

# A giant rhinocerotoid (Mammalia, Perissodactyla) from the Late Oligocene of north-central Anatolia (Turkey)

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Received 3 March 2006; accepted for publication 4 June 2007

A giant rhinocerotoid is described for the first time south of the Black Sea, in Turkey. The single specimen, a fragmentary radius referred to *Paraceratherium* sp., originates from conglomerates nearby at Gözükizilli, in the Çankiri–Çorum Tertiary basin. These layers correspond to the Lower member of the Kizilirmak Formation. The same locality (Gözükizilli-2) yields also the small rhinocerotid *Protaceratherium* sp., cf. *P. albigense* (Roman, 1912). Three other mammal localities (Gözükizilli-1, in the Lower Member of the formation, with several rodent species; Tepe 641 and Kizilirmak, in the Upper Member, with a diversified micro- and macro-mammal fauna) allow us to refer the Kizilirmak Formation as a whole to the Late Oligocene. All the observed taxa have strong Asian and/or European affinities, which precludes any geographical insulation for this part of Anatolia during the Late Oligocene. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 152, 581–592.

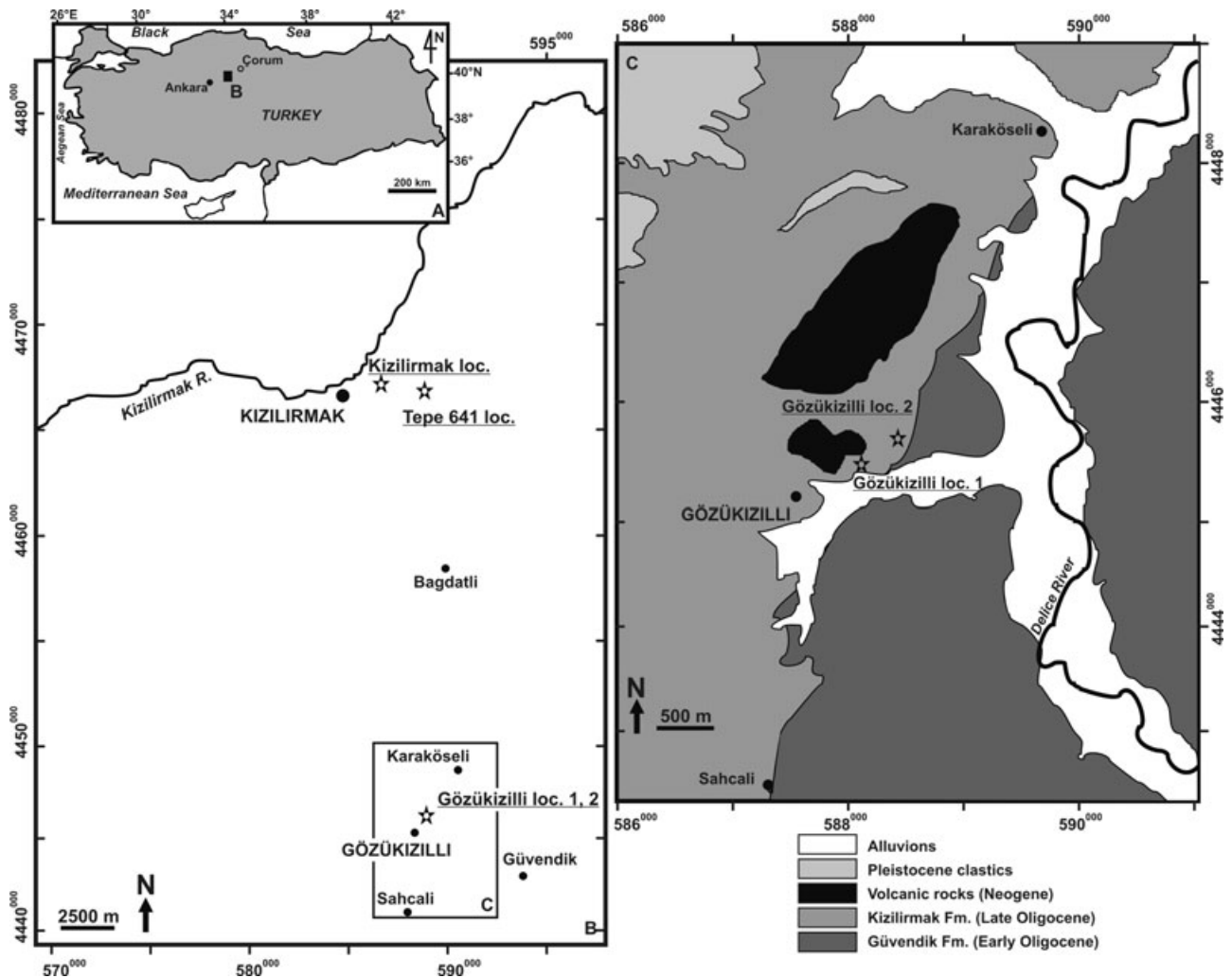
ADDITIONAL KEYWORDS: indricothere – palaeogeography – *Paraceratherium* – vertebrate palaeontology.

## INTRODUCTION

The indricotheres are extinct giant rhinocerotoids known in the Eocene of western North America and from the Middle Eocene to the Late Oligocene in Eurasia (Russell & Zhai, 1987; Lucas & Sobus, 1989; Welcomme *et al.*, 2001; Antoine *et al.*, 2004). The hornless rhinos, which many authors consider to have been the largest land mammals that have existed, were widespread during the Oligocene in Asia (Pakistan, China, Mongolia, Russia, Kazakhstan; Forster-Cooper, 1911, 1913a, b, 1915, 1924, 1934; Borissiak, 1915, 1923; Pavlova, 1922; Teilhard de Chardin, 1926; Granger & Gregory, 1936; Gromova, 1959; Lucas & Sobus, 1989; Antoine *et al.*, 2004). In addition, a few specimens have been mentioned in recent decades from Eastern Europe (Yugoslavia, Bulgaria, Romania; Nikolov & Heissig, 1985; Lucas & Sobus, 1989; Spassov, 1989; Codrea, 2000) and the Caucasus (Georgia; Gabunia, 1955, 1964, 1966).

This article deals with the discovery of a single specimen – a broken and damaged radius – unearthed in June 2002 near the village of Gözükizilli, c. 20 km south of Kizilirmak (Fig. 1), during part of a joint project by the Muséum National d'Histoire Naturelle in Paris and the Maden Tektik ve Arama in Ankara (Karadenizli *et al.*, 2003). This radius, unquestionably referable to an indricothere (on the basis of size and morphological features), is the first evidence of a giant rhinocerotoid in Asia Minor. It was found associated with a magnum of a small rhinocerotid in grey fluvial conglomerates (Fig. 1: Gözükizilli-2 locality; Fig. 2) from the Lower Member (Mbr) of the Kizilirmak Formation (Fm.). These conglomerates overlie grey lacustrine clays (Fig. 1: Gözükizilli-1 locality), which have yielded a diversified micromammal fauna, notably Late Oligocene rodents (Ünay, Bruijn & Saraç, 2003). In addition, the recent discovery of two mammal localities (Kizilirmak and Tepe 641; Fig. 1) in the upper member of the Kizilirmak Fm. sheds a new light on the age of this formation as a whole (Karadenizli *et al.*, 2003).

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**Figure 1.** Location map of Late Oligocene mammal localities and sections from the Kizilirmak Fm. (Çankiri-Çorum Basin, north central Anatolia, Turkey). A, map of Turkey; B, location of Kizilirmak, Gözükizilli and other cities; C, geological sketch map of the Gözükizilli area. GK-1, Gözükizilli-1 (Lower Mbr); GK-2, Gözükizilli-2 (Lower Mbr); Kizilirmak (Upper Mbr); Tepe 641 (Upper Mbr). In B and C, the coordinates are UTM.

## SYSTEMATICS

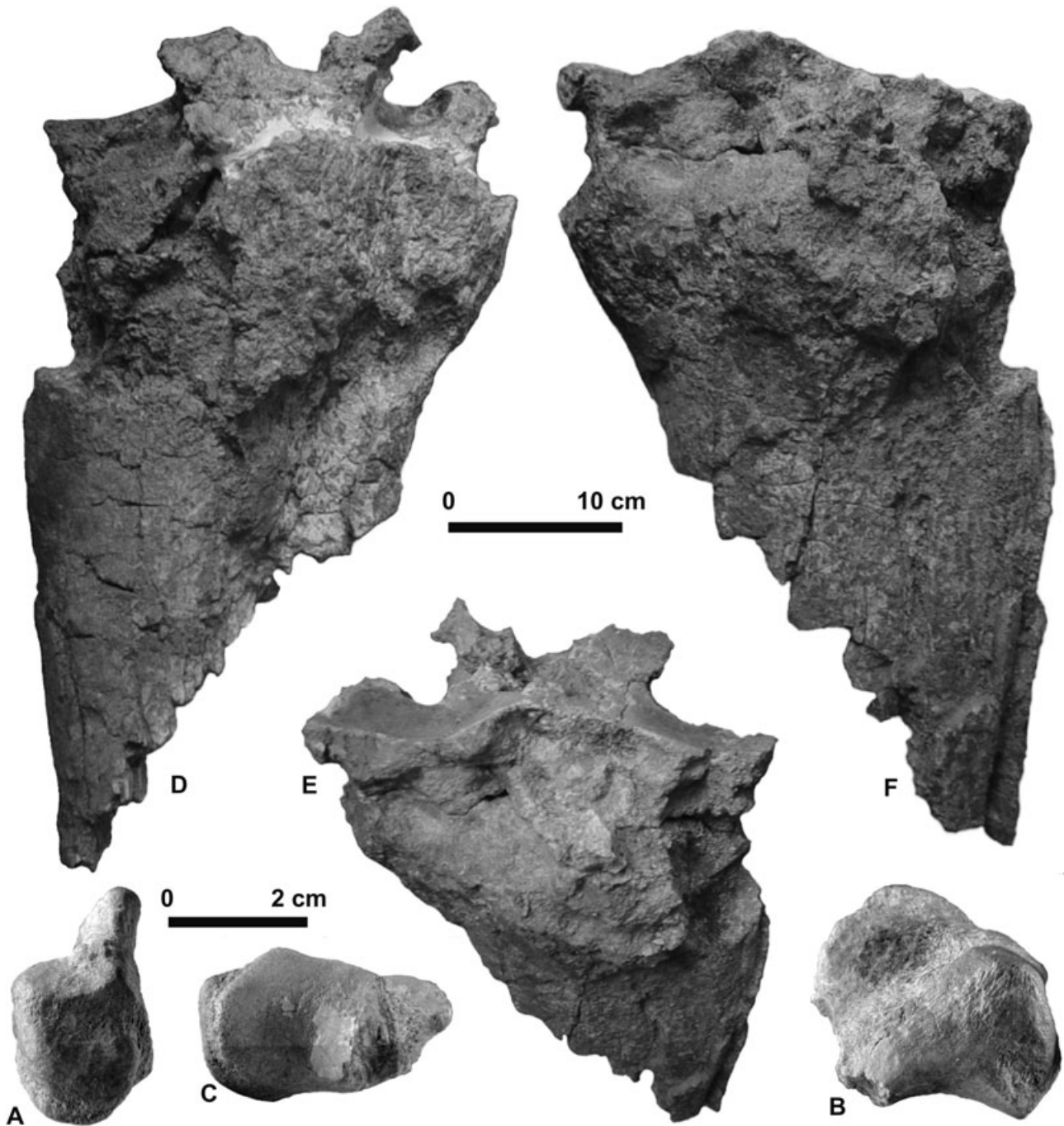
The use of the taxon *Rhinoceroidea* Gray, 1821 follows Prothero, Guérin & Manning (1989) rather than McKenna & Bell (1997): it is the clade formed by rhinocerotids, hyracodontids and amynodontids. Even though the genus *Indricotherium* Borissiak, 1915 is considered here as a junior synonym of *Paraceratherium* Forster-Cooper, 1911, the subfamily name *Indricotheriinae* Borissiak, 1923 is used (1) because 'when the name of a type genus of a nominal family group taxon is considered to be a junior synonym of the name of another nominal genus, the family group name is not to be replaced on that account alone' (ICZN 1999: 46, article 40.1), and (2) because the name *Indrico-*

*theriinae* 'has priority over Osborn's (1923: 13) names *Baluchitheriinae* and *Paraceratheriinae* (imprint date on Borissiak, 1923 is March; on Osborn, 1923, it is May)', according to Lucas & Sobus (1989: 362).

ORDER PERISSODACTYLA OWEN, 1848  
 SUPERFAMILY RHINOCEROIDEA GRAY, 1821  
 FAMILY RHINOCEROTIDAE GRAY, 1821  
 GENUS *PROTACERATHERIUM* ABEL, 1910  
*PROTACERATHERIUM* SP., CF. *PROTACERATHERIUM*  
*ALBIGENSE* (ROMAN, 1912)

FIGURE 2A–C

*Material available:* GK-2-1, anterior fragment of an eroded left magnum (Fig. 2A–C), housed in the

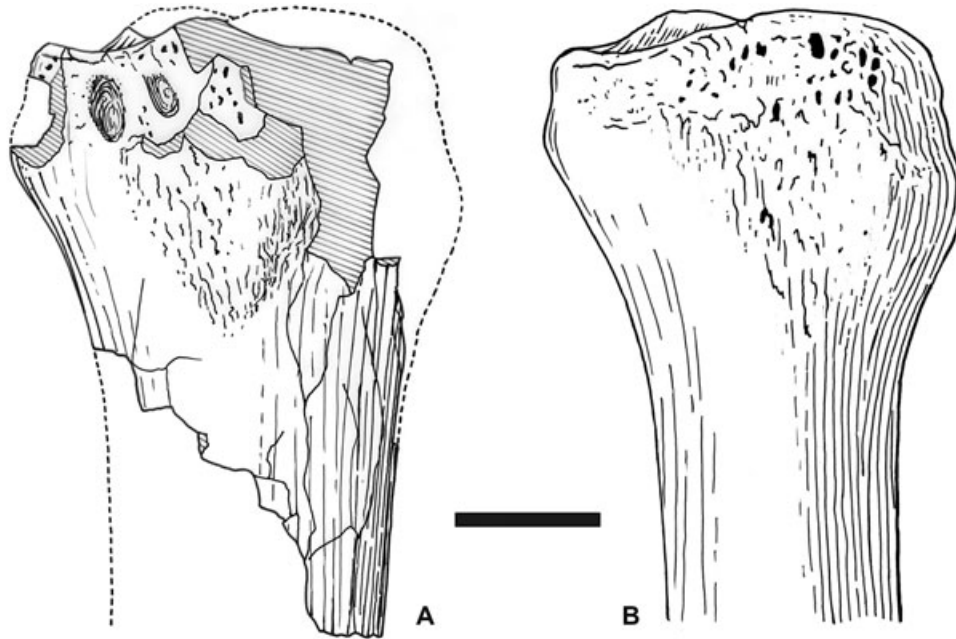


**Figure 2.** *Protaceratherium* sp. cf. *Protaceratherium albigense* (Roman, 1912). Left fragmentary magnum (GK-2-1). Gözükizilli-2 locality (Çankiri-Çorum Basin, Central Anatolia, Turkey). Late Oligocene. A, anterior view; B, medial view; C, distal view. Scale bar = 2 cm. *Paraceratherium* sp. Right radius, proximal end (GK-2-2). Gözükizilli-2 locality (Çankiri-Çorum Basin, Central Anatolia, Turkey). Late Oligocene. D, anterior view; E, posterior view; F, antero-proximal view. Scale bar = 10 cm.

Natural History Museum of the Maden Tektik ve Arama (MTA) in Ankara. Gözükizilli-2 loc., Lower Mbr of the Kızılırmak Fm. (north-central Anatolia). Late Oligocene (Ünay *et al.*, 2003; this work). For location, see Figure 1.

*Description and comparison*

The bone is small and slender (anterior transverse diameter = 22.7 mm; anterior height = 22 mm; maximal height *c.* 37 mm; McIII-facet transverse diameter = 22 mm). The surface is quite severely



**Figure 3.** A, *Paraceratherium* sp. Right radius, proximal end (GK-2-2) in anterior view. Locus 2, Gözükizilli (Çankiri-Çorum Basin, Central Anatolia, Turkey); B, *Paraceratherium transouralicum*. Right radius, detail of the proximal end (AMNH 26166) in anterior view, after Granger & Gregory (1936: 43, fig. 24). Scale bar = 10 cm.

eroded in places. The bone is broken in front of the posterior tuberosity. In anterior view, the anterior side is square, with a regularly convex distal border, while the proximal, lateral and medial borders are straight. The insertion of the *M. extensor digitorum* is a thick and wide tubercle which occupies the central part of the anterior side. It is very prominent in its latero-distal tip. The dorsal process is slender. When compared with the proximo-distal axis, its obliquity is *c.* 40°. In medial view, the dorsal process (for the semilunate) is semicircular (diameter = 25 mm) and posteriorly displaced. It is separated from the anterior side by a smooth inflection. Due to erosion, the medial facets (for the trapezoid and the second metacarpal) are not preserved. The distal facet is regularly concave, with a large diameter. As an inference, the third metacarpal is likely to bear a wide antero-posterior diameter. In lateral view, the articular facets are eroded. In distal view, the facet for the third metacarpal shows a convex anterior border and straight subparallel lateral borders. The size, shape and morphological features of GK-2-1 closely match those of the magnums referred to *Protaceratherium albigense* (Roman, 1912) from the early Late Oligocene of Marseilles, France (P. O. Antoine, pers. observ.), and, to a lesser degree, with that of *P. minutum* (Cuvier, 1822) from the Early Miocene of Laugnac, France (de Bonis, 1973). The latter differs by having a narrower anterior side and the absence of a posteriorly displaced dorsal process (de Bonis, 1973:

fig. 48.7). No direct comparison can be made with *P. betpakdalense* (Borissiak, 1938) from the Late Oligocene to earliest Miocene of the 'Aral suite' in Kazakhstan (de Bonis *et al.*, 1997), for which no magnum is available.

#### FAMILY HYRACODONTIDAE COPE, 1879

#### SUBFAMILY INDRICOTHERIINAE BORISSIAK, 1923

#### GENUS *PARACERATHERIUM* FORSTER-COOPER, 1911

#### *PARACERATHERIUM* SP.

#### FIGURES 2D–F AND 3

*Material available:* GK-2-2, proximal fragment of a right radius from a large adult individual (Fig. 2D–F), housed in the Natural History Museum of the Maden Tektik ve Arama (MTA) in Ankara. Gözükizilli-2 loc., Lower Mbr of the Kizilirmak Fm. (north-central Anatolia). Late Oligocene (Ünay *et al.*, 2003; this work). For location, see Figure 1.

#### *Description and comparison*

GK-2-2 is a fragmentary right radius from an adult individual (proximal epiphysis and diaphysis fused); only the proximal third is preserved, including the proximal part of the diaphysis. More distal fragments of the same bone were found *in situ*, scattered as a result of weathering. The bone was lying on its anterior side, at the bottom of a conglomerate lens 30 cm thick. The proximal articulation has furrows, some over several centimetres in diameter; they may origi-

**Table 1.** Comparison of measurements of radii (mm) from large indricothere rhinocerotoids, after Pavlova (1922), Forster-Cooper (1924), Teilhard de Chardin (1926), Granger & Gregory (1936), Gromova (1959), and personal observation by P.-O.A. (*Paraceratherium bugtiense*: Bugti Hills, Balochistan)

Measurement	<i>Paraceratherium</i> sp. Gözükizilli (this work)	<i>Paraceratherium</i> <i>bugtiense</i> (our unpubl. data)	<i>Paraceratherium</i> <i>prohorovi</i> (Borissiak, 1939)	' <i>Indricotherium</i> ' <i>transouralicum</i> (Pavlova, 1922)
Length	pres. 490; est. 1200	–	665; 731; 985	960–1220
prox. end				
TD	pres. 270; est. 310	170 – (> 235)	180–342	241–est. 290
APD	pres. 210	100 – (> 158)	114–205	178–est. 250
Prox. art.				
TD	pres. 270; est. 280	170–220	?	est. 260
med. hum. fac.				
TD	pres. 135; est. 160	–	100–193	123
APD	> 108	105 – (> 120)	85–100	121
lat. hum. fac.				
TD	135	–	70–146	108
APD	pres. 114; est. 140	75 – (> 93)	70–84	?
lat. ulna fac.				
H	pres. 60; est. 80	–	?	?
min. dia.				
TD	est. 185	90–125	110–185	147–est. 160
APD	pres. 80; est. > 100	75–90	70–112	92–est. 110

*Baluchitherium grangeri* is here considered a junior synonym of *Indricotherium transouralicum*, as stated by Lucas & Sobus (1989). The measurements provided by Granger & Gregory (1936) for '*B. grangeri*' are included in the corresponding column.

APD, antero-posterior diameter; art., articulation; dia., diaphysis; est., estimated; H, height; hum., humerus; min., minimal; pres., preserved; prox., proximal; TD, transverse diameter.

nate from post-mortem predation. The proximal extremity is not deformed, while the diaphysis displays longitudinal cracks and is crushed in its posterior side. The preserved part is very large (Table 1), with an estimated bone length of *c.* 1200 mm (estimated by comparison with available radii from other indricotheres; Table 1). The cortical part (substantia corticalis) of the diaphysis exceeds 32 mm in thickness. GK-2-2 displays characteristic proportions of a cursorial rhinocerotoid. The proximal end is wide and deep (transverse diameter *c.* 310 mm; antero-posterior diameter greater than 210 mm), nearly three times larger than the mean values observed in living black rhinos (Guérin, 1980: 85, table 9). It is widened laterally with respect to the diaphysis.

In proximal view, the humerus articulation shows a pear-like outline, with a concave anterior border and a larger medial part. It consists of two cochleae occupying most of the proximal surface. The medial cochlea has largely been destroyed while the lateral one is better preserved (Fig. 2F). Both cochleae are biconcave. The lateral cochlea is much smaller but more concave. It shows a trapezoidal outline in proximal view (Fig. 2F) and lacks any lateral extension corresponding to the capitulum humeri. Such mor-

phology is characteristic of the Rhinocerotioidea among Perissodactyla. Contiguous with the posterior border of the lateral cochlea, a small part of the lateral ulna facet is visible. It is oblique both transversely and sagittally.

The anterior side is badly damaged in its proximal part. In anterior view, the median ridge between the biconcave humerus facets is very smooth, and it forms a dihedral angle of about 135° (Fig. 2E). As a consequence, the preserved part of the proximal border of the bone is 'W' shaped. The anterior side displays a wide and salient axial tubercle, with a rough surface. This tubercle is located very proximally. It forms an equilateral triangle (140 mm wide) tapering distally and corresponding to the insertion for the *M. biceps brachii*. In most rhinocerotoids, this insertion is flat or depressed (Antoine, 2002). Indeed, only indricothere hyracodontids bear such a salient insertion among Rhinocerotioidea (e.g. Granger & Gregory, 1936: fig. 24). There is a shallow vertical groove on the lateral half of the anterior side, externally from the insertion of the *M. biceps brachii*. More distally, the anterior surface of the diaphysis is smooth and regular. The proximal articulation and the medial border of the diaphysis form an angle of *c.* 100°

(the medial border is broken proximally). The lateral border is strongly convex in its proximal part: the maximal width of the bone (c. 310 mm) is situated c. 80 mm below the proximal end. In this area is the insertion for the *M. extensor digitorum communis* (Guérin, 1980: 83–84, fig. 11). Distally to this maximal width, the diaphysis tapers quickly. This tapering is stronger laterally than medially, the lateral border being very oblique from the vertical (Fig. 2D).

In lateral view, the proximal articulation is much higher posteriorly than anteriorly, which is extremely prominent along the median ridge between the cochleae. This obliquity is similarly observed in most fossil and living rhinos (Guérin, 1980).

The posterior side of the bone probably suffered from a long period of exposure to erosion and/or post-mortem predation: it is still more badly damaged than the anterior side. In posterior view, the highest part of the bone corresponds to the limit between the cochleae for the humerus. The medial ulna facet is not preserved. The lateral ulna facet is wide, as is constantly observed among Rhinocerotidae. It is preserved in two places (Fig. 2D): (1) a flat and crescent-like surface near the axis of the bone and contiguous to the proximal humerus facet – it is oblique transversely and vertically (about 50° from the vertical); (2) a centimetre-sized surface, 60 mm more distally than the former – it is simultaneously oblique and concave transversally, and flat antero-posteriorly. Distally to the articulate region, the axial part of the posterior side forms a salient ridge which separates two deep and wide depressions. These depressions are covered by a rough surface, indicating a tight contact with the ulna by means of a strong *membrana interossea*.

In distal view, the diaphysis is ovoid in cross-section.

Although fragmentary, the specimen from Gözükiçilli-2 displays a combination of size and shape that fits only with the radii referred to large indricothere rhinocerotoids (Table 1): for instance, other megamammals such as elephantoids bear reduced and slender radii with respect to their body size. Lucas & Sobus (1989) published the last systematic revision of indricotheres, with four valid genera recognized within the subfamily Indricotheriinae Borissiak, 1923: the small-sized genera *Forstercooperia* Wood, 1939 and *Juxia* Chow & Chiu, 1964, mostly recorded from Eocene localities in Asia, and the large-sized genera *Urtinotherium* Chow & Chiu, 1963, from the Early Oligocene of Asia, and *Paraceratherium* Forster-Cooper, 1911, from the late Early and Late Oligocene of Asia and eastern Europe. In that sense, *Paraceratherium* includes all species previously referred to *Thaumastotherium* Forster-Cooper, 1913a, *Baluchitherium* Forster-Cooper, 1913b, *Indricothe-*

*rium* Borissiak, 1915, *Aralotherium* Borissiak, 1939 and *Dzungariotherium* Chiu, 1973. By contrast, other authors (e.g. Gromova, 1959; Spassov, 1989; Fortelius & Kappelman, 1993) consider *Indricotherium* and *Paraceratherium* as distinct genera.

Pending a forthcoming systematic revision of the phylogeny of indricotheres, the views of Lucas & Sobus (1989) are followed: a single Oligocene genus, *Paraceratherium*, with four valid species – *P. bugtiense* (Pilgrim, 1910) from the Bugti Hills of Pakistan (Pilgrim, 1910; Forster-Cooper, 1913a, b, 1924, 1934; Welcomme *et al.*, 1999, 2001; Antoine *et al.*, 2004); *P. transouralicum* (Pavlova, 1922) and *P. prohorovi* (Borissiak, 1939) from Asia and south-eastern Europe (Osborn, 1923; Granger & Gregory, 1936; Gromova, 1959; Nikolov & Heissig, 1985; Codrea, 2000); and *P. orgosensis* (Chiu, 1973) from China (Chiu, 1973; Xu & Wang, 1978).

No direct comparison can be made with *Paraceratherium orgosensis* or *Urtinotherium* Chow & Chiu, 1963, nor with the controversial indricothere *Benaratherium callistrati* Gabunia, 1955 from the Late Oligocene of Georgia (Gabunia, 1964), because no radius is available for these latter taxa.

By contrast, GK-2-2 shows no substantial morphological difference with the radii of *P. bugtiense* recently found in the Late Oligocene of the Bugti Hills, Pakistan, and particularly with those from the type locality of this species (Lundo-Chur J2; Welcomme *et al.*, 2001; Antoine *et al.*, 2004; our unpubl. data): the surface of the bone is rough, with a very thick *pars corticalis*; there are two cochleae for the humerus, slightly asymmetric and separated by a smooth ridge, the lateral one being biconcave; the posterior part of the humeral articulation is much higher than the anterior border; the insertion for the *M. biceps brachii* is wide, salient and triangular; the diaphysis tapers strongly distally from the proximal end; and there is a shallow vertical groove on the lateral half of the anterior side, externally from the insertion of the *M. biceps brachii*. The specimen from Gözükiçilli-2 is larger than the largest radius referred to *P. bugtiense* (Table 1).

In addition, GK-2-2 is very similar to the largest specimen attributed to *Baluchitherium grangeri* Osborn, 1923 by Granger & Gregory (1936: 43, fig. 24); the latter is a junior synonym of *P. transouralicum* according to Lucas & Sobus (1989: 367). On a metrical basis, they are equivalent (Table 1; Fig. 3). In *P. prohorovi* from the Aral Suite of Kazakhstan, the size distribution of the radii appears bimodal (Table 1; Gromova, 1959) while the morphology is constant. A similar bimodality, probably reflecting a strong sexual dimorphism, is observed for the 'frequency distribution of mass estimates' in *P. transouralicum* (Fortelius & Kappelman, 1993: 96). The same occurs in *P. bugtiense*

from Pakistan (Antoine *et al.*, 2004). This phenomenon has long been debated for indricotheres, especially concerning its taxonomic implications (i.e. Lucas & Sobus, 1989 vs. Spassov, 1989; Fortelius & Kappelman, 1993; Antoine *et al.*, 2004).

Therefore, and pending the discovery of supplementary material, we propose to refer the indricothere from Gözükizilli-2 to *Paraceratherium* sp., further presuming that the radius belongs to a large individual, i.e. most probably to a male.

#### AGE OF THE KIZILIRMAK FORMATION

Prior to 2002, a single mammal locality was known in the Kizilirmak Fm. (Gözükizilli-1; Ünay *et al.*, 2003). Several mammal localities were discovered within the Kizilirmak Fm. during the 2002 fieldwork (Gözükizilli-2 in the Lower Mbr; Tepe 641 and Kizilirmak in the Upper Mbr). The corresponding faunas (listed below) allow us to infer a time range for this formation.

##### GÖZÜKIZILLI-1 (FIG. 1C)

The faunal list provided by Ünay *et al.* (2003) is as follows, with familial assignment in square brackets for the taxa identified at the species/genus level:

- aff. *Sayimys* sp. [Ctenodactylidae],
- Ctenodactylidae gen. B. sp. 1,
- Dipodidae indet.,
- *Eucricetodon* sp. 2 [Cricetidae],
- *Eucricetodon* sp. 3 [Cricetidae],
- *Glirulus* sp. [Gliridae],
- *Bransatoglis* cf. *complicatus* [Gliridae]

A similar assemblage, with ctenodactylids and cricetids, is reported in the Central Anatolian locality of Yeniköy, assumed to be coeval with the Gözükizilli site (Ünay *et al.*, 2003).

##### GÖZÜKIZILLI-2 (FIG. 1C)

Although poorly diversified and imprecisely identified, both rhinocerotoids provide a rather precise age for Gözükizilli-2: the rhinocerotid *Protaceratherium* has a good record from the late Early Oligocene to the Early Miocene in Eurasia (MP24 to MN 4; Marivaux, 1999; Antoine, Bulot & Ginsburg, 2000; Antoine *et al.*, 2003). The species showing the closest affinities with the currently described specimen is *P. albigense* (Roman, 1912), which has an MP 24–28 stratigraphic range (Uhlir, 1999; Antoine *et al.*, 2003). Moreover, this species has recently been described in late Early to early Late Oligocene coastal deposits from Turkish Thrace (Saraç, 2003). The giant rhino *Paraceratherium* occurs from the late Early to the latest Oligocene

in Asia and Eastern Europe (Lucas & Sobus, 1989; Prothero *et al.*, 1989; Lucas, Kordikova & Emry, 1998; Meng & McKenna, 1998; Welcomme *et al.*, 2001; Antoine *et al.*, 2004). Unfortunately, no morphological evolution can be ascertained for the whole interval of the genus – especially on postcranials – which does not allow further direct precision regarding the age of the Gözükizilli-2 locality. Yet, a Late Oligocene age can be inferred for Gözükizilli-2 thanks to its stratigraphic position, intercalated between a Late Oligocene locality (Gözükizilli-1 in the Lower Mbr) and two Late to latest Oligocene loci (Tepe 641 and Kizilirmak in the Upper Mbr; see below).

##### TEPE 641 (FIG. 1C)

The provisional mammal list is:

- *Iberomeryx* cf. *parvus* Gabunia, 1964 [majority among artiodactyls],
- Tragulidae indet. sp. 1
- ?*Palaeohypsodontus* sp.,
- Cervoidea gen. et sp. indet. (size of *Procervulus Dremotherium*),
- ?*Feliformia* indet. (small),
- Rhinocerotidae gen. et sp. indet.,
- Rhinocerotidae gen. et sp. indet.,
- Rodentia, gen. et sp. indet.,
- Lagomorpha, gen. et sp. indet.

##### KIZILIRMAK (FIG. 1C)

The provisional faunal mammal list is:

- *Iberomeryx* cf. *parvus* Gabunia, 1964,
- Tragulidae indet. sp. 1 [same as that of Tepe 641; majority among artiodactyls]
- Carnivora indet., sp. 1,
- Carnivora indet., sp. 2,
- Rhinocerotidae gen. et sp. indet.,
- Rodentia, gen. et sp. indet.,
- Lagomorpha, gen. et sp. indet.

A coeval age can be hypothesized for Tepe 641 and Kizilirmak, based on both lithostratigraphy (floodplain deposits in the Upper Mbr of the Kizilirmak Fm.) and biostratigraphy. The difference between these localities (e.g. in the relative abundance of artiodactyls) is probably due to taphonomical bias (most remains were damaged by predators or scavengers).

In Tepe 641, the small and slender *Iberomeryx* cf. *parvus* is represented by 20 cheek teeth (and dozens of isolated postcranials) with typical lophiomerycid features, such as the lingual opening of the anterior and posterior fossettes on lower molars (Janis, 1987: 214, fig. 10). Both the lack of any parastyle on the upper molars and the backward elongation of the metaconid on the fourth premolar distinguish

the genus *Iberomeryx*, as demonstrated by Métais *et al.* (2001). This genus is known throughout the Oligocene in Eurasia (Gabunia, 1964; Sudre, 1984; Janis, 1987; Nanda & Sahni, 1990; Sudre & Blondel, 1996; Métais *et al.*, 2001). The closest affinities exist with the type species, *I. parvus*, from the Late Oligocene of Georgia (Gabunia, 1964, 1966; Sudre, 1984). However, *Iberomeryx* from Tepe 641 seems to be more advanced than any known species of the genus, especially in possessing very elongate lower molars and a strong lingual cingulum on all the upper molars.

The recognition of *?Palaeohypsodontus* sp. is based on two fragmentary molars. These teeth are as hypsodont as bovid teeth, but their structures are very simple. A state-of-the-art revision of *Palaeohypsodontus* has recently been made (Métais *et al.*, 2003), showing that this puzzling genus was a hypsodont traguloid rather than a precocious bovid. Indeed, unambiguous remains of *Palaeohypsodontus* are restricted to two localities from Mongolia (Early and Late Oligocene; Vislobokova & Daxner-Höck, 2002) and the Lundo-Chur J2 locality in Baluchistan (Late Oligocene; Métais *et al.*, 2003). The occurrence of *Palaeohypsodontus* in Central Anatolia would widely expand westward the geographical range of this puzzling ruminant genus.

The morphological advancement of *Iberomeryx* tends to indicate a latest Oligocene age for Tepe 641, as *Iberomeryx* and *Palaeohypsodontus* have a strictly Oligocene record (Métais *et al.*, 2003).

#### PALAEOGEOGRAPHY

Among the mammals recognized in the Kizilirmak Fm., three groups (rhinocerotoids, ruminants, rodents) allow us to enhance the palaeogeographical relationships of north Central Anatolia during the Late Oligocene.

The small rhinocerotid from Gözükişilli-2 has closest affinities with *Protaceratherium albigense* from western and central Europe and Turkish Thrace (Antoine *et al.*, 2003; Saraç, 2003). Indricotheres are essentially recorded in Asia (Antoine *et al.*, 2004). Yet, a few Oligocene localities have yielded scarce indricothere remains around the Black Sea, in the Caucasus and Eastern Europe (Fig. 4). Indeed, Gözükişilli is the first indricothere-bearing locality south of the Paratethys (an area more or less corresponding to the recent Black Sea; Fig. 4). Among the ruminants recognized in the Kizilirmak Fm. deposits, *Iberomeryx* has a strict western Asian record (Janis, 1987), while the occurrence of a probable *Palaeohypsodontus* would widely expand westward the geographical range of this puzzling ruminant genus, thus fae only recognized in Mongolia and Pakistan (Vislobokova & Daxner-Höck, 2002; Métais *et al.*, 2003). Dawson

(2003: 98) states that, during the Oligocene, 'in Asia [the strong endemic development of rodents] can be seen most clearly in the array of ctenodactylids and in Europe of glirids and theridomyids'. In fact, the Oligocene spatial distribution of Ctenodactylidae is limited westward to Anatolia (de Bruijn, 1999; Dawson, 2003). Among this poor Anatolian record, Gözükişilli is the westernmost locality where this endemic Asian rodent group occurs (Ünay *et al.*, 2003). At the same time, Gözükişilli-1 is the first Oligocene glirid-bearing locality (Ünay *et al.*, 2003), as the Gliridae were previously restricted to European Oligocene localities. Similarly, some other Anatolian Oligocene localities have yielded the anthracotheres *Anthracotherium* and *Elomeryx*, which have a wide Eurasian distribution (Russell *et al.*, 1982; Saraç, 2003).

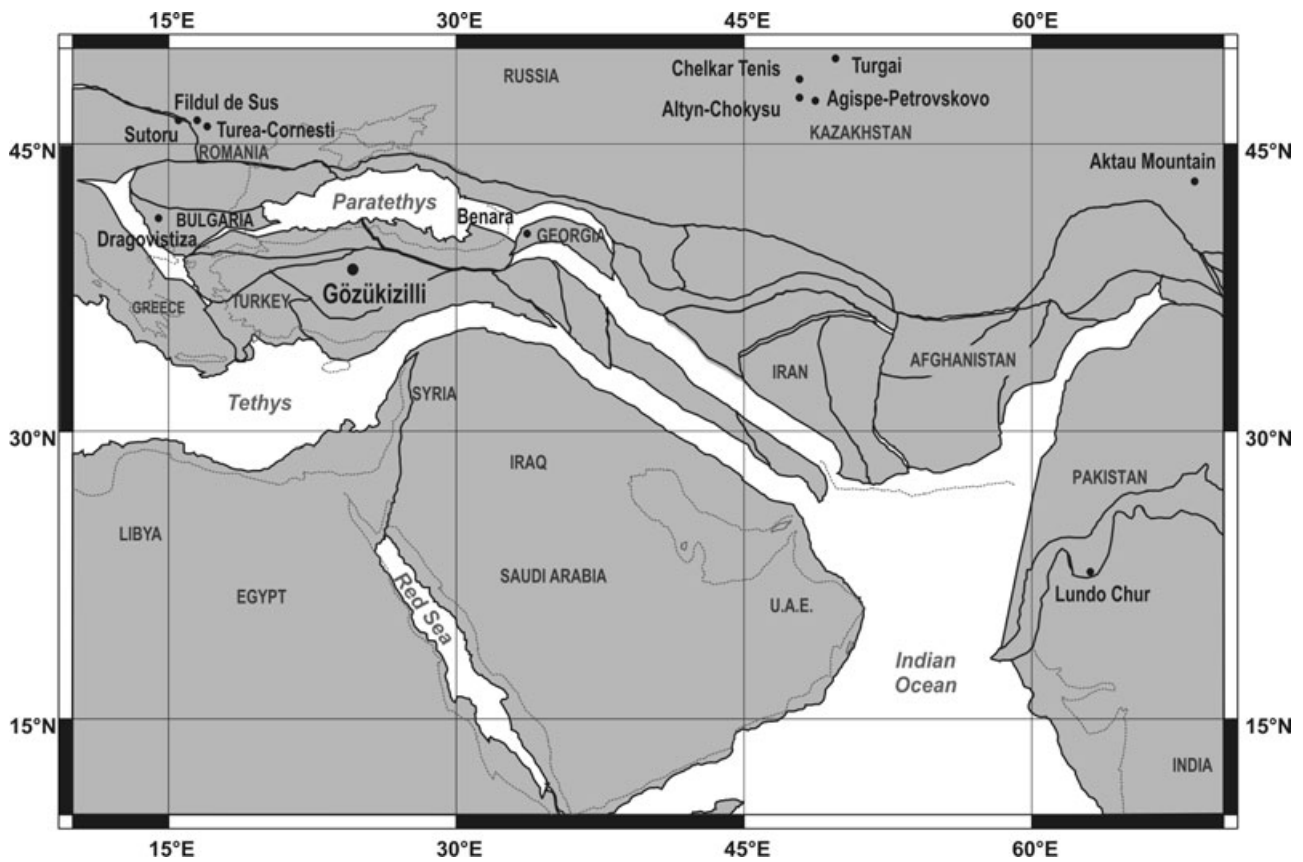
The Late Oligocene mammal faunas from Anatolia share several elements with more or less coeval faunas from Pakistan and Mongolia (*Paraceratherium*, *Palaeohypsodontus* and ctenodactylids; Dashzeveg, 1990; Métais *et al.*, 2003; Antoine *et al.*, 2004), Georgia (*Iberomeryx* and an indricothere), Central Europe (*Anthracotherium* and *Paraceratherium*) and Western Europe (*Protaceratherium*, *Anthracotherium* and glirids). In summary, these strong affinities with both Asia (including the Indian subcontinent) and Europe do not support any island hypothesis for the Late Oligocene of Anatolia. In contrast, the mammal faunas from the Late Oligocene Kizilirmak Fm. of north central Anatolia have not thus far yielded any taxon of Arabo-African affinity.

On an environmental point of view, ctenodactylid rodents (Gözükişilli-1; Lower Mbr) and hypsodont herbivores such as *?Palaeohypsodontus* and lagomorphs (Tepe 641 and Kizilirmak; Upper Mbr) occur mainly in Shandgolian (Early Oligocene) and Tabenbulukian (Late Oligocene) localities of Mongolia and China (McKenna & Bell, 1997; Wang, 1997; Meng & McKenna, 1998; Métais *et al.*, 2003). This kind of assemblage strongly suggests the existence of abrasive vegetation in the surroundings, likely to occur in rather open habitats (Wang, 1997). By contrast, the glirids *Glirulus* and *Bransatoglis* (Gözükişilli-1; Lower Mbr) were most probably scansorial rodents typical of forest habitats (Hartenberger, 1994), while the unidentified tragulid (Tepe 641 and Kizilirmak; Upper Mbr) rather tends to indicate a water-related forested environment (Rössner, 1997; Gentry, Rössner & Heizmann, 1999).

#### ACKNOWLEDGEMENTS

The 2002 fieldwork in the Çankiri-Çorum basin was funded by TÜBİTAK, the CNRS (ECLIPSE Program), and the Faculty of Sciences of the University of





**Figure 4.** Palaeogeographical map of Middle East and south-west Asia illustrating the geographical distribution of Oligocene indricotheres around the Paratethys, in Kazakhstan and in Pakistan. After Petronijevic & Thenius (1957), Gromova (1959), Gabunia & Iliescu (1960), Gabunia (1964), Nikolov & Heissig (1985), Lucas & Sobus (1989), Spassov (1989), Lucas & Bayshashov (1996), Lucas & Emry (1996), Lucas *et al.* (1998), Codrea (2000), Welcomme *et al.* (2001) and Antoine *et al.* (2004). Source for map construction: [http://www.odsn.de/odsn/services/palaeomap/adv\\_map.html](http://www.odsn.de/odsn/services/palaeomap/adv_map.html)

Ankara. Gürol Seyitoglu and Baki Varol (Fen Fakültesi, Jeoloji Mühendisliği Bölümü, Ankara), Arzu Gül (Denizli University), Raquel Lopez Antonanzas and Fabien Knoll (Muséum National d'Histoire Naturelle, Paris) contributed to this field trip. Grégoire Métails provided useful literature sources (and advice) for the identification of the artiodactyls from Tepe 641 and Kizilirmak. This article is dedicated to the memory of Annie Antoine.

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