upward to a lacustrine unit (Turabi Formation) mainly deposited in swamp environments (Fig. 3c). A layer in this formation yielded a crocodile tooth together with abundant fish bones and teeth, and some charophytes (*Nitellopsis* sp.) indicating shallow lake conditions (less than 10 m deep).

The lake deposits are conformably overlain by a red bed unit (Cincevat Formation) composed of flood plain, caliche and ephemeral stream deposits (Fig. 3d). A layer close to the base of this unit yielded some micromammalian fossils together with terrestrial small gastropods.

The last Neogene depositional unit outcrops around Tuzluca town, and it consists of thick evaporites (Tuzluca Formation), mainly composed of bedded halite and gypsum, formed in the saline pan and shallow saline lake environments, respectively.

## Material and methods

The fossil material described in this article was collected during a field trip carried out by the authors in May 2010. The specimens are stored in the Natural History Museum of the Turkish Geological Survey (Maden Tektik ve Arama (MTA)), in Ankara.

We found vertebrate remains at three localities from three successive formations. The rhinocerotoid limb bones have been found on a surface outcrop, some bones still in place, in the Güngörmez Formation at a locality about 8 km NW of Tuzluca and about 3 km N to Güngören village (Fig. 3a, b). The GPS coordinates of the locality are 40°05' 29.07" N and 43°34'20.37" E.

The Turabi Formation has been sampled at a locality situated about 4 km N of Tuzluca (GPS coordinates 40°03' 17.82" N and 43°44'2.18" E) (Fig. 3c). The screenwash of about 60 kg of sediment yielded many fish teeth and bones, one crocodile tooth and also two gyrogonites of charophytes determined as *Nitellopsis* sp.

A third locality, sampled at about 800 m north of the crossroads of Tuzluca, Kars and Erzurum, on the right bank of the road to Kars, yielded some remains of micromammals. This locality is situated at the lower part of the Cincevat Formation (Fig. 3d). Its GPS coordinates are 40°06'51.77" N and 43°37' 38.42" E. The fossiliferous horizon is formed of clays, rich in montmorillonite, and it contains relatively abundant shells of small gastropods. About 100 kg of matrix that we processed yielded four molars of cricetid rodents, three teeth

of an erinaceid insectivore and some unidentifiable tooth fragments of a lagomorph.

Except when mentioned, the dimensions are given in millimetres. The rhinocerotoid specimens were oriented following the protocol of Guérin (1980).

The anatomical abbreviations are: antero-posterior diameter (APD), diaphysis (dia), distal (dist), estimated (est), height (H), length (L), musculus (M; muscle), maximal (max), minimal (min), preserved (pres), proximal (prox), transverse diameter (TD).

The institutional abbreviations are: American Museum of Natural History, New York, USA (AMNH), Natural History Museum of the Turkish Geological Survey (*Maden Tektik ve Arama Genel Müdürlüğü*), Ankara, Turkey (MTA).

## Systematic paleontology

Order Crocodylia Gmelin, 1788  
 Superfamily Alligatoroidea Gray, 1844  
 Subfamily Diplocyonodontinae Brochu, 1999  
 Genus *Diplocynodon* Pomel, 1847  
*Diplocynodon* sp.

## Material

One tooth (Tuz-6), crown height >6.3 mm (the tip is broken), maximum basal width 2.8 mm.

## Locality

Dark clays in a ravine about 4 km north of Tuzluca town, Turabi Formation (Fig. 3c).

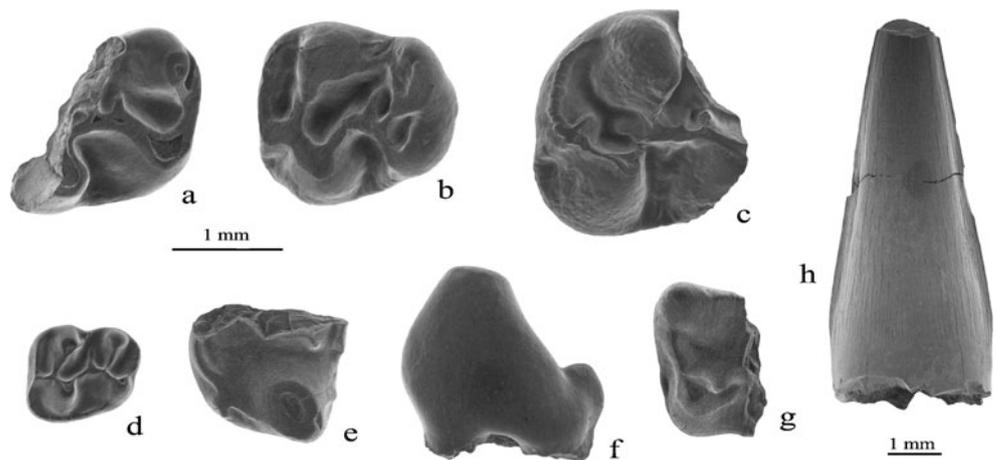
## Description and discussion

The crown is sharp and moderately curved lingually. The enamel is wrinkled, and it bears one anterior and one posterior sharp ridges all along the tooth depth (Fig. 4h).

The size of tooth indicates a small crocodile, no longer than 2 m in comparison to the extant species of the group. Such small and sharp teeth with anterior and posterior ridges are well-known for the species grouped in Alligatoroidea, and particularly in *Diplocynodon*, which is a common genus in Late Paleogene and Early Neogene of Eurasia (Ginsburg and Bulot 1997). Because of its great similarities with those of *Diplocynodon*, the unique tooth from the Turabi Formation is determined as *Diplocynodon* sp.

The record of a crocodile tooth in the Turabi Formation is of great interest for the environment and in some extent for the age of these deposits. Crocodiles are thermophilic

**Fig. 4** Small mammals from the Cincevat Formation (a–g) and a crocodile tooth from the Turabi Formation (h). *Cricetodon* cf. *meini*: a fragment of left M2, b left M3, c posterior part of right m1; *Vallaris* sp.: d left M2; Erinaceidae g. and sp. indet.: e fragment of right P3, f left p3, g posterior part of right m1; *Diplocynodon* sp.: h a tooth from lingual view



reptiles, and their extant relatives live exclusively or mostly in tropical and subtropical climates. It is assumed that their past representatives inhabited similar environmental conditions. Studies on the European vertebrate faunas and their biodiversity dynamics in relation with climatic and environmental parameters showed that the relative abundance of thermophilic taxa is closely controlled by mean annual temperatures (MAT) and the minimal cold month temperatures (mCMT). For most parts of Europe, MAT was between 15°C and 20°C during Paleogene and Early Miocene, while mCMT was above 5°C. MAT and mCMT show a sudden drop at about 14 Ma, leading to the extinction or at least to a great diversity drop of the thermophilic taxa, including crocodiles (Böhme 2003). The occurrence of a crocodile implies that the Turabi Formation deposited under subtropical warm environments. In addition, the crocodiles need the existence of permanent water, which is in agreement with the dominantly lacustrine sediments of the Turabi Formation.

Paleontological studies showed that crocodiles are well documented in Europe between Late Eocene and Early Miocene, but scarcely in a few sites of Middle Miocene (Ginsburg and Bulot 1997; Böhme 2003). In western and central Europe, their last occurrence is at the locality of Anwil (Switzerland) dated to about 13.5 Ma (Böhme 2003). However, Antunes (1994) noted that in the Iberian Peninsula the record of crocodiles reaches the earliest Late Miocene (MN9, 9.7–11.1 Ma), as well as in the Italian Peninsula (Kotsakis et al. 2004). The youngest European crocodile record (*Crocodylus* sp.) is reported from the Mio-Pliocene transition at Gargano in southern Italy (Delfino et al. 2007). The Middle and Late Miocene record in these regions consists in fact of littoral marine crocodiles referred to the genera *Tomistoma* and *Gavialis*, while *Crocodylus* sp. at Gargano, which is an African immigrant during the Messinian sea level drop. In Eastern Europe, Huene and Nikolov (1963) described a species of

crocodile named *Diplocynodon levantinicum* from the lignite mine near Radajevo in the western Maritsa Basin. They dated this fossil as “Mittel Pliocäne”, which corresponds to the Late Miocene in the present chronological charts. Ginsburg and Bulot (1997) demonstrated that the Radajevo crocodile remains, in particular the dentary, fit morphologically with that of *Diplocynodon rateli* from Saint-Gérard Le-Puy in France, dated to MN2 mammal zone, i.e. Late Aquitanian. The coal seams (with crocodiles) in the western Maritsa Basin are overlain by Vallesian sediments (Böhme, personal communication), so *D. levantinicum* from Radajevo is most probably of Middle Miocene age.

In Turkey, crocodiles are poorly documented. As far as we know from the available literature, no fossil crocodile has been described up today. Saraç (2003) mentioned the record of crocodiles in the Early Miocene localities of Alahıdır (Salihli-Manisa) and Baloluk (Yahyalı-Kayseri). According to the “fosFARbase” database (Böhme and Ilg 2003), 20 localities in Turkey yielded crocodiles, all with *Diplocynodon* sp. Their ages span from the Oligocene to the Middle Miocene, the youngest locality being Çandır in central Anatolia, dated to MN 5 ca. 16–16.5 Ma (Begun et al. 2003). In this database, there is no reference to any publication, and it is apparently built on personal observations of its authors. From this review, it can be assumed that the age of the Turabi crocodile locality might be Early Miocene or older.

This site in the Turabi Formation also yielded many lacustrine fish remains and a few gyrogonites of charophytes determined as *Nitelopsis* sp. This indicates calm and relatively shallow water environments.

Order Insectivora Bowdich, 1821

Family Erinaceidae Fischer de Waldheim, 1817

Erinaceidae genus and species indet.

## Material

Fragment of right P3, left p3 ( $1.67 \times 0.92$ ) and posterior half of a right lower molar ( $- \times 1.27$ ) (catalogue numbers Tuz-7 to 9).

## Locality

Right bank of the road from Tuzluca to Kars, about 8 km NNW of Tuzluca town, Cincevat Formation.

## Description and discussion

Three teeth from the Cincevat Formation are attributed to an erinaceid. The P3 is badly broken (Fig. 4e). It has a strong protocone, which is anteriorly situated. The hypocone is a tenuous bulge, of which is issued a ridge developed all along the posterior margin of the tooth. The p3 is two rooted (Fig. 4f). The outline of the occlusal surface is elliptical. The posterior margin is rounded and bears a well-identified small cusp. On the fragment of a lower molar (Fig. 4g), the hypoconid has an anterior ridge directed toward the protoconid. The posterior cingulum is weak.

This material is too poor and the characters that these teeth display are too scant to identify the genus to which they may belong. Their size and the morphology of their occlusal pattern recall small-sized erinaceid species that are numerous in the Late Oligocene and Miocene of Turkey (Hook Ostende 1992, 2001).

Order Rodentia Bowdich, 1821  
 Family Cricetidae Rochebrune, 1883  
 Genus *Cricetodon* Lartet, 1851  
*Cricetodon* cf. *meini* Freudenthal, 1963

## Material

A fragmentary left M2 ( $- \times 1.60$  mm), a left M3 ( $1.66 \times 1.53$  mm) and the posterior half of a right m1 ( $- \times 1.84$ ) (catalogue numbers Tuz-10 to 12).

## Locality

Right bank of the road from Tuzluca to Kars, about 8 km NNW of Tuzluca town, Cincevat Formation.

## Description and discussion

These teeth are brachydont and have globular cusps. The M2 has a short mesoloph, an anteriorly directed sinus, a short metalophule connected to the posteroloph, and a posterosinus still prominent (Fig. 4a). The M3 has the

posterior portion reduced (Fig. 4b). The labial anteroloph is a low ridge while the lingual anteroloph is a strong loph. The anterosinus is deep and open labially. The protoloph and metaloph are anteriorly oblique and connected to the anterior arm of the protocone and hypocone, respectively. The sinus is transverse, the mesoloph is strong but divided in two parts, the labial part being connected to the metalophule. The posteroloph is reduced but the posterosinus forms a deep fossette between the hypocone and posteroloph; this fossette is open posteriorly. There are three roots. The m1 has a longitudinal ridge rather central, a short mesolophid, a transverse sinusid, a strong ectomesolophid reaching the ectostylid, and a wide posterosinusid partly closed by the strong posterolophid, which joins the base of the entoconid (Fig. 4c). The posterolophid has an anterior spur, which is an equivalent of the posterior arm of the hypoconid that exists in some primitive cricetids.

The globular shape of the main cusps and the thick ridges between them prevent to compare these molars to that of *Deperetomys*. The bulk of their characters fit with that of the species referred to the genus *Cricetodon*. The size of these molars is smaller than that of the Middle Miocene species of this genus, such as *Cricetodon sansaniensis*, *Cricetodon hungaricus*, *Cricetodon jotae*, *Cricetodon pasalarensis* and *Cricetodon candirensis*, but falls in the variation of the species like *Cricetodon tobieni* (MN4, Turkey), *Cricetodon meini* (MN4-5, Europe) or *Cricetodon* n. sp. from Horlak 2 (MN4) (De Bruijn et al. 1993), and in the upper limit of *Cricetodon aliveriensis* (MN4, Greece; Klein Hofmeijer and De Bruijn 1988). These molars display some primitive features such as the presence of a strong posterosinus on the M2 and M3, anteriorly oblique lophs on the M3, and a complete ectomesolophid on the m1. The ectomesolophid on the m1 is observed in the species *Cricetodon kasapligili*, *Cricetodon tobieni*, *Cricetodon aliveriensis*, and on some specimens of *Cricetodon meini*. These species are all dated to the late Early Miocene, or slightly younger. This character is lost in the species such as *Cricetodon pasalarensis*, *Cricetodon candirensis*, *Cricetodon cariensis*, and *Cricetodon hungaricus*, all dated to the Middle Miocene. In summary, this material belongs to a primitive cricetodontine that we tentatively compare to *Cricetodon meini* because of its similarities in size and the occlusal pattern of the molars.

Genus *Vallaris* Wessels, Theocharopoulos, De Bruijn and Ünay, 2001  
*Vallaris* sp.

## Material

Left M2 ( $0.89 \times 0.78$  mm), Tuz-13.

## Locality

Right bank of the road from Tuzluca to Kars, about 8 km NNW of Tuzluca town, Cincevat Formation.

## Description and discussion

The unique M2 (0.89×0.78 mm) belong to a very small cricetid (Fig. 4d). The crown is extremely low. On its occlusal outline, the posterior part is slightly narrower than the anterior part. The labial and lingual anterolophs are equally strong. The protolophule is simple and connected to the anterior arm of the protocone. The metalophule is anteriorly oblique and connected to the anterior arm of the hypoconid. The mesoloph is moderately developed. The sinus is wide, transverse and lingually closed by a thick cingulum, which is in continuation of the lingual anteroloph. The roots are missing.

This tooth obviously belongs to a small-sized cricetid. We compared it with all small-sized species of the genera *Democricetodon* and *Megacricetodon*, which are common in Early–Middle Miocene localities all over Eurasia. This M2 is smaller than the M2 of the smallest species of these genera, i.e. *Democricetodon anatolicus* Theocharopoulos 2000 and *Megacricetodon tautavelensis* Lazzari and Aguilar, 2007. The smallest species ever described for *Democricetodon* is *D. anatolicus* from Harami and Kılçak (MN1/2, Central Turkey) in which the M2 measures 1.02×0.92 mm (range for 17 specimens is 0.96–1.05×0.88–1.05) (Theocharopoulos 2000). In addition, the M2 of *Democricetodon* species has double and symmetric protolophule, and the lingual cingulum is absent or weak. The smallest species of *Megacricetodon*, *M. tautavelensis* from Blanquatière 1 (MN4/5, Southern France) has M2 measuring 0.98×0.86 mm (range for 78 specimens is 0.83–1.07×0.75–0.95) (Lazzari and Aguilar 2007). The M2 of *Megacricetodon* species is generally elongated, higher crowned, usually has a paracone with a posterior spur, and simple or double protolophule.

Both the size and morphology of this M2 fit with that of *Vallaris zappai* Wessels et al. 2001 from the localities of Keseköy (Bolu dept.) and Sabuncubeli (Manisa dept.) in Turkey (Wessels et al. 2001; De Bruijn et al. 2006). Both localities are dated to late Early Miocene (MN3 zone). Although no marked difference is observed between this tooth and the M2s described by Wessels et al. (2001) from Keseköy, the type locality of *V. zappai*, the single M2 from Tuzluca cannot allow species determination. Wessels et al. (2001) referred this taxon to the Myocricetodontinae, underlining its interest as a basal form of this subfamily and potentially ancestor to later genera such as *Sindemys*, *Punjabemys* and *Myocricetodon*. The attribution of *Vallaris*, as well as *Sindemys*, to the subfamily Myocricetodontinae

is a matter of debate, which is out of the purpose of the present study.

Order Perissodactyla Owen, 1848

Superfamily Rhinocerotoida Gray, 1821

Family Hyracodontidae Cope, 1879

Subfamily Indricotheriinae Borissiak, 1923

Genus *Paraceratherium* Forster-Cooper, 1911

*Paraceratherium* sp.

## Material

Tuz-04, thoracic vertebra (adult), fragmentary centrum; Tuz-01, left humerus (large adult), broken in two parts; Tuz-02, left radius (middle-sized adult), distal end; Tuz-05, diaphysis of a right Mc4 (gigantic adult); see Fig. 5a–f.

## Locality

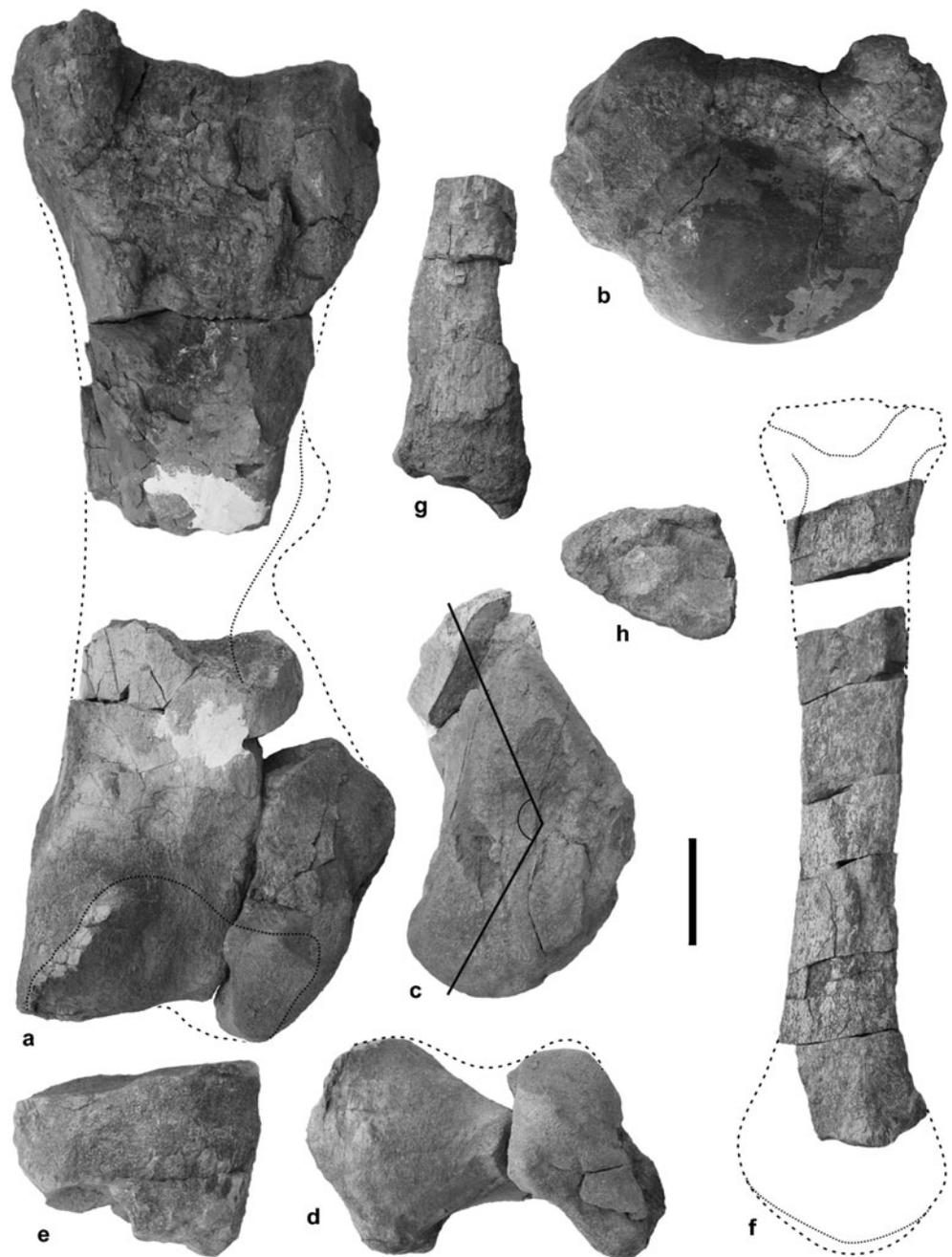
About 3 km north of Güngören village, Güngörmez Formation, Kağızman-Tuzluca Basin, Northeastern Anatolia.

## Description and comparison

Tuz-04 is a fragmentary centrum of a vertebra (pres TD=150; max pres H=98; pres APD=126). Although no costal facet is preserved, Tuz-04 is interpreted as an 11<sup>th</sup> to 13<sup>th</sup> thoracic vertebra, due to (1) the isometric and cordiform shape of the ventral part in anterior and posterior views, (2) the absence of a ventral crest and ventrally displaced transverse processes, and (3) the regular convexity/concavity of the intervertebral facets. This tentative identification is consistent with most rhinocerotoid vertebrae (Hünemann 1989; van der Made 2010: Figs. 16–17; POA, personal observation). More precisely, and given its dimensions, Tuz-04 fits the detailed description of thoracic vertebrae of *Paraceratherium transouralicum* (= *Baluchitherium grangeri* sensu Granger and Gregory 1936; = *Indricotherium transouralicum* sensu Gromova 1959) as provided by Granger and Gregory (1936: 29–32, Figs. 14–15).

The left humerus Tuz-01 belongs to a large adult individual (i.e. equivalent to grade II, sensu Granger and Gregory 1936). It is quite complete, but split off into two distinct parts (proximal and distal ends) without any connection between them (Fig. 5a). However, and with comparison to other available humeri of indricotheres (e.g. Forster-Cooper 1923; Granger and Gregory 1936; Gromova 1959; Gabunia 1964), its length could be estimated at ca. 970 mm (Table 1). The proximal part is well preserved, even if the cortical layer has disappeared by places. The proximal end is large (TD=375; APD=340), D-shaped in

**Fig. 5** a–f *Paraceratherium* sp. from the Late Oligocene of the Kağızman-Tuzluca Basin, Eastern Turkey. Tuz-01, left humerus (large adult), broken into two parts, in anterior view (a), proximal view (b), lateral view of the distal end with the angle between the diaphysis and the distal trochlea ca. 130° (c), and distal view (d). Tuz-02, distal end of a left radius (middle-sized adult), in posterior view (e). Tuz-05, diaphysis of a right Mc4 (large adult), in medial view (f). g–h, Rhinocerotidae, gen. et sp. indet. Tuz-03, distal end of a right tibia, in medial view (g) and distal view (h). Dashed lines suggest preferred hypothetical reconstructions (long dashes are used for outlining the bones and short dashes for outlining finer structures, such as cristae or articular facets), based on Forster-Cooper (1923), Granger and Gregory (1936), and/or Gromova (1959). Scale bar=10 cm



proximal view, with a rounded posterior side and a subrectilinear anterior one (Fig. 5b). The scapular facet (caput humeri) is huge (TD=210; transverse linear L=300; APD=270), biconvex (much more sagittally than transversely), oval, and elongated transversely. It faces upward, as in *Paraceratherium bugtiense* from the Bugti Hills, Pakistan (= *Baluchitherium osborni*; Forster-Cooper 1923: 43, Fig. 9) and *P. transouralicum* from Mongolia (Granger and Gregory 1936). The tuberculum majus (=trochiter major) forms a large anterolateral process, slightly higher than the head (i.e. much lower than in rhinocerotids) and separate from the lower and more extended posterolateral

process (convexity of the tuberculum majus) by a sulcus. A shallow groove lies next to the lateral border of the caput humeri, separating it from the tuberculum majus. The concerned area is facing upward; it displays a dozen vascular foramina. At the anteromedial angle of the proximal head, the tuberculum minus is extremely developed, much more elevated than the tuberculum majus, and forming a huge process frontward as in *P. bugtiense* (Forster-Cooper 1923: 43, Fig. 9). On the anterior side, both the crista tuberculi minoris and the crista tuberculi majoris are developed and converging distally. In medial view, the collum humeri is not marked at all. In proximal

**Table 1** Compared measurements of humeri from large Oligocene indricothere rhinocerotoids, after Pavlova (1922), Osborn (1923), Forster-Cooper (1924), Granger and Gregory (1936), Gromova (1959), Fortelius and Kappelman (1993), personal observation by POA, and the current work

Measurements	<i>Paraceratherium</i> sp. Güngören (this work)	<i>Paraceratherium bugtiense</i> (Pilgrim 1910)	<i>Paraceratherium prohorovi</i> (Borissiak 1939)	“ <i>Indricotherium</i> ” <i>transouralicum</i> (Pavlova 1922)
Length				
L	Est 970	840–848	623	est. 900–est. 1200
Prox end				
TD	375	>230–238	200	242–(376)
APD	340	>180 to 199	177	–
Prox art				
TD	210	–	–	–
APD	270	–	–	–
Min dia				
TD	(200)	167	122–156	–
APD	(152)	122 to >125	109–112	–
Lat epic				
TD	308	318	219–270	312
Dist end				
TD	240	220–235	184–194	272
APD	210	188	128–155	195
Dist art				
TD	(230)	164–(170)	–	–
Dist art med				
TD	Est 140	100	–	–
APD	175	(100)–118	–	–
Dist art min				
APD	95	67–87	–	–
Dist art lat				
TD	Est 90	64–(70)	–	–
APD	130	80–105	–	–

*Baluchitherium osborni* and *Baluchitherium grangeri* are here considered as junior synonyms of *I. transouralicum* and of *P. bugtiense*, respectively, as stated by Lucas and Sobus (1989). The measurements provided by Granger and Gregory (1936) for “*B. grangeri*” are included in the corresponding column

APD antero-posterior diameter, ART articulation, DIA diaphysis, EPIC epicondyle (epicondylus), EST estimated, L length, MIN minimal, PRES preserved, PROX proximal, TD transverse diameter

view, the sulcus intertubercularis is wide and shallow (Fig. 5b). The parts of the diaphysis corresponding to the subscapular muscle, the tuberositas deltoidea, and most of the crista humeralis are damaged and/or lacking (Fig. 5a). In its median part, the diaphysis has an ovoid cross section, wider than deep (TD min≈200; APD min≈152). The epicondylus lateralis is wide (TD=308) and located ca. 210 mm above the distal end. In anterior view, the edge of the crista supracondylaris lateralis forms a dihedron with an angle ca. 105°, similar to what is observed in *P. bugtiense* (Forster-Cooper 1923: 43, Fig. 9) and in *Paraceratherium prohorovi* from Kazakhstan (Gromova 1959: pl. 10), but lesser than in *P. transouralicum* (ca. 130° in AMNH 29166; Granger and Gregory 1936: Fig. 23A) and *Benaratherium callistrati* from Georgia (ca. 130° in n°7/340; Gabunia

1964: 93, Fig. 48). The fossa coronoidea and the fossa radialis are shallow. In lateral view, the angle between the diaphysis and the distal end equals ca. 130° (Fig. 5c), i.e. less than in *P. transouralicum* (ca. 145° in AMNH 29166; Granger and Gregory 1936: Fig. 23B), and more than in recent rhinocerotids (e.g. ca. 115° in *Diceros bicornis*; Guérin 1980: 81, Fig. 10). There is no distal expansion of the epicondylus lateralis, as in *P. transouralicum*, *P. prohorovi* and *P. bugtiense*, but contrary to what is observed in most rhinocerotids (Antoine, 2002). Most of the distal articulation is badly eroded, but the wide radius-facet (TD≈230) shows three parts: a large and conical medial lip (TD≈140; APD max=175), narrowing laterally (down to ca. 95 mm), a smaller lateral lip, widening laterally (APD ranging from ca. 95 mm up to 128 mm), and

a lateralmost cylindrical condyle ( $APD \approx 130$ ). This shape, i.e. devoid of capitulum humeri, is typical of rhinocerotoids among mammals (e.g. Antoine, 2002); it further impedes referring this specimen to a large elephantoid of similar gigantic dimensions, such as *Mammuthus meridionalis* (Christiansen 2004). In lateral view, the epicondylus lateralis shows a small central pit in its anterior side, surrounded proximally by a smooth and curved prominence. This area is probably central to the insertion of the *M. extensor carpi radialis*. In posterior view, the fossa olecrani is wide, low, and strikingly shallow ( $TD=150$ ;  $APD \approx 60$ ;  $H \approx 110$ ), which corresponds to the classical indricothere pattern. In distal view, the epicondylus medialis is small, thick, and short both transversely and sagittally, while the epicondylus lateralis is extremely developed postero-laterally (Fig. 5d). As a consequence, the distal end is as deep laterally as medially (lateral  $APD =$  medial  $APD \approx 210$ ). A similar morphology is observed in *P. bugtiense* (J2-PB48; our unpublished data).

Only the distal end of the left radius Tuz-02 is preserved. It belongs to a middle-sized adult (grade III sensu Granger and Gregory 1936;  $TD=230$ ;  $APD=160$ ). As such, it may not belong to the same individual as the humerus Tuz-01 (large adult: Grade-II). The cortical surface is generally well preserved and most articular facets are observable. In anterior view, the gutter for the *M. extensor carpi* is absent, like in *P. prohorovi* (visible in distal view; Gromova 1959; Fig. 12) and *P. bugtiense* (POA, personal observation), but contrary to *P. transouralicum*, in which this gutter is deep and wide (Granger and Gregory 1936: Fig. 24A); the anterodistal edge is sigmoid and oblique, the scaphoid-facet being much more distal than the ulna-facet. The distal outline is more angular, due to the still more distal position and flat shape of the posterior part of the scaphoid-facet. In medio-distal view, the scaphoid-facet is also sigmoid, first concave and forming a right dihedron in its anterior half, then regularly convex in its posterior half. Such morphology recalls what is observed in undescribed specimens referred to *Paraceratherium* sp. from the Oligocene of North Central Anatolia (Bağatlı-1; POA, personal observation) and, to a lesser extent, the concerned shape of radii and scaphoids of *P. bugtiense* from the Oligocene of the Bugti Hills, Pakistan (Forster-Cooper 1923: Figs. 13, 18; POA, personal observation). Gromova (1959) does not provide any illustration for the concerned part of the radius of *P. prohorovi*. The scaphoid-facet seems to be rather similar in *P. transouralicum* (AMNH 29166; Granger and Gregory 1936: Fig. 24). In lateral view, only the anterior part of the ulna-facet is preserved ( $H=40$ ). Above it, the smooth bone surface indicates that the ulna and the radius were neither fused nor in contact along their diaphyses. In posterior view, the medial expansion of the scaphoid-facet is not preserved (Fig. 5e); the ulna-facet is flat and oriented

at ca.  $45^\circ$  with respect to the vertical line (Fig. 5e). In distal view, the distal end forms a transversely elongated oval, similar to what is observed in *P. prohorovi* (Gromova 1959, Fig. 12) and *P. bugtiense*. The D-shaped scaphoid-facet ( $TD=78$ ;  $APD=100$ ) is much more prominent than the concave and depressed semilunate-facet ( $TD=68$ ;  $APD \approx 97$ ), the medial border of which is sagittal, subvertical, and ca. 40 mm high, as in *P. prohorovi* (Gromova 1959, Fig. 12) and *P. bugtiense*. The lateral part of the distal articulation is badly damaged, which impedes stating on the presence/absence of a pyramidal-facet.

Tuz-05 is a straight and narrow shaft (Fig. 5f), broken into two disconnected parts and almost devoid of any cortical and/or articular surface (est pres  $L=595$ ). Shape and proportions discard referral to a humerus, a radius, a femur, a tibia, or central metapodials (e.g. Granger and Gregory 1936; Gromova 1959). It is too much slender for being part of an ulna and too much robust for being a fibula (Granger and Gregory 1936: 48, Fig. 29). Besides, the absence of a planar symmetry impedes considering it as a processus spinosus of a thoracic vertebra (Granger and Gregory 1936). The proximodistal and sagittal elongation of the concerned specimen, as well as its distal widening and its gigantic size, are only consistent with lateral metapodials of indricotheriines. Given the hypothesized orientation of the bone (flat and straight side next to the central – and always much larger – metapodial; insertion of the *M. interosseus* reaching the distal third of the diaphysis), it may correspond to the body of a right Mc4. Tuz-05 compares well with the Mc4s of *P. bugtiense* (partly reconstructed; Forster-Cooper 1923: 48, Fig. 13) and *P. prohorovi* (Gromova 1959: pl. 20, Fig. 3) whereas it is much straighter in anterior view than the Mc2 and Mc4 of *P. transouralicum* illustrated by Granger and Gregory (1936: 46, Fig. 27). The latter two are twice smaller than Tuz-05, which inferred complete length is estimated at ca. 790 mm (Fig. 5f). In cross section, Tuz-05 is mostly oval, transversely compressed, and sagittally elongated, especially in its proximal part (prox  $TD > 48$ ; prox  $APD > 125$ ; min  $TD$  dia  $\approx 52$ ; min  $APD$  dia = 91). The medial side is straight and flat, while the lateral side is more rounded. The distal end is more robust, with a semi-circular cross section (dist  $TD > 98$ ; dist  $APD > 140$ ) and the ignition of what could have been a distal cochlea (Fig. 5f). This identification is tentative, as to our knowledge, no metapodial of such a huge size was recorded in the available indricotheriine record so far (Forster-Cooper 1923; Granger and Gregory 1936; Gromova 1959; Fortelius and Kappelman 1993; our unpubl. data).

## Discussion

The morphological features observed in Tuz-01, Tuz-02, Tuz-04, and Tuz-05 allow referring them to an indricotheriine rhinocerotoid, probably documenting a single species.

In the last taxonomic revision of the subfamily Indricotheriinae, Lucas and Sobus (1989) recognized only two valid large-sized genera: *Urtinotherium* Chow and Chiu, 1963, from the early Oligocene of Asia (no postcranial material available), and *Paraceratherium* Forster-Cooper, 1911, from the late early and late Oligocene of Asia and Eastern Europe. *Paraceratherium* includes notably the species previously referred to *Baluchitherium* Forster-Cooper, 1913b and *Indricotherium* Borissiak, 1915, i.e. *P. bugtiense* (Pilgrim, 1910) from the Bugti Hills of Pakistan (Pilgrim 1910; Forster-Cooper 1913a, 1913b, 1924, 1934; Welcomme et al. 1999, 2001; Antoine et al. 2004), *P. transouralicum* (Pavlova, 1922) and *P. prohorovi* (Borissiak, 1939) from Asia and southeastern Europe (Osborn 1923; Granger and Gregory 1936; Gromova 1959; Nikolov and Heissig 1985; Codrea 2000), and *P. orgosensis* (Chiu, 1973) from China (Chiu 1973; Xu and Wang 1978). Other authors, such as Gromova (1959), Spassov (1989), or Fortelius and Kappelman (1993) do consider *Indricotherium* and *Paraceratherium* as distinct genera. *B. callistrati* Gabunia, 1955 is an indricothere of controversial affinities from the late Oligocene of Georgia (Gabunia 1964). Given its hypodigm, this taxon could not be directly compared with the present specimens, except for the distal part of the humerus.

The humerus Tuz-01, the fragmentary radius Tuz-02, and the putative Mc4 Tuz-05 compare very well with those of *P. bugtiense*, from the Oligocene of Pakistan (humerus and Mc4; Forster-Cooper 1923) and of *P. prohorovi*, from the Oligocene of Kazakhstan (humerus, radius, and Mc4; Gromova 1959), from which they do not differ significantly. On the other hand, the shape of the humerus (lateral edge of the crista supracondylaris lateralis forming an angle ca. 105°; angle of ca. 130° between the diaphysis and the distal trochlea in lateral view) and the morphology of the radius (absence of a distal gutter for the M. extensor carpi; oval outline for the distal end in distal view) are quite distinct in *P. transouralicum* (= *B. grangeri*; Granger and Gregory 1936) and in *B. callistrati* (Gabunia, 1964). The characteristics of the putative Mc4 Tuz-05 would tend to confirm this clustering, whereas the vertebral centrum Tuz-04 is of no use for such a purpose. The present specimens are therefore tentatively referred to as *Paraceratherium* sp.

As far as the concerned postcranial elements are significant for  $\alpha$ -taxonomy, *Paraceratherium* sp. from the Kağızman-Tuzluca Basin (this work), *Paraceratherium* sp. from central Anatolia (Antoine et al. 2008), *P. bugtiense*, and *P. prohorovi* appear much similar one to each other than to *P. transouralicum* and to *B. callistrati*. If confirmed on a phylogenetic ground (i.e. on a much wider sample), this would justify splitting again *Paraceratherium* Forster-Cooper, 1911 and *Indricotherium* Borissiak, 1915, the latter

being monotypic and restricted to *I. transouralicum* Pavlova, 1922, which “*B. callistrati* Gabunia, 1955” would perhaps be a junior synonym.

Family Rhinocerotidae Gray, 1821

Rhinocerotidae genus and species indet.

Material

Tuz-03, right tibia, distal end.

Locality

As for *Paraceratherium* sp.

Description and comparison

Tuz-03 is the distal part of a right tibia belonging to an adult individual. It is badly damaged by places (e.g. anterior and medial sides of the diaphysis; anterodistal and posterodistal edges). This bone (pres L=320; TD>104; APD>81) was smaller and slenderer than any tibia referred to an Oligocene indricotheriine (Forster-Cooper 1923; Granger and Gregory 1936; Gromova 1959). On the other hand, this size is consistent with that of large rhinocerotids, such as the widespread teleoceratines *Brachypotherium* and *Diaceratherium* (Cerdeño 1993), or the enigmatic chilothere-like *Aprotodon smithwoodwardi* from the late Oligocene of the Bugti Hills, Pakistan (Métais et al. 2009; POA, personal observation). The diaphysis is tear-shaped in cross section, with a sharp lateral edge (margo interosseus): the tibia and the fibula were only in contact in the distalmost 100 mm, but the fibula-facet is not preserved. The anterodistal groove is not observable (damaged area). In medial view, there is no medio-distal gutter corresponding to the tendon of the M. tibialis posterior (Fig. 5f). The malleolus medialis is high, triangular, acute, and medially pinched (i.e. with a subvertical medial edge). Such morphology discards any referral to indricotheriines, which have a low and rounded symmetrical malleolus medialis (Forster-Cooper 1923: 45, Fig. 12; Granger and Gregory 1936: Fig. 29; Gromova 1959: pl. 11, Fig. 1), but it recalls what is observed in most Oligocene rhinocerotids (Antoine 2002: 212–213). In distal view (Fig. 5g), the distal end has a trapezoidal outline, with a very small lateral side (TD>158; APD≈125). The anterior and medial borders form a right angle and the posterior edge is oblique. Again, this trapezoidal outline recalls the plesiomorphic rhinocerotid pattern (e.g. *Ronzotherium filholi* and *Pleuroceros blanfordi*; Antoine 2002: 210, Fig. 247; Antoine et al. 2010: 150, Fig. 7), quite distinct from the rectangular indricotheriine pattern, as exemplified in *P. prohorovi* (Gromova 1959: pl. 12, Fig. 2). The astragalus-facet (TD>135; APD≈90) consists of two

cochleae. The medial one is deeper (larger APD) and more biconcave than the sub-planar lateral cochlea. Both cochleae are separated by a smooth sagittal edge, forming an angle ca. 135° in transverse longitudinal section. In medial view (Fig. 5g), the distal articulation (astragalus cochlea) is oriented down- and frontward, contrary to what occurs in indricotheriines (facing downward; Forster-Cooper 1923: 45, Fig. 12A; Granger and Gregory 1936: 48, Fig. 29B).

## Discussion

On both metrical and morphological grounds, this fragmentary tibia cannot be referred to an indricotheriine rhinocerotoid. Yet, the concerned morphology (high, acute and medially pinched malleolus medialis; trapezoidal distal outline; astragalus cochlea oriented down- and frontward) is consistent with most large Oligocene-early Miocene rhinocerotids, such as the teleoceratines *Diaceratherium* and *Brachypotherium* (Cerdeño 1993) or the stem rhinocerotid *Mesaceratherium* (e.g. Antoine et al. 2010). Given the concerned stratigraphical interval, the large size of this tibia—for a rhinocerotid—might be indicative of either a large teleoceratine (*Diaceratherium* or *Brachypotherium*) or the enigmatic rhinocerotid *Aprotodon*, recorded in the late Oligocene and the earliest Miocene of Asia (Qiu and Xie 1997; Métails et al. 2009) but for which tibiae are not known so far. However, this specimen is not sufficient to ensure any identification at tribe, genus, and/or species level.

## Conclusions

### Age of the deposits

Based on such a restricted postcranial sample—therefore likely not to be pertinent at a wider scale—the indricotheriine rhinocerotoid from Kağızman-Tuzluca Basin seems to be more closely related to *P. bugtiense* (from Pakistan), *P. prohorovi* (from eastern Kazakhstan), and *Paraceratherium* sp. from North central Anatolia than to *P. transouralicum* (from Mongolia, Inner Mongolia and Kazakhstan) and *B. callistrati* (from Georgia).

*Paraceratherium* occurs in Asia and Eastern Europe throughout the late early to late Oligocene (for review, Antoine et al. 2008). The Turkish record of indricotheres was so far restricted to the Late Oligocene of the Çankırı-Çorum Basin (Antoine et al. 2008).

A similar rhinocerotoid association (rhinocerotid+*Paraceratherium* sp.) was described in the late Oligocene of Pakistan (Antoine et al. 2003, 2004; Métails et al. 2009) and of Turkey (Antoine et al. 2008). Consequently, a Late

Oligocene age is attributed to the Göngörmez Formation, which yielded the rhinocerotoid remains.

The age of the overlying Turabi Formation is tentatively determined as Early Miocene based unique occurrence of a crocodile. As discussed above, crocodiles become extinct or widely reduced in middle latitudes of northern hemisphere by the end of the Early Miocene.

The overlying Cincevat Formation yielded, at a level close to its base, a small mammalian fauna including insectivores, rodents and some tooth fragments of lagomorphs. The much interesting species for the age of this locality are *Cricetodon* cf. *meini* and *Vallaris* sp. The latter form is only known in Turkey from the localities of Keseköy and Sabuncubeli, both dated to MN 3 mammal zone, i.e. late Early Miocene. The species *C. meini* has a wide distribution in western, central and southeastern Europe in the localities dated to the late Early Miocene and basal Middle Miocene (MN 4 and MN 5 mammal zones). Consequently, an age of late Early Miocene is suggested for the fossiliferous level. This age attribution implies that the Cincevat Formation might span across the Early–Middle Miocene boundary.

### Paleobiogeography

The vertebrate localities in the Kağızman-Tuzluca Basin yielded an indricotheriine rhinocerotoid of Late Oligocene age, a crocodile, an erinaceid and two cricetids of Early Miocene. The dispersal history of these groups is of great interest to enlighten paleobiogeographic relationships of Eastern Anatolia with the neighbouring landmasses.

Giant rhinocerotoids, or Indricotheriinae, were flourishing in Eurasia during the Oligocene (e.g. Lucas and Sobus 1989). They are particularly well documented in South Asia (Pilgrim 1910; Forster-Cooper 1911, 1924; Antoine et al. 2004), Central Asia (Borissiak 1915; Pavlova 1922; Osborn 1923; Granger and Gregory 1936; Gromova 1959; Lucas and Bayshashov 1996), and China (Chow and Chiu 1963; Chiu 1973; Xu and Wang 1978). The Oligocene of Asia Minor and Southeastern Europe also yielded indricotheres in the last decades, first in Georgia (Gabunia 1955, 1964), in Montenegro (Petronijevic and Thenius 1957), in Bulgaria (Nikolov and Heissig 1985), and in Romania (Codrea 2000), then in Turkey (Gözükızıllı, North central Anatolia; Antoine et al. 2008). Along with a diversified mammal assemblage, the latter report notably attested to strong faunal affinities between central Anatolia and adjacent areas such as Europe and Asia, including Greater India, throughout late Oligocene times (Antoine et al. 2008). Indeed, during the Late Oligocene, the indricotheres had their largest dispersal, from Mongolia to the Balkans. This implies continuity of landmasses and similarity of environmental conditions across this large area. This assumption

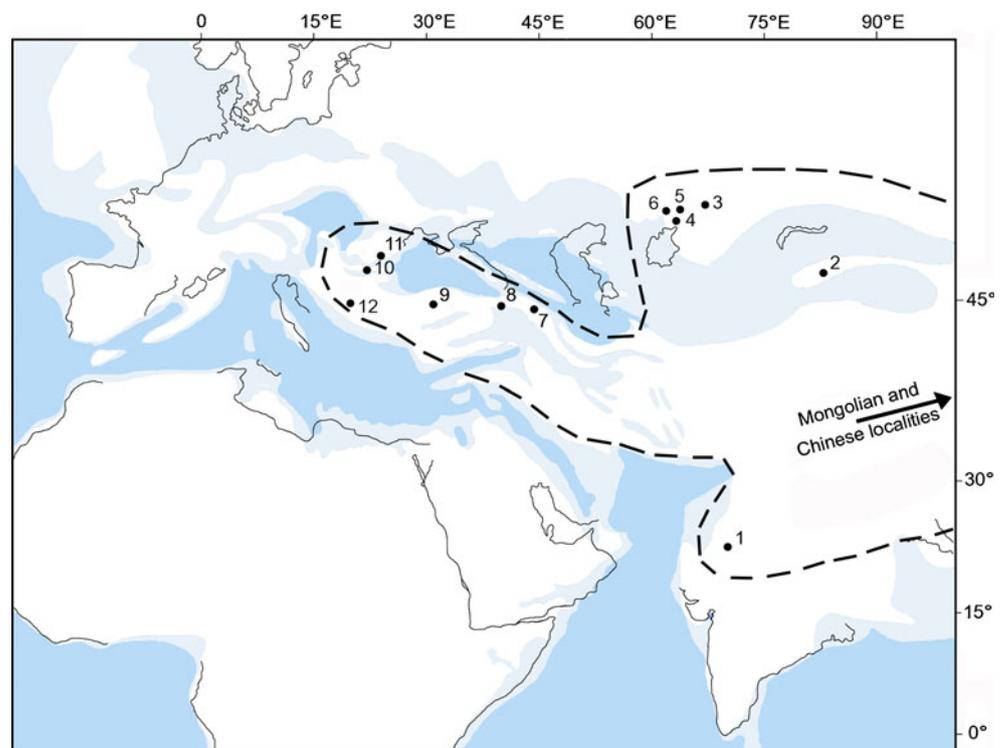
contradicts the paleogeographic maps that indicates an Anatolian land almost isolated from the neighbour continents by divers branches of the Neo-Tethys during the Late Oligocene (Rögl 1998; Meulenkamp and Sissingh 2003; Popov et al. 2004). In these maps the Anatolian land is connected to Asia via Elbroz and Kopet Dagh highlands landbridge. The paleogeographic map of Barrier and Vrielynck (2008) draws also several shallow sea barriers between the Anatolian land and Central Asia, but separated from the Arabian Plate by a narrowed Neo-Tethys Ocean. At any case, the distribution of indricotheres during the Late Oligocene from Mongolia in the east to Montenegro in the Balkan Peninsula shows that this group was well successful in occupying such a large area despite some marine barriers that paleogeographic maps unanimously places on their routes (Fig. 6). Our findings support the interpretation by Şengör et al. (2008), who posited the presence of a wide fore-arc region extending from the Katawaz Basin in southeastern Afghanistan via the Pakistani and Iranian Makran all the way into eastern Turkey. The Serravallian marine fossils collected by Gelati (1975) near Lake Van had suggested that parts of this accretionary prism had remained under water until then. But it now appears that the northerly parts of this accretionary prism had already surfaced in the Late Oligocene and allowed land animals to wander along it, as it is expected from a developing subduction-accretion complex.

Perea et al. (2010) drawn a similar paleogeographic scenario by studying phylogenetic relationships of Leucis-

cinae (Teleostei, Cyprinidae) inferred from both mitochondrial and nuclear gene data. According to their molecular evolutionary rate based on a relaxed molecular clock and all-gene database, the main Mediterranean leuciscine lineages originated in Asia and diversified during the Oligocene. These authors hypothesize the presence of a continuous landmass (Balkanian/Anatolian/Iranian landmass) during the Early Oligocene, which enabled the dispersal of these freshwater fishes from Asia to Europe and to the Mediterranean realm. They “propose an initial leuciscine colonization of Europe from southwestern Asia via the Balkanian–Anatolian–Iranian landmass at the beginning of the Early Oligocene”. However, according to these authors, “marine connections fragmented this landmass around 28 mya into the huge Balkanian and Anatolian islands” (Perea et al. 2010, p. 17). The latter paleogeographic scenario does not fit with the presence of indricotheres during the Late Oligocene in territories spanning from East Asia to the Balkans, because such a continuous extension of the “indricothere fauna” implies connected landmasses all along their dispersal areas.

The crocodile tooth found at the Turabi Formation belongs to a taxon, *Diplocynodon* sp., having a large dispersal in time (Early Eocene–Middle Miocene) and space (all southern and central Europe, from Portugal to Turkey; Ginsburg and Bulot 1997; Böhme and Ilg 2003). The Turabi locality is therefore the easternmost occurrence of this crocodile, enlarging somewhat its dispersal area to the east.

**Fig. 6** Probable dispersal area of the indricotherines during the Oligocene (dashed lines) on a palinspastic map of the Late Rupelian (after Barrier and Vrielynck 2008, modified). The localities which yielded indricothere rhinocerotoids are 1, Lundo Chur (Pakistan); 2, Aktau Mountain; 3, Turgai; 4, Agispe-Petrovskovo; 5, Altyn Shokysu; 6, Chelkar Tenis (Kazakhstan); 7, Benara (Georgia); 8, Tuzluca; 9, Gözükiçilli (Turkey); 10, Dragovishtiza (Bulgaria); 11, Turea Cornesti, Fildu Tetis and Sutoru (Romania); 12, Ivangrad (Montenegro)



The muroid rodent *Vallaris* sp. from the Cincevat Formation remains restricted to Turkey during the Early Miocene. In the late Early Miocene, the genus *Cricetodon*, recorded in the same locality, is well-known in Turkey during the Early and Middle Miocene. This genus is accepted as originated in western Asia (De Bruijn et al. 1993). It spreads out suddenly to all Eurasia ca. 17 Ma (MN 4 mammalian zone), and it is thereafter reported as well from China, Central Asia and Central and Western Europe.

In conclusion, the Anatolian land seems to have close terrestrial connections with Asia and the Balkans during the Late Oligocene and with Asia and Europe during the Early Miocene.

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