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Denis Geraads, Gerçek Saraç. Rhinocerotidae from the Middle Miocene Hominoid Locality of Çandır (Turkey). *Courier Forschungsinstitut Senckenberg*, 2003, 240, pp.217-231. halshs-00009915

HAL Id: halshs-00009915

<https://shs.hal.science/halshs-00009915>

Submitted on 3 Apr 2006

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Rhinocerotidae from the Middle Miocene Hominoid Locality of Çandır (Turkey).

1 figure, 2 plates

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Abstract.- The rhinocerotid material collected at Çandır during the last 20 years is compared with that from other Middle Miocene localities. More specimens of the 3 species identified by HEISSIG (1976), *Beliajevina grimmi*, *Aceratherium* sp and *Brachypotherium* cf *brachypus*, are described, and we have been able to add a fourth species to the list, cf *Lartetotherium* sp. The Çandır Rhinos provide little biochronological information, but are useful for paleoecological reconstruction; they point towards an open landscape surrounding a lake margin.

Key-words: Middle Miocene, Turkey, Mammalia, Perissodactyla, Rhinocerotidae

Introduction

In 1976, K.HEISSIG published his study of the rhinocerotid material collected by the German team led by O.SICKENBERG. He recognized 3 species. *Hispanotherium grimmi*, an Elasmothere, was considered closer to the type-species of this genus, *H. matritense* from Spain, than to other Elasmotheres. He distinguished *Aceratherium* aff *tetradactylum* from the material of the type-locality, Sansan, by some dental and tarsal features. *Brachypotherium brachypus* is a species common in Europe. We have not seen the German collection, but HEISSIG'S careful descriptions allow reliable comparisons to be made. We describe below

more material of the three species already mentioned by HEISSIG, and we have been able to add a fourth rhino species to the Çandır list. Some descriptions had already been provided (in Turkish) by SARAÇ, and the present paper is a revision and enlargement of this preliminary study. The fossils collected by I.TEKKAYA and co-workers are housed in the MTA Museum, those collected under the direction of E.GÜLEÇ between 1989 and 1997 are housed in the DTCTF, Ankara.

In contrast to most other mammalian groups, rhinocerotids are often treated as though their identifications were self-evident. While it is common to find isolated teeth or postcranial bones identified to species, reasons for doing so are seldom stated. A much studied bone, the astragalus, is almost always identified to species, with the most common criteria being smaller size and lower proportions of *Aceratherium* (fig.1). In the Çandır sample the situation is not so simple. For example, an *Aceratherium* is present among the 4 non-brachypotherine astragali the dimensions of which all fall within the supposed Dicerorhinine range of Europe. Comparison of bones assigned to the same species by various authors also demonstrates that some of their identifications must be erroneous. The right process would be to try to sort out the whole collection from one locality into two or more satisfactorily homogeneous groups (as done, e.g. by CERDEÑO 1996). This might often prove difficult, however, because examination of large samples of sympatric and synchronic populations has shown, first (GERAADS 1988) that it may be extremely difficult to separate the postcranial bones of two species of similar size, second (HARRISSON & MANNING 1983) that intra-specific variability is great.

Figure 1 about here

Since most rhino species are defined on skulls and teeth, one might expect the problem not to occur with teeth, but aside from some highly characteristic groups (elasmotheres, brachypothere), Middle Miocene rhinos are very homogeneous in their dental morphology, and assigning fragmentary remains to one particular species is often a hazardous task. The problem is further complicated by the high frequency of parallel evolution. This is why we prefer to leave some of the Çandır Rhinos in open nomenclature.

Materials and Methods

All measurements are in mm, and taken according to GUÉRIN (1980). Uppercase letters denote upper teeth, lowercase letters are for lower teeth.

Systematic description

Aceratherium KAUP, 1834

Aceratherium sp

Several genera (*Dromoaceratherium*, *Plesiaceratherium*, *Mesaceratherium*, *Hoploaceratherium*, *Acerorhinus*, *Alicornops*...) have been recognised among Middle Miocene *Aceratherium*-like rhinos. There is no doubt indeed that the latter genus is not homogeneous, but since most of these "genera" correspond to poorly defined evolutionary grades rather than to clades, and that an agreement is far from being reached, we shall use the name *Aceratherium* as a super-genus.

Dentition

ÇA-1210 is a maxillary fragment with DP2-DP4 (Pl.1, Fig.1). The rear of the nasal notch is at the level of the middle of DP2 and is thus short. All milk premolars are much longer than broad, with DP2 almost as long as DP3. The DP2 is much narrower anteriorly

than posteriorly. It has a strong mesostyle and weak paracone and metacone ribs. The protoloph is connected by a narrow bridge to the ectoloph, and directed postero-lingually, but the protocone is not distinct. A long slender crochet joins both the crista and an antecrochet, closing a pre- and a medifossette. The cingulum is strong anteriorly and posteriorly, but it is interrupted lingually. The protoloph of DP3 and DP4 are recurved posteriorly with anterior and posterior grooves isolating the protocone, and there is also an anterior groove on the metaloph. The crochet is very long, and there is a weak crista on DP3. The ectoloph has a strong protocone rib. Anterior and posterior cingula are weaker than on DP2.

Plate 1 about here

These teeth are similar to those of *A. incisivum* or *A. tetradactylum*, and especially to the *A. aff. tetradactylum* from Paşalar (FORTELIUS 1990), the only differences being perhaps that the anterior part of DP2 is very long at Çandır, and the lingual cingulum reduced. Still, on the basis of these milk teeth alone, specific identity between the Çandır and Paşalar *Aceratherium* is highly probable.

Measurements: DP2: 36.8 x 31; DP3: 38.5 x 34.2; DP4: 41.4 x 36.1

ÇA-1211 are 3 right upper premolars, P2-P4, from the same individual (Pl.2, Fig.1).

Their maximum dimensions are: P2: 29.4 x 35.1; P3: 32.4 x 43.9; P4: - x 46.5

They are well worn, but not extremely so. There is a thin cement cover on the external side of P3-P4. P2 is much smaller than P3, especially transversely. In this feature this *Aceratherium* is more like *A. lumiarensis* (ANTUNES & GINSBURG 1983, pl.4, fig.4b; pl.5, fig.2a) than like most later species, but a still earlier species, *A. platyodon*, also has a large P2 (MERMIER 1896).

Plate 2 about here

The cingulum is continuous around the lingual side of all 3 premolars. This is undoubtedly a primitive feature, present in all early Miocene species, *A. platyodon*, *A. lumiarense*, *A. fahlbuschi*, often present in *A. simorreense*, but usually absent in *A. tetradactylum* and *A. incisivum*.

A small medifossette is present on P2-P3, but not on P4. Crochet and crista are weak, as in most *Aceratherium*.

The most noticeable feature of these premolars is the union of the protocone and hypocone, closing the median valley high above the base. The Çandır premolars described by HEISSIG (1976, pl.4, fig.1-2) display the same feature, thus this is not an individual anomaly. A tendency towards closure of the median valley can still be seen in some Astaracian and early Vallesian *Aceratherium* (ALBERDI & al. 1981, in *A. simorreense*; KAUP 1834, fig.5, in *A. incisivum*) but this feature is constant in *A. platyodon* and *A. lumiarense*. However, in these latter species, the metaloph is shorter than the protoloph, while it is as long in Çandır.

ÇA-1212 is a fragment of upper tooth-row, with most of M2 and M3. These teeth are less characteristic than the premolars. The protocone is well set off from the protoloph, and flattened at the base. The teeth are well worn, but the crochet was certainly not strong. In this character again, the Çandır *Aceratherium* is more primitive than *A. tetradactylum* and *A. simorreense*, in which the crochet is better developed.

ÇA-1213 is a left mandibular ramus with i2, p2, p4, m2 and m3 (Pl.2, Fig.2). The mandibular corpus is rather low, and not much higher below m3 than below p2. The lower border of the corpus is gently convex below the tooth-row, but rather straight below the diastema, which is rather long. The symphysis reaches the level of the anterior lobe of the

missing p3. The anterior border of the ascending ramus is inclined backwards, and curves upwards far behind m3.

The incisors are dorso-ventrally compressed, rather vertically inserted, and close to the midline, with no indication of smaller incisors between them. The jugal teeth are much worn and display no noticeable feature.

Aceratherium mandibles are not easily distinguished from those of other rhinos. At Eppelsheim, KAUP'S type material of *A. incisivum* can be distinguished from its sympatric horned rhino, *Dihoplus schleiermacheri*, by its small teeth relative to mandibular size, low corpus, especially below the molars, with an almost straight lower border (the same characters are present at Höwenegg: HÜNERMANN 1989, pl.2), very high ascending ramus, stronger incisors and longer premolars. *A. tetradactylum* (GUÉRIN 1980, pl.3) differs from its sympatric *L. sansaniense* by roughly the same set of characters, but the difference is much less clear-cut. Other mandibles referred to *A. incisivum* (GUÉRIN 1980, pl.9, A2, from Montredon; CERDEÑO & SANCHEZ 1998, from Cerro de los Batallones; PAVLOV 1914, pl.5, fig.1c, from Tchobroutchi) or *A. simorreense* (ALBERDI & al. 1981, from Los Valles; CERDEÑO 1989, pl.9, from Toril-3) display such a great variety of shapes that it is impossible to assign them all to the same genus.

It is thus hard to compare the Çandır mandible with other species, since most of them do not have well-established characteristics. The incisors look more vertical than in *A. tetradactylum* or *A. incisivum*, and are more like those of *A. simorreense*, and perhaps especially like those of *Plesiaceratherium fahlbuschi* (HEISSIG 1984, fig.146) but this species has a p1 and a shorter diastema.

Postcrania

A left distal humerus, an almost complete right radius and a proximal left ulna, although certainly from at least two different individuals, fit rather well together, and are most probably from the same species. Few characteristic features are visible on the humerus, but the radius and ulna are definitely not of *Beliajevina*, a rhino of similar size also present at Çandır, and all three bones are best referred to *Aceratherium*.

a) Humerus: ÇA-1224 is a distal half, incomplete laterally. The *epicondylus lateralis* is much more salient, both medially and posteriorly than in *Brachypotherium*. The coronoid fossa is high and deep, the trochlea looks broader than that referred to *Dicerorhinus* by GENTRY (1987, fig.36).

Measurements

	Distal width max.	Distal width artic.	min.A-P diameter trochlea	max.distal A-P epiphysis
ÇA-1224	□ 117	75	39	90
<i>A.tetradactylum</i> Sansan	121	-	-	90
<i>A.incisivum</i> Höwenegg	107-120	82-87	39-42	85-93

b) Radius : ÇA-1225 is rather small but stout. The medial part of the proximal articular surface is roughly rectangular. This bone differs from that of *Beliajevina grimmi* in many respects (HEISSIG 1976: 38-41):

- in anterior view, the anterior border of the humeral facet is less sloping;
- the insertion of the *biceps brachialis* is central, if not medial, as in most rhinos, instead of lateral as in *B.grimmi*.
- the inter-osseous area is divided into two parts, while it is "einfach" in *B.grimmi*.

- there is a large facet for the pyramidal at the distal end, a characteristic feature of the Aceratheriini according to YAN DEFA & HEISSIG (1986: 91). This articulation is lacking in *B.grimmi* (HEISSIG 1976: 41), but also in *A. incisivum* (HÜNERMANN 1989, Fig.32).

Measurements

	ÇA-1225	<i>A. tetradactylum</i> GUÉRIN 1980 (N=3-4)	<i>A. simorreense</i> GUÉRIN 1980 (N=3-6)	<i>A. incisivum</i> HÜNERMANN 1989
Length	270	346	296	305
Min.width shaft	47.5	50	45	48
Distal width, max.	78.5	88	80	83
Distal width, artic.	63.5	73	69	71

This bone is thus smaller but more massive than that of both *A. tetradactylum* and *A. simorreense*, and more like *A. incisivum*. It seems best, however, to assign it to the genus *Aceratherium* s.l.

A proximal fragment (ÇA 93-XI-6, DTCF) is about the same size, and differs by the same characters from that of *B.grimmi*. We also refer it to *Aceratherium*, although it differs from ÇA-1225 by its broader (antero-posteriorly) medial part of the humeral facet.

c) Ulna : A proximal end, ÇA-1226 (max. transverse width: 65), is also much different from that of *B.grimmi* (HEISSIG 1976: 41-42, fig.7):

- both lips of the *processus anconaeus* are subequal in size, as in the *A. aff. tetradactylum* from Çandır (HEISSIG 1976, fig.27) while the lateral one is much longer in *B. grimmi*;

- the radial facets are set at an obtuse angle on the humeral one, instead of at a right or acute angle in *B.grimmi*;
- the diaphysis is not narrowed immediately below the epiphysis.

d) Metacarpals : ÇA-1227, ÇA-1228 and ÇA-1229 are proximal left McII, McIII and McIV, whose sizes match radius ÇA-1225. McIII much differs from that of *B.grimmi* (HEISSIG 1976, fig.12, 14) by its strong curvature in anterior view (its lateral part overhangs McIV), by its palmar facet for McIV which is large and facing laterally, instead of small and facing slightly upwards, and by its probable shortness. The proximal border of the lateral face is almost straight, and more closely resembles *Plesiaceratherium* (YAN DEFA & HEISSIG 1986, fig.12) than *A. tetradactylum*. Of the lateral facets for McIV, the posterior is much larger than the anterior one, and has a straight upper border, as in *A. tetradactylum* (KLAITS 1973: 322).

Measurements:

	McII, ÇA-1227	McIII, ÇA-1228	McIV, ÇA-1229
Prox.width, max.	34	48.4	28.5
A-P, max.	26	38.7	34
Min.width shaft	27.4	35.2	-

e) Tibia : The distal epiphysis ÇA-1231 much differs from that of *Beliajevina* by its great breadth relative to its antero-posterior dimension (cf measurements), and by the stronger obliquity of the articulation.

Measurements

ÇA-1231	<i>A.tetradactylum</i>	<i>A.simorreense</i>	<i>A.incisivum</i>	<i>B.grimmi</i>
	Sansan	N = 3-4	Höwenegg	Sofça

		GUÉRIN 1980		HÜNERMANN 1989	HEISSIG 1976
Dist.width, max.	82.5	88 (N=4)	84	79-98	87
Distal width, artic.	60	74 (N=1)	66	55-61	65
Distal A-P, max.	55	63 (N=4)	58	59-62	67
Distal A-P, artic.	42	51 (N=1)	46	47-48	52

f) Astragalus : There is no clear-cut difference allowing the distinction between the astragali of *Aceratherium* and *Dicerorhinus* s.l. Usually, the astragalus of *Aceratherium* is rather low, the trochlea is not very broad and separated by a narrow sulcus from the distal facets, its lateral lip has a regular slope, calcaneal facet 2 is isolated. Unfortunately, these differences are valid only as rules and are sometimes subtle.

The astragalus ÇA-1215 differs from ÇA-1209 in that calcaneal facet 2 joins facet 3 (as in the one figured by HEISSIG 1976, fig.29) and in the stronger medial tuberosity, but the bones are otherwise similar. The trochlea is less asymmetrical than in *A.tetradactylum* and more like *A.simorrense* (GUÉRIN 1980: 311-312) but the difference is far from being well established. In size, they fit better *A.tetradactylum* than *A.simorrense*, which is a small species.

Measurements

	Height	Max width	Trochlea width	Distal width artic.	Distal width max.
ÇA-1209	69	76.4	50.5	66	67.5
ÇA-1215	62	80	50	67	72

g) Calcaneus : ÇA-1216 is a right calcaneus, which fits well the astragalus ÇA-1215. The articular part is short compared with the non-articular one. Unfortunately, precise comparative data on the proportions of the calcaneus are lacking. The *sustentaculum tali* is much extended medially, and the cuboid facet is broad as in *A.tetradactylum*.

Measurements:

Max.length = 101; width of sustentaculum = 71; *tuber calcis*: transverse = 41
dorso-plantar = 54.5

h) Mt II : A proximal MtII differs from that of *B.grimmi* by the lack of dorso-plantar convexity of the proximal facet and the roundness of the anterior lateral facet. The narrowness of the epiphysis fits *Aceratherium* better than *Lartetotherium* (CERDEÑO 1986, pl.2, fig.1), and its small size fits *A.simorrense* better than *A.tetradactylum*.

Measurements

	ÇA-1232	<i>A.simorrense</i>			<i>A.tetradactylum</i>
		Paracuellos	Los Valles	Höwenegg	Sansan/Steinheim
		CERDEÑO 1989	ALBERDI & al.1981	GUÉRIN 1980	GUÉRIN 1980
Prox., A-P	32.2	28-32.7	31.1-35.6	33.5-37	35-41.5
Prox., transv	21.8	19-20.3	20-23.2	25.5-27.5	25.5-21

i) MtIII-MtIV : ÇA-1238 and ÇA-1240 are the proximal parts of a left MtIII and a right MtIV, probably of the same species. They differ from *B.grimmi* by the facets between them not being in the same plane, and by the transverse rather than antero-posterior extension of the proximal articular facet of MtIV. They look like *Aceratherium* in these features, but one must be very cautious again, because the proximal MtIII referred to *L.sansaniense* by CERDEÑO

(1986, pl.II, fig.3) differs as much as possible from the one referred to the same species by GUÉRIN (1980, fig.53, D1) ! None of these figures resemble ÇA-1238. These metapodials are relatively larger than the MtII above, but we prefer to assign them to *Aceratherium* because they match those of this genus more closely.

Measurements (proximal, transverse x A-P):

MtIII ÇA-1238 : 50.7 x 37+ ; MtIV ÇA-1240 : 42 x 39

The *Aceratherium* from Çandır is rather primitive in its upper teeth, and peculiar by its short and stout radius and metapodials. It is probably the same species as at Paşalar, but it looks different from the classical European contemporaneous forms. It is quite possible that it is indeed a new species, but more complete material is needed before its precise relationships can be established.

Beliajevina HEISSIG, 1974

Type-species: *Rh.caucasicus* BORISSIAK, 1935

This genus is often included in the Elasmotheriini, but the validity of this tribe is disputable. The characters that define it (FORTELIUS & HEISSIG 1989) are far from being clear-cut or may be subject to parallel evolution. It is strange that, using the same cladistic methodology, CERDEÑO (1995, 1996) reached a completely different conclusion, separating the group in two, and that PROTHERO & al. (1986), who considered only *Elasmotherium*, found still another tree.

Within the Elasmotheriini, FORTELIUS & HEISSIG (1989) reached the conclusion, based upon tooth characters, that both the Elasmothere from Çandır, formerly included in the mainly Spanish genus *Hispanotherium*, and the one from Paşalar, that HEISSIG (1974) had included in his genus *Beliajevina*, must be included in *Begertherium* (whose type-species, *B.borissiakii*, is

from Mongolia), leaving in a different group both the Spanish species *H.matritense*, and the Siwalik *Caementodon oettingenae* HEISSIG. This has, of course, important biogeographic implications, and could only be accepted with strong arguments. However, some of those put forward by FORTELIUS & HEISSIG appear to us insufficiently documented:

- the postfossette is said to be shorter on the premolars of the Spanish *Hispanotherium*, but we cannot see any difference in this respect between *H.matritense* (ANTUNES & GINSBURG 1983, pl.15, fig.1) and *B. grimmi* (HEISSIG 1976, pl.1, fig.4);

- the premolars are said to be higher in *Begertherium*, but very few unworn teeth are known. In Turkey, unworn molars are known only from Paşalar;

- *Begertherium* is said to have reduced incisors, but this is also true of *H.matritense* (ANTUNES & GINSBURG 1983, pl.12,fig.3e).

CERDEÑO (1996) held a completely different view, including several "genera", *C.oettingenae*, *B.borissiaki*, *H.grimmi*, in one and the same species, *H.matritense*. Discrepancies between these various systematic arrangements are so great that we prefer to take a conservative view, and include the Çandır species in the genus defined upon *B.tekkayai* of Paşalar. This clade is not better supported, but it has the advantage of not having any dubious biogeographic implications.

Beliajevina grimmi (HEISSIG, 1974)

Dentition

There are 4 upper teeth of *B.grimmi*: two much worn right M1, a moderately worn left M2, and a much worn left M3, (Pl.1, Fig.6-8). None of the M1s is worn enough to be associated with the worn M3, so these 4 teeth represent at least 3 individuals.

These teeth are similar to those already described (HEISSIG 1974, 1976) for this species, so that there is no need to describe them in detail. There are vertical grooves

demarcating the hypocone, and stronger ones demarcating the protocone. The antecrochet is strong (and fuses with the metaloph on one M1), the crochet is small, and there is a minute crista. The metaloph is not so short as in *B.tekkayai* from Paşalar. The external wall is sinuous. There is a thick cement cover, and the enamel is rugose.

Measurements (all permanent teeth numbered ÇA-1214):

	M1	M1	M2	M3
Basal length	-	-	33	□ 50
Anterior width	43	41+	44	□ 43
Posterior width	41	37	37	

Postcrania

Very few bones can be assigned to this genus, which looks therefore much rarer than in the German collection; this can easily be explained by a difference in the precise collecting spots, because such differences in relative abundance are also found among the Çandır Ruminants (see GERAADS et al. this volume).

ÇA-1207 and ÇA-1208 are right MtIII and MtIV. They display the characteristic features of *B.grimmi*: both articular facets between them are almost in the same plane (in *H.matritense* from Spain, they are in different planes: IÑIGO & CERDEÑO 1997, fig.6.10), and the proximal MtIV facet is longer antero-posteriorly than transversely.

ÇA-1234 (Pl.1, Fig.5) is a right astragalus, larger than, but morphologically not much different from those assigned to *Aceratherium*. Calcaneal facet 2 is united with facet 3, which is transversely elongated. The trochlea is not very asymmetrical, and almost reaches the distal facets. The cuboid facet is much broader anteriorly than posteriorly. All these features match those illustrated by HEISSIG (1976, fig.20-21) for *B.grimmi*.

Measurements:

	Height	Max width	Trochlea width	Distal width artic.	Distal width max.
ÇA-1234	77	90	56	77	79.5

ÇA-1206 is a proximal fragment of McII. It differs from that assigned to *Aceratherium* in the more obtuse angle between the trapezoid and magnum facets, and in the slightly concave outline of the former in anterior view. There is no demarcation line between the magnum and McIII facets. The identification to *B.grimmi* is far from certain, however, because the bone is also rather similar to the one described as *Mesaceratherium simorreense* by HEISSIG (1976, fig.31).

Brachypotherium ROGER, 1904

Type-species: *B.brachypus*

Diagnosis: HEISSIG 1976: 80.

Brachypotherium sp cf *B.brachypus* (LARTET in LAURILLARD, 1848)

Type-locality: Sansan.

Diagnosis: HEISSIG 1976: 81.

No teeth of this species have been found in Çandır. HEISSIG (1976) described an incomplete distal humerus and 3 astragali, and there is more skeletal material in MTA, described below.

Postcrania

a) Humerus : ÇA-1217 (Pl.1, Fig.3) is a complete bone, but the proximal half is somewhat crushed. The bone is similar to that of *Diaceratherium aurelianense* from Artenay (CERDEÑO 1993, pl.II, fig.3), but more slender, although the difference is probably less than it appears, because the humerus from Artenay is strongly crushed. Still, the Çandır humerus looks remarkably slender for a rhino. As in *D.aurelianense*, the lateral tuberosity is recurved above the bicipital groove, as in modern *Dicerorhinus sumatrensis*, or fossil *Dicerorhinus* (e.g. GENTRY 1987, fig.36), but it is stronger. The distal end is extremely different from that of non-brachyothere Rhinos. When the bone is held vertically, the trochlea lies almost directly below the shaft, instead of more cranially. This is of course related to the greater weight of the animal, which has pillar-like limbs, like elephants. The palmar part of the epitrochlea (*epicondylus medialis*) is broken, but it was certainly very weak. The *epicondylus lateralis* is well preserved, and both its palmar and lateral extensions are also very short. The olecranon fossa is quite small and low. The trochlea is broad and low, with shallow central groove, and a medially stretched medial lip. Above the coronoid fossa, a crest separates the scars for *m.extensor carpi radialis* and for *m.extensor digitalis communis*.

Measurements:

	<i>B.cf brachypus</i>		<i>D.aurelianense</i>	<i>B.goldfussi</i>
	ÇA-1217	Çandır HEISSIG 1976	Artenay CERDEÑO 1993	Steinheim ROGER 1900
Max. length	490	-	455	-
Distal width, artic	102	95	97	100-110
Distal A-P, artic.	96.5	83	105	-
Distal width, max.	147	-	140	150-160

b) Pyramidal : Two pyramidals are the only carpal bones preserved in the MTA collection. They are much lower than bones referred to *H.grimmi* by HEISSIG (1976, fig.9) or to *Aceratherium* by KLAITS (1973, pl.2, fig.8-9) and more like *Brachypotherium* (HEISSIG 1976, fig.37; KLAITS 1973, pl.2, fig.10). Another similarity with the latter genus lies in the very low distal facet for the lunar but, in contrast to *Brachypotherium*, the antero-medial height is not much greater than the postero-lateral one (ibid.) and the ulnar facet is not so concave. Still, we refer them to this genus because they are too low to be satisfactorily assigned to *Aceratherium*.

Measurements:

	ÇA-1219	no number
Antero-medial height	48.5	50
Minimum height	" 33	" 32.5
Length of medio-palmar face	" 42	" 42.5

c) Metacarpals : Two metacarpals, McII and McIV, both almost complete but in a rather bad state of preservation, must belong to *Brachypotherium*. McIV is strongly crushed transversely.

Measurements

McII	<i>B.brachypus</i>			<i>B.goldfussi</i>	<i>B.heinzellini</i>	
	ÇA	Malartic	Sansan	Steinheim	Zelten	Rusinga
	1220	CERDEÑO 1993	KLAITS 1973	ROGER 1900	HAMILTON 1973	HOOIJER 1966
Length	140	150	-	100-132	149	130
Min.width shaft	46.5	46.3	-	38-40	53	45
Dist. width max.	57	53.4	-	-	57	50
Dist. width artic.	45	45.6	-	-	48	-
McIV Length	134	132.6	130-140	116-130	?103	110-113

The palmar facet for the McIII on the McIV has an elliptical outline, as in *B.aurelianense* (CERDEÑO 1993: 37) instead of rectangular in *B.brachypus* of Sansan (KLAITS 1973). It is impossible to tell whether a McV was present. According to KLAITS (1973: 322), it was absent in *B.brachypus* but, according to CERDEÑO (1993: 53), it is sometimes present, as in *D.aurelianense*.

d) Tibia : The complete tibia ÇA-1218 is very similar in its proportions to those of Simorre (Malartic); it is more massive than in earlier sites (GINSBURG & BULOT, 1984, pl.IV, fig.1; CERDEÑO, 1993, pl.III, fig.8). The astragalus surface is broad (instead of "assez carrée" in *D.aurelianense*) shallow, and less oblique than in other rhinos, and distal processes are shorter than in *D.aurelianense*. On the whole, the bone is clearly more advanced than that of the latter species.

Measurements

	ÇA-1218	Malartic			Artenay	Bézian	Stätzling
		CERDEÑO			CERDEÑO	G.&B.	ROGER
		1993			1993	1984	1900
Length	302	317.5	310	308	307	351	300
Prox. width	125	124.6	128.5	137.8	130	126	145
Min.width shaft	56	62	59.5	60	60.6	57.4	-
Dist. width, max.	102	-	103	106	98	104	100
Distal A-P max.	70	-	72.8	68	71	76	-
Dist. width, artic.	80	-	86	84	69	-	-
Distal A-P, artic.	53	-	54	57	56	-	-

e) Astragalus : ÇA-1223 (Pl.1, Fig.2) fits the above mentioned tibia well and differs in several respects from the 4 other astragali from Çandır. It is lower and broader, the pulley is less asymmetrical, with a shallower median gorge, its lateral lip does not overhang calcaneal facet 2, facets 1 and 2 on the plantar face are continuous, facet 3 is absent or extremely small, facet 1 is long proximo-distally but only weakly concave, and the cuboid facet is very broad. In this last character, and in the fusion between facets 1 and 2, this specimen differs from the ones described by HEISSIG from the same locality, demonstrating intra-specific variability, since specific identity is not doubtful.

Measurements:

ÇA-1223 Height = 67.5 ; Max width = 92? ; Trochlea width = 66

The astragalus of *B.brachypus* is much lower in comparison to its length than that of *D.aurelianense* (CERDEÑO 1993, fig.1). The relative size and positions of the calcaneal facets are variable (variable presence between facets 1 and 2, size of facet 3) but the distal

prolongation of facet 1 looks constant (CERDEÑO 1993, pl.VI, fig.8; AZANZA & al. 1993, pl.III, fig.1b; HOOIJER 1963, pl.VIII, fig.7; GINSBURG & BULOT 1984, pl.IV, fig.3b).

As in other Mammals, astragalus is the most commonly found bone in *Brachypotherium*, and this bone has often been studied. CERDEÑO (1993: 60-61) centered her discussion on the distinction between *Prosantorhinus*, *D.aurelianense* and *B.brachypus*, but the consideration of *B.brachypus* alone leads to an unexpected result. It had already been noted (e.g. GENTRY 1987, table 3) that the proportions of this bone change with time, the most recent specimens being lower in relation to width, thus more “ typical ”. What is more surprising is that the astragali that are lower are also smaller: height is positively allometric on width (fig. 1). This means that the change of proportions, far from being a consequence of weight, results from an adaptative morpho-functional change.

cf *Lartetotherium* sp.

ÇA-1236 (Pl.2, Fig.3) is an almost unworn right DP2 (max.length = 37; max.breadth = 36). The ectoloph is gently convex, except for a strong mesostyle. The protoloph is fully connected to the ectoloph; the protocone is not demarcated. The crochet and the crista enclose a shallow medifossette. The metaloph is almost transverse, and the postfossette much reduced. The cingulum is weaker than in *Aceratherium*, but still strong, and continuous along the mesial, lingual and distal borders, except at the base of the hypocone. This tooth differs from the DP2 of *Aceratherium* ÇA-1210 by its completely different proportions, and there is no doubt that it does not belong to this genus, but to a Rhinocerotinae.

In *Hispanotherium* from Spain (CERDEÑO & ALBERDI 1983, Fig.1C), dP2 has roughly the same proportions and orientation of the lophes, but the protocone and hypocone are connected, as in the premolars, and the DP2 of *Beliajevina* was thus certainly very different from ÇA-1236

Several Middle and Upper Miocene Rhinos have DP2s much more similar to ÇA-1236. Indeed, had this tooth been found in the Upper Miocene, we would have referred it without much hesitation to *Ceratotherium neumayri*. The Middle Miocene East and North African species "*Dicerorhinus*" *leakeyi* and *Paradiceros mukirii* are smaller, and the lingual cingulum is weaker (HOOIJER 1966, 1968; GUÉRIN 1976). The mesostyle is perhaps weaker in the Vallesian "*D. primaevus* ARAMBOURG (actually a Dicerotini: GERAADS 1986), from Algeria (ARAMBOURG 1959). We could not find any description of the DP2 of *Lartetotherium sansaniense* in the literature. However, SANTAFE-LLOPIS & CASANOVAS-CLADELLAS have described and illustrated (1992, pl.1, fig.1), from Polinyà, a maxilla with DP2-DP4, that they referred to *A. incisivum*, but in which the shortness of DP2 is unlike this species. We believe that it could belong instead to *L. sansaniense*, a species also mentioned from this site. If our identification is correct, the DP2 of the latter species would be quite similar to ÇA-1236.

The astragalus ÇA-1239 (Pl.1, Fig.4) is very different from all others. It is very high, the trochlea is widely separated from the distal facets, the cuboid facet is very narrow anteriorly, the navicular facet is little transversely elongated but broad anteroposteriorly. Calcaneal facet 2 is large and united with facet 3, the fibular facet is very short and broad. This bone is certainly not of *Aceratherium* or *Beliajevina*, and more "*Dicerorhinus*-like". The trochlea is asymmetric, while that of *Paradiceros* from the middle Miocene of Kenya is, remarkably, almost symmetrical (HOOIJER 1968, pl.3, fig.3). The bone is much like that of *L. sansaniense* (CERDEÑO 1986, pl.1) but a specific, or even generic identity cannot be taken for granted. Still, this astragalus confirms beyond doubt the occurrence of a true horned rhino at Çandır.

Measurements:

Height	Max width	Trochlea width	Distal width	Distal width
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				artic.	max.
ÇA-1239	80	87	60	70	73.5

Of the larger calcanei, ÇA-1241 is incomplete, but it fits the astragalus ÇA-1239 well. Its tuber was certainly rather long, and the anterior process pointed rather than squat. We assign it to *Lartetotherium* with some doubt.

Measurement: width of sustentaculum = 69

We refrain from attempting a species level identification based upon a single milk-tooth and an astragalus, but it is clear that a fourth species of Rhino is present at Çandır.

Results and Discussion

The rhinocerotid fauna of Çandır shares, at least at first sight, several taxa with those of western Europe, where *Hispanotherium matritense*, *Aceratherium tetradactylum*, *Brachypotherium brachypus* and *Lartetotherium sansaniense* are relatively common species in the Middle Miocene. The similarity is perhaps not so close, however, because specific, if not generic, identity of the Anatolian and European forms is far from certain. Uncertainty arises first from the almost complete lack of skull material in the Middle Miocene of Turkey. The diversity of skull characters in Elasmotheres and Aceratheres, both with a rather uniform tooth morphology, prevents any reliable conclusion to be drawn from teeth only. The lower Siwaliks of the Pakistan also have similar taxa (*Caementodon* and *Brachypotherium*) and the most common Rhino of the MTA collection, *Aceratherium*, has some peculiarities (primitive teeth, short and robust distal limbs), which set it aside from the best-known European forms and specific identity is unlikely. On the whole, there is little reason to believe that the

biogeographic affinities of the Çandır rhinos lie more with European than with Asiatic species.

Biochronological conclusions are also difficult. In western Europe, *Hispanotherium* is restricted to zone MN 4 & MN 5 (GINSBURG & al., 1987), but this genus or closely related ones survive much later in Asia. *Brachypotherium* and *Aceratherium* are also known until the upper Miocene.

Ecological interpretations are less ambiguous. *Brachypotherium* has often been compared to Hippos, and was certainly a marsh or lake dweller. According to GUÉRIN (1980), *Aceratherium* favoured wet forested areas; its teeth, however, are not very low-crowned, and it was probably a mixed-feeder. *Beliajevina grimmi*, on the contrary, with its very high-crowned teeth and slender limbs, was certainly an open-country rhino. This association points therefore to a wooded lake-margin, surrounded by a more steppe or savannah-like landscape. Discrepancies in the proportions of the four taxa among the German and MTA-DTCF collections probably result, as for Ruminants, from different depositional environments at the various collecting spots (but only the DTCF material, which is very scarce, has its precise provenance data).

Acknowledgements

We are particularly grateful to Prof.ERKSIN GÜLEÇ for having entrusted us with the study of the Çandır rhinos. Many thanks also to BARIS KARABAGLI, head of the MTA Museum, for her permission to work there and for her constant help, and to all people who allowed D.G. to study material in their care: L.GINSBURG, F.RENOULT, B.SENUT (Muséum National d'Histoire Naturelle, Paris), A.CURRENT, A.W.GENTRY (Natural History Museum, London). The missions of D.G. in Turkey were funded by the "Programme

Paléoenvironnement, évolution des Hominidés" of the Centre National de la Recherche Scientifique.

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Captions to plates

Plate 1

Fig.1: *Aceratherium* sp., DP2-DP4 ÇA-1210. Fig.2: *Brachypotherium* sp., astragalus ÇA-1223. Fig.3: *Brachypotherium* sp., humerus ÇA-1217. Fig.4: cf *Lartetotherium* sp., astragalus ÇA-1239. Fig.5: *Beliajevina grimmi*, astragalus ÇA-1234. Fig.6-8: *Beliajevina grimmi*, M1 M2 and M3 ÇA-1214. Scale = 25 mm for Figs.1 and 6-8, 50 mm for Fig. 2, 4, 5, 100 mm for Fig.3.

Plate 2

Fig.1: *Aceratherium* sp., P2-P4 ÇA-1211 in occlusal (1A) and lingual (1B) views. Fig.2: *Aceratherium* sp., mandible ÇA-1213 in upper (2A) and lingual (2B) views; 2C: occlusal view of the teeth, p4 and m1-m2. Fig.3: cf *Lartetotherium* sp., DP2 ÇA-1236 in labial (3A) and occlusal (3B) views. Scale = 10 cm for Fig.2, 5 cm for Figs 1 and 3.

Caption to figure

Figure 1 : Plot of height vs maximum width of some Middle and Upper Miocene Rhino astragali