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Ruminants, other than Giraffidae from the middle Miocene hominoid locality of Çandır (Turkey).

9 figures, 3 plates

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Abstract.- There are six Ruminant species at Çandır, not including the Giraffid *Giraffokeryx*. The smallest one is a *Micromeryx*, a genus left as *Eupecora incertae sedis*, but its determination at species level must await full revision of the genus. A large rare form is provisionally referred to *Palaeomeryx*. Also rare is a new species of the primitive cervid *Heteroprox*, with antlers similar to the European ones, but with quite a different dentition. Bovids are much more common, with the hypsodont genera *Turcocerus* and *Hypsodontus*, and the more generalised *Tethytragus*. The ruminants provide no evidence for putting Çandır later than Paşalar, but they reveal ecological differences, Çandır Locality 3 being especially open.

Key-words.- Middle Miocene, Turkey, Mammalia, Artiodactyla, Ruminantia

## Introduction

The middle Miocene site of Çandır, 60 km N-E of Ankara, has long been known for having yielded the hominoid primate *Griphopithecus alpani* (TEKKAYA). Following excavations by German paleontologists (SICKENBERG et al. 1975), KÖHLER (1987) described bovids from several Turkish Neogene localities, including Çandır. From this site, she listed *Caprotragoides potwaricus*, *Hypsodontus pronaticornis* n.sp. and *Turcocerus gracilis* nov.gen., nov.sp. New excavations led by I.TEKKAYA in the '80s greatly increased the sample, kept in the MTA Museum; it has, however, the drawback that not all specimens are precisely

registered as to their exact provenance, except some of those from Locality 1, labelled AÇHÜ. From 1989 onwards, E.GÜLEÇ conducted new excavations at Çandır, this time with precise recording of the location of all specimens. Both her collection of Ruminants (housed in the DTCF, and labelled ÇA), and TEKKAYA'S, are studied here. The sites closest to Çandır are Paşalar (ALPAGUT, 1990) and İnönü (GERAADS & al., 1995).

## Materials and Methods

In the following descriptions, upper tooth rows are supposed to be horizontal, “ horn ” refers to any kind of cranial appendage, uppercase letters refer to upper teeth, lowercase letters to lower teeth, and measurements are in millimetres. Abbreviations are : DTCF: Dil ve Tarih Cografya Fakültesi, Ankara; MTA: Maden Tetkik ve Arama, Ankara; MGL : Musée Guimet, Lyons ; MNHN : Muséum National d'Histoire Naturelle, Paris.

## Systematic description

Family indet.

*Micromeryx* LARTET, 1851

*Micromeryx* sp., aff *Micromeryx flourensianus* LARTET, 1851

This taxon is not uncommon at Çandır, even though it was probably more easily overlooked during excavations than larger Ruminants. It is mostly represented by mandibular fragments and some postcrania.

Description: the premolar row is not very long. The p3 has the parastylid distinct from the paraconid, and an oblique metaconid crest. The morphology of p4 is varies little on the 8 specimens (Fig. 1); the metaconid forms a complete lingual wall connecting the paraconid, which is little distinct from the parastylid (less so than in the later Spanish site of Los Valles:

MORALES & SORIA 1981). The labial groove separating the talonid from the trigonid is deep, but the eocristid remains continuous. The entoconid may tend to become isolated from the main cristid.

Figure 1 about here

The molars are not very brachyodont; ectostylids are present, as well as metastylids, at least in the upper half of the crown. The *Palaeomeryx* fold may or may not be present, even on unworn teeth. The third lobe of m3 forms a complete loop, and is not much smaller than each of the first two lobes.

Dental measurements :

	p2-p4	m1-m3
ÇA 91-72 (Loc. 3)	14.5	
ÇA 92-35 (Loc. 3)		23.1
ÇA 92-89 (Loc. 3)	14	
ÇA 93-5 (Loc. 3)	15.2	
AÇHÜ 1103		25.4
AÇHÜ 1104		26.2
AÇHÜ 1105	15.6	
AÇHÜ 1107	15.2	
AÇHÜ 1108		25.6
AÇHÜ 1109		25.6
AÇHÜ 1110	17	25.7

Postcranial bones are mostly characterized by their small size (dimensions of the tali, fig.2). No distal metatarsal has been found at Çandır.

Figure 2 about here

Comparisons: *Micromeryx* is mainly a Middle Miocene genus, hornless or the antlers of which are unknown, easily recognisable by its small size, but also very characteristic by some morphological features, such as the strongly molarized p4 and the large size of the third lobe of m3 (as already noted by LARTET 1851). It has traditionally been placed within the Cervidae (or at least Cervoidea), mainly because FILHOL (1890) figured a metatarsal with a roofed-over distal groove. However, GENTRY (1990) remarked that the teeth from Paşalar that he referred to ?*Micromeryx* sp. “ are not definitely cervid ”. My examination of the material from La Grive housed in Musée Guimet, Lyons, convinced me that no argument allows the placement of *Micromeryx* within cervids :

- 1) numerous metatarsals, either complete ones or distal parts, of the right size for *Micromeryx* but for no other Ruminant at La Grive (except a very rare one), display all intermediate conditions between a fully open distal groove, as in Bovids and Giraffids, and a closed one. In the latter case, however, the channel remains superficial, with the distal opening less plantar than in Cervids. Whether or not this variation relates to time-succession of the two main localities of La Grive is not known, but, in any case, this variability prevents use of this character in familial attribution of *Micromeryx*.
- 2) a fragment of skull, LGr 3004, as yet unpublished, displays some original features. There is a large alveolus for an upper canine, extending backwards as far as the middle of dP2, and this canine was therefore relatively as large as in *Moschus* or *Hydropotes*. Although the muzzle is somewhat dorso-ventrally crushed, it can be seen that a small (relatively smaller

than in *Hydropotes*) lachrymal vacuity was almost certainly present, but the lachrymal bone is flat, and there was certainly not the slightest trace of a pre-orbital fossa. There is a single large lachrymal foramen inside the orbit, while almost all cervids, including *Hydropotes*, have two, a derived condition found in very few other Ruminants, (LEINDERS & HEINTZ 1980 ; BOUVRAIN & al. 1989). Above the lachrymal foramen, probably just above the lachrymo-frontal suture, the orbital margin is notched, as in some other Ruminants (e.g. *Cephalophus*). Still higher, the orbital margin is imperfectly preserved ; a wide depression in the frontal is pierced by several accessory foramina in front of the supra-orbital foramen. It is most likely that the latter was not really a foramen, but only a notch in the orbital margin. In any case, the position and shape of this foramen is more reminiscent of *Moschus* and *Hydropotes* than of other Ruminants.

3) Both *Moschus* and *Micromeryx* have a molarized p4, an unusual feature for a small Ruminant.

The main argument against a close relationship between *Moschus* and *Micromeryx* is the morphology of the lower molars which, in *Moschus*, have no metastylid, but a strong fold descending backwards from the metaconid ; this fold, also found in Tragulids and *Bachitherium*, is a primitive feature lost in the Eupecora. *Micromeryx* should therefore be left as Eupecora *incertae sedis*.

There are significant size differences between the *Micromeryx* from various localities. At Çandır, the metacarpal (ÇA 92-83 from Loc.3) is 96 mm long, with a distal width of 13.1 mm, while three specimens from La Grive in MGL are 75.7, 76.5 and 87 mm long, with distal widths of 12.4, 12 and 10.5 mm respectively. The tali (Fig. 2) are also larger than at La Grive, where the medial height is usually in the range 14.5-15 mm, the distal width in the range 9.5-10 mm. In turn, the *Micromeryx* from La Grive is larger than that of Sansan, where the length of a metatarsal is given by FILHOL as 88-92 mm, instead of 100-110 mm at La Grive. There is

no clear consistent morphological difference in the teeth, but the molars from La Grive are shorter than those from Çandır, especially relative to the premolars. The Turkish teeth are more like those of *M.styriacus* THENIUS, 1950, from Göriach.

	p2-p4	m1-m3	index of means
La Grive	15.8-18 (mean 16.3 ; N = 8)	20.8-22.7 (mean 22 ; N = 5)	74
Çandır	14.5-17 (mean 15.2 ; N = 6)	23.1-26.2 (mean 25.3 ; N = 6)	60

The Çandır *Micromeryx* is, therefore, certainly different from that of La Grive, and probably still more different from that of Sansan, type-locality of *M. flourensianus*. It should perhaps be referred to *M. styriacus* because of its large size, but I prefer to leave it close to *M. flourensianus*, which is the oldest name, until the systematics of the genus is settled. The interesting point is that both in the larger size and the shorter premolar row, the Çandır *Micromeryx* looks more evolved than that of La Grive, although it is in all probability earlier. It is about of the same size as the ? *Micromeryx* of Paşalar (GENTRY 1990, fig.3,N-S), but the latter is somewhat different: it is perhaps less hypsodont, the basal pillars are small or absent, there is no metastylid, and no *Palaeomeryx*-fold. It is difficult to relate these differences to chronology, and there are perhaps two lineages in Turkey as well as in Europe.

Family indet.

*Palaeomeryx* VON MEYER, 1834

cf *Palaeomeryx* sp

A number of large brachyodont Ruminant teeth, mainly from the Middle Miocene of Europe, have long been united under this generic name, but recent discoveries (see review in DURANTHON et al. 1995) have shown that several taxa have probably been confused. None of

them has been described in detail yet, so that even their familial affinities remain doubtful. It is well established that they have a closed distal gully on metatarsal, like cervids, but their skull appendages are said to be independent from the frontal, as in modern Giraffes. Çandır has yielded some teeth and postcrania, most of them from Loc.1.

The teeth are only slightly smaller than those of *Giraffokeryx*, but readily identifiable because of their strong brachyodonty, *Palaeomeryx* fold on lower molars, strong forwardly inclined paracone rib on upper molars, and strong cingulum. Limb bones are less easily identifiable, except the talus, which has a strongly concave external face, and a sharp narrow internal lip of the tibial trochlea (see dimensions in GERAADS & ASLAN, this volume). A distal metatarsal has the distal channel penetrating deeply into the bone. These characters are similar to those of the “ classic ” French *Palaeomeryx*, but the absence of skull precludes any precise attribution.

There is also in MTA the cast of an upper right canine said to be from Çandır, but we could not find the original specimen. There is no doubt that it is a Ruminant canine. It is curved backwards and outwards, with a sharp posterior edge and a rounded anterior face. The tip is worn on the anterior face (i.e. on the antero-inferior side, in the living animal). It compares favorably with a tooth from La Grive (N° 2621 in Musée Guimet, Lyon), except that it is larger (at crown-root junction: 21.5 x 13.5, length of crown:  $\pm$  65 instead of 18 x 11, L  $\pm$  30). It most probably belongs to *Palaeomeryx*.

Family Cervidae

*Heteroprox* STEHLIN, 1928

*Heteroprox anatoliensis* sp.nov.

Type : AÇHÜ-311, right horn with the complete pedicle (Pl.1, Fig.1) . Housed in the MTA Museum, Ankara.



Referred material: ÇA 92-7, from Loc.1, DTCF, Ankara, a mandible with p2-m1 (Fig. 3); AÇHÜ-310, left horn with part of the pedicle (Pl.1, Fig.2); Several tooth-rows and isolated teeth. I have not systematically tried to recognize cervid bones among those attributed to *Tethytragus*, which is of similar size, but no bone is obviously cervid, and *H. anatolicus* is certainly much less common than *Tethytragus*.

Diagnosis : A species of *Heteroprox* with horns similar to those of the type-species, *H. larteti* from Sansan, but with a protoconal fold on the upper molars, and a *Palaeomeryx* fold on the lower molars ; p4 with shallow labial groove and expanded metaconid.

Plate 1 and figure 3 about here

Description : Both horns differ in size and are certainly from two different individuals. A fragment of frontal is preserved on AÇHÜ-311, so that side and orientation of the horn can be determined. On the type at least, the pedicle is very long, about as long as the “ antler ” itself, and it was probably from a young individual. It is slightly concave externally in front view, and its section is somewhat compressed transversely. The "antler" consists of a single fork. Its base, where it joins the pedicle, and where the burr is in true cervids, is thickened and ornamented with deep grooves and strong ridges, but there is no clear limit at all between the fork and the pedicle, and nothing suggests that the "antlers" could have been deciduous.

However, STEHLIN (1928) and GINSBURG & CROUZEL (1976) have put forward some good arguments showing that this was probably the case in European *Heteroprox*. The anterior tine is slightly curved backwards, but about in line with the pedicle. It is perhaps slightly shorter and more transversely compressed than the posterior one, which makes an angle of about 30° with the pedicle. There is no indication of an incipient third tine, such as the one present at

Sansan (GINSBURG & CROUZEL, 1976), but this, again, could be because both "antlers" are from juveniles.

Measurements :

	AÇHÜ-310	AÇHÜ-311
Pedicle: AP x transverse	19 x 14	17 x 12.7
"burr": " "	35 x 19.5	33.5 x 18
Length of posterior tine	90	-

These characters are so similar to those described for *Heteroprox larteti* at Steinheim (STEHLIN 1928 ; HEIZMANN 1976), Klein-Hadersdorf (THENIUS 1948) and especially Sansan, type-locality of this species (LARTET 1890, pl.37 ; GINSBURG & CROUZEL 1976) that there is no doubt about the close similarity of the Çandır species with this primitive cervid, which had not hitherto been mentioned outside Europe. By the absence of clear limit between "antler" and pedicle, Çandır horns are more like those of Sansan than like those of the younger site of Steinheim (on a specimen from this site in MGL, the transitional area between pedicle and antler is not more than 3mm long).

The dentition is mainly known by several mandibular fragments and teeth. All come from Loc.1, except two teeth from Loc.3. One of them is an upper molar (12 x 14.2) with a protoconal fold. As no other non-Bovid Ruminant of this size occur in Çandır, these dentitions can be referred without doubt to the same species as the two horns described above.

## Measurements :

	p2-p4	m1-m3
ÇA 92-7 (Loc. 1)	28.6	39.5
AÇHÜ 1098		39
AÇHÜ 1211	29.9	
AÇHÜ 1236		38.3

These teeth differ from those described as *?Stephanocemas* at Paşalar (GENTRY 1990) by the protoconal fold on upper molars, and the presence of a paraconid on p4.

Surprisingly, these dentitions (Fig.3) are also much different from those described by GINSBURG & CROUZEL (1976) for *H.larteti* of Sansan. At Çandır :

- p2 is wider posteriorly than in the middle;
- p3 is also narrower anteriorly; the paraconid and parastyloid may be poorly distinct; the metaconid forms a distinct cuspid, absent at Sansan according to GINSBURG & CROUZEL (1976), and it further has a posteriorly directed expansion ;
- the anterior part of p4 is similar to that of p3; the metaconid is distinctly enlarged, forming an incipient lingual wall on all 5 specimens of this tooth; the labial groove is much shallower than at Sansan. The orientation of the entoconid is variable: it may be oblique, as at Sansan, or it may tend to have a more mesio-distal axis, in line with the metaconid;
- all lower molars have a distinct *Palaeomeryx*-fold, which is almost absent at Sansan.

Both at Sansan and Çandır, the association between horns and teeth is not in doubt, so that these differences imply a specific distinction. The Çandır teeth are more like those of the earlier cervid *Procervulus dichotomus*, which has more primitive horns than those of *Heteroprox* : they are more slender and without any difference in ornamentation between “ antler ” and pedicle. However, the metaconid of p4 has an anterior outgrowth, a derived

character. The Çandır teeth are perhaps a little more evolved than those of *P.dichotomus* (GINSBURG & BULOT, 1987, fig.47) by their metaconid more expanded on p3 and p4, and their stronger metastylids on molars, but other specimens of this species also have large metaconids on premolars (e.g. M672, from Foissin, in Fac. Sciences Lyons).

Given the importance of parallelism in the evolution of Ruminant dentition, these similarities should not be overestimated, but the diachronism in the evolution of horns and lower premolars indicate that the split between European and Turkish lineages of *Heteroprox* occurred earlier than Çandır.

#### Family Bovidae

*Turcocerus* KÖHLER, 1987

= *Sinomioceros* CHEN, 1988

Type-species : *Oioceros ? grangeri* PILGRIM, 1934

*Turcocerus gracilis* KÖHLER, 1987

KÖHLER (1987) described *T. gracilis* from Çandır and summarised its differences from the type-species, *T. grangeri* from the Tung Gur Formation of Mongolia. E.GÜLEÇ'S excavations have greatly increased the sample from the Turkish locality, but the skull of this species remains unknown. No specimen is undoubtedly from Loc.1 and, although many of TEKKAYA'S specimens are of uncertain provenance, *Turcocerus* is certainly much more common in Loc.3 than in Loc.1.

The size of the Çandır horns (including those described by KÖHLER, 1987) is rather homogeneous, contrasting with the great variation found at İnönü, that GERAADS & al. (1995) explained by sexual dimorphism and ontogenic changes. Çandır horns would all be adults and less sexually dimorphic (Fig.4 and Pl.2, Fig.1).

A fragment of mandible with dp4-m2 has an unworn m2 measuring 12.2 x 7 with an height of 14 mm: it is therefore greatly hypsodont. All other specimens are adults; the anterior valley of p4 is usually widely open (KÖHLER, 1987, fig.25), but one specimen (ÇA 92-88, Fig. 5) has the paraconid strongly expanded backwards, almost closing the valley.

Plate 2 about here

Figures 4 & 5 about here

Dental measurements :

	p2-p4	m1-m3	p2-m3
Loc.3, surface	20.5	37	57
ÇA 90-47(Loc.3)	25.5	38.6	
ÇA 91-160( " )	20.7	34	54.9
ÇA 92-88( " )	20.6	37.7	57.6
ÇA 92-98( " )	20.7	35	55.5
MTA 83-96		38.1	
MTA 83-275		36.5	
MTA 83-300	22.2		
MTA 5119		35.4	
MTA 5123		37	
MTA 5131		37.9	
MTA 5163		40.4	
MTA 5194		37.4	

MTA 5202

38.7

Comparisons: Despite the smaller size and some tooth differences, *T. gracilis* is so similar in its horn-core morphology to *T. grangeri* that it can be confidently assigned to the genus *Turcocerus*. Several other species from China have been referred by CHEN (1988) to his genus *Sinomioceros* (a synonym of *Turcocerus*), but the horns of most of them are unknown. However, the horn-core figured by BOHLIN (1938, pl.7, fig.8) is almost identical to the Turkish specimens and generic, if not specific, identity is likely. The genus *Turcocerus* is therefore widely distributed, but remains poorly known, except its type-species.

*Hypsodontus* SOKOLOV, 1949 ?

*Hypsodontus ? pronaticornis* KÖHLER, 1987

*Hypsodontus* has already been described from Çandır and Paşalar by KÖHLER (1987), from Paşalar by GENTRY (1990) and from İnönü by GERAADS & al. (1995), and little more need be added to these descriptions.

Köhler had surmised from the morphology of a juvenile horn-core that its orientation was sharply different from that of the adult specimens, but a juvenile frontlet, n° ÇA 91-113, has small horn-cores inserted vertically, quite similarly to the adult ones. The latter have a rounded cross-section, without keel, a homonymous torsion and poor spiralisation, mainly visible in side view, the anterior border being concave. They are, on the average, smaller than at İnönü (Fig.6).

Figure 6 about here

The teeth are noticeable by their large size and hypsodonty, and short premolar rows, obviously denoting grazing habits. This is confirmed by the very high and oblique mandibular ramus; it is still more so in the adult than in (more complete) juvenile mandible of Pl.3, Fig.4.

Dental measurements (all from Loc.3):

	p2-p4	m1-m3	p2-m3
ÇA 89-12	34	71	105
ÇA 90-8		71.1	
ÇA 90-24	33.3		
ÇA 91-91		65.5	
ÇA 92-2	37.5	74	
ÇA 92-37	34.5	66	100.2
ÇA 92-178	36.8	67.7	103.5
MTA 1022		73.5	
MTA 5040		72.5	
MTA 5041		66	
MTA 5045	34.5		
MTA 5052	36.2		

Plate 3 about here

There are 3 metapodials that almost certainly belong to *Hypsodontus*. Only the metatarsals can be measured (lengths are estimated, because the distal epiphyses are missing):

AÇH-1082	Length ± 290	Prox.W	31.7	min.W of shaft	20.3
AÇH-1085	± 270		31.2		19.4

The type-specimen of the type-species of *Hypsodontus*, *H. miocenicus* SOKOLOV, 1949, is a fragment of mandible with two molars from Byelomyechyetskaia, a locality

probably older than Çandır. GABUNIA (1973, fig.33) illustrated under the same name a fragment of a horn-core similar to those of Çandır (and İnönü) but smaller. *H. ? pronaticornis*, the type-locality of which is Çandır, might be descended from *H. miocenicus*, but the material of the latter species is so poor that it is hard to be sure that they are really of the same genus. Indeed, it would probably be better to leave both the generic and specific names for the holotype only. Another species of about the same size is *H. serbicus* PAVLOVIC, 1969 from Prebreza, Serbia, which has larger horns, spiralled rather than simply twisted on their axis. They much look like large specimens of *Turcocerus gracilis* but the teeth are also much larger. However, this raises the question of the relationships between *Hypsodontus* and *Turcocerus*. At Çandır, the distinction is obvious because of the great size difference, but this criterion does not work elsewhere, because most other species are intermediate in size. Tooth differences are few and unlikely to be of generic value. Goat folds are perhaps stronger in *Turcocerus* and the labial rib of the paracone is stronger in *Hypsodontus*. The greatest difference, in fact, lies in the shape of the skull and mandible. *Turcocerus grangeri*, the type-species of *Turcocerus*, has a skull of "normal" shape, with the orbit not very far from M3, its anterior border being at the level of the middle of this tooth in side view, and with the temporo-mandibular articulation not much above the tooth-row. In *H. serbicus*, on the contrary, and still more in *H. ? pronaticornis*, the maxilla is very deep below the orbit, which is well behind the tooth-row, and the ascending ramus of the mandible is extremely lengthened, reminiscent of the modern Alcelaphines; combined with the shallow corpus below the molars. This gives the *H. ? pronaticornis* mandible a very characteristic appearance. There is little doubt, therefore, that *H. serbicus* is more closely related to *H. ? pronaticornis* than either is to *T. grangeri*, and a generic distinction is certainly needed. The shape of *T. gracilis* horn-cores, the lack of frontal sinuses, the long constricted pedicles make the generic assignment of the small Çandır species probably correct. Its horns are much less slender than



those of *Kubanotragus sokolovi* (GABUNIA 1973, fig.34) but this does not preclude phyletic relationships.

DE BONIS & al. (1998) considered that *Kubanotragus* GABUNIA is a junior synonym of *Hypsodontus* SOKOLOV, and that this name should be restricted to the bovid from Byelomyechyetskaia and Chios, which has small long slender horn-cores. I cannot accept this synonymy, because the type mandible of *Hypsodontus miocenicus* is much too large to belong to the same species as the type horn-core of *K. sokolovi*, unless the latter is a female, but in this case it is hard to draw conclusions about the distinction between the male ones (which would then be known by a single fragment: GABUNIA 1973: fig.33) and those from Çandır. I think it wiser to keep *Kubanotragus* for the smaller (and earlier) horns.

*Tethytragus* AZANZA & MORALES, 1994

*Tethytragus koehlerae* AZANZA & MORALES, 1994

This Bovid was described by KÖHLER (1987) under the name *Caprotragoides potwaricus*, but AZANZA & MORALES (1994) have demonstrated that it belongs in fact to a new taxon, that they called *T. koehlerae*. It is by far the most common large mammal at Çandır, with numerous horns and tooth-rows, a few frontlets and some other skull elements.

#### Description

a) Skull : AÇH-263 (MTA 82-58; Pl.1, Fig.3 and Pl.3, Fig.2) is the posterior part of a hornless (and therefore female) skull, somewhat crushed, almost certainly from Loc.3. There are very few Cervids at this locality, and a set of morphological features make it almost certain that it belongs to the Bovidae, although not demonstrated :

- the tympano-hyal emarginates the lateral side of the bulla, much forward of the post-glenoid process ; in cervids it is more posterior, contacting the post-glenoid process, or its forward-directed flange ;

- the mastoid exposure on the occipital face is very large ; dorso-laterally to the occipital condyles, it is even broader than the occipital bone.

- the post-glenoid foramen is small, and the bulla is large, in contrast to most cervids.

Other features of this skull, which I consider as belonging to *T. koehlerae*, are :

- the basioccipital is rectangular, with posterior tuberosities strong but little expanded laterally, but anterior ones large, although not very salient, and without anterior groove or keel in the middle ;

- although this area is crushed, there is no doubt that the *foramen ovale* was quite small, probably smaller than in all Recent bovids except some *Cephalophus*. Its orientation cannot be determined.

Except those of the basioccipital, probably linked with the presence of relatively large horns in males, these characters are mostly primitive, and do not help much to solve the question of the systematic position of *Tethytragus*. It confirms, however, that the female of the most primitive bovids were hornless : this contrasts with the hypothesis of THENIUS (1951) who attributed large ornamented horns from Nikolsburg, type-locality of *Caprotragoides stehlini*, to males and smaller ones to females. Indeed all measurements provided by this author fall within the range of Çandır *Tethytragus*, where there is no bimodality in horn-core dimensions. Female *Eotragus* skulls are also hornless, and I have compared AÇH-263 with the skulls of *Eotragus* from Sansan in MNHN, but the latter (FILHOL 1890, pl.39, fig.6) are incomplete and badly preserved, especially their basicrania. The main differences are that, in *Eotragus*, the fronto-parietal suture is concave forward instead of convex, that the mid-frontal suture is elevated (but it is also elevated in a fragmentary male skull of *T. koehlerae*, ÇA 91-109), and that the temporal lines are more strongly marked, even in the female, and approximate more closely at the rear of the skull. The angular region of the mandible is strongly expanded (Pl.2, Fig.2).

b) Horn-cores : They are without keels or transverse ridges, moderately compressed transversely, less convex laterally than medially, and with a variable curvature backwards : it is usually strong, but may be absent, as e.g. in AÇHÜ-150. There is also usually a slight, but clear, sigmoid curvature in front view, with divergence first increasing, but the tips re-approaching; there is, therefore, an incipient anticlockwise torsion in the right horn (Pl.3, Fig.1, 3). As noted by AZANZA & MORALES (1994), this distinguishes them from those of *T. langai* from Spain. Another difference with the Spanish species is the long pedicle, especially anteriorly. Their dimensions are given Fig.7.

Figure 7 about here

c) Dentition : It provided to AZANZA & MORALES (1994) the main basis of distinction between *Tethytragus* and *Gentrytragus*, the latter showing grazing adaptations, such as more hypsodont teeth, shorter premolars, molarized p4, and flatter lingual walls on lower molars. *T. koehlerae* differs from *T. langai* by its more molarized p4, on the average, despite the fact that Çandır probably pre-dates the Spanish localities (AZANZA & MORALES 1994, fig.6).

Dimensions of lower tooth-rows are :

Length p2-p4 :	Loc.1	N = 11	L = 24.6-29.1 (mean 27.2)
	Loc.3	N = 34	L = 22.8-28.9 (mean 26.1)
	Pooled	N = 45	L = 22.8-29.1 (mean 26.4)
Length m1-m3	Loc.1	N = 29	L = 36.3-44.3 (mean 39.5)
	Loc.3	N = 71	L = 35.6-46.0 (mean 39.0)
	Pooled	N = 100	L = 35.6-46.0 (mean 39.1)

Fig.8 is a plot of premolar vs. molar length of the complete tooth-rows.

Figure 8 about here

d) Limb-bones : They are referred to *Tethytragus* on the basis of size. As usual, the most common ones are the tali, whose size allow the recognition of several well separated groups, probably of systematic value (Fig. 2). There are also several metacarpals, but their size variation is perhaps too great for a single population, and some of them could be of *Heteroprox*. There is no well-preserved adult metatarsal, but it seems that this bone was somewhat larger than the metacarpal, probably a primitive character for bovids.

#### Measurements (all from Loc.3)

##### Humerus :

ÇA 91-65 (not the same individual as the radius) Distal articular width = 23.8 ; minimum antero-posterior thickness = 12.3

##### Radii :

ÇA 91-121	171	26.7(articular)	17.5
ÇA 91-143	163	( " )	17.6
ÇA 91-92	155		14
ÇA 91-65(juvenile)	152	21.3	14.8

##### Metacarpals :

ÇA 92-62	L = 162	prox.width= 17.5	mid-length w.= 11.2	distal w.= 18.8
ÇA 92-16	168		12	24
ÇA 91-70	153.5	17.8	11	19.5
ÇA 91-144			13	23.9
ÇA 91-158	179	22	14.5	21.6
ÇA 90-41	156.5	18	10.8	18.8

##### Metatarsals :

MTA 83-125	L = ca.200	prox. width = 21	mid-length width = 13.5
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MTA 83-149	ca.170	19.8	11.6
ÇA 91-56(juvenile)	167	17.8	10.5

### Discussion

There is no doubt that the Çandır species should not be assigned to *C. potwaricus*, as was done by KÖHLER (1987), since this species is insufficiently known. The distinction from *Tethytragus stehlini* is maintained here, although it is admittedly more questionable. This species was erected by THENIUS (1951) for horn-cores from Nikolsburg which could be of the same species as at Paşalar (as was supposed by GENTRY 1990) and Çandır, but no tooth has been described from this locality, so that specific identity remains doubtful. Two similar incomplete horn-cores (N° LGr-529-530 in MGL) are also known from La Grive, where they are probably co-specific with some dental remains, many of them labelled “*Caprotragoides*” by J.VAN DER MADE. They are indeed similar to the Çandır teeth, but are perhaps less hypsodont, with sometimes a double crescent on the third lobe of m3, and a long sagittally oriented metaconid on p4 (as in Çandır “*Hispanomeryx*”). One of the fragmentary mandibles (N° LGr-6014) has a very high ramus below m3, with the concavity of its lower border below the rear of this tooth ; both characters are very different from those of the Çandır species, where the ramus is low, with a widely expanded angular area. This raises the possibility of the existence of an European species, different from *T. koehlerae* (and from *T. langai*). This European species is likely to be the one described by THENIUS, and it is therefore wiser to restrain the name of *T. stehlini* to it.

### The case of *Hispanomeryx* at Çandır

The genus *Hispanomeryx* was founded by MORALES & al.(1981) for a small Vallesian Ruminant from Spain with short premolars, long isolated metaconid on p4, weak metastylid

on molars, and large third lobe on the m3, which has a lingual wall. Several of these features are reminiscent of *Micromeryx*. MOYÁ-SOLÁ (1986) referred to the same genus some specimens from Çandır ; illustrations provided by this author show that the Turkish specimens are about 30% larger, that the premolars are of normal size, the metastylids of molars not very weak, and the third lobe of m3 not so large, and the Çandır specimens do not seem to share any significant feature with the Spanish ones. On the other hand, they appear to be very similar to *T. koehlerae*. The specimens illustrated by Moyá-Solá are near the upper limit, but within the size range of *T. koehlerae* ; in the latter species, an incipient lingual wall may also be present along the third lobe of m3, and the entoconid of p4 may be isolated from the main crest ; specimen MTA 5107 (Fig. 9) is the most *Hispanomeryx*-like. The only remaining difference are that the metaconid of p4 of the specimen figured by MOYÁ-SOLÁ is slightly stronger than in all specimens of *T. koehlerae* that I have seen, and that it is lower crowned. I believe that more material is needed before another taxon should be added to the faunal list.

Figure 9 about here

In conclusion, this study of the material collected by the Turkish teams at Çandır has significantly improved our knowledge of these Middle Miocene Ruminants. *Heteroprox*, recognized for the first time in Turkey, is probably present also at Paşalar, but belongs to a lineage distinct from the European one. *Turcocerus*, also known from İnönü, remains poorly known. Its grouping with *Hypsodontus* is little supported, but certainly neither is related to Upper Miocene bovids. These grazing Bovids appear as specialized offshoots of the first bovid radiation. *Tethytragus* is now known by a few relatively complete specimens but their mostly primitive characters do not help to solve the question of its systematic position. In fact,

none of the Çandır Ruminants can satisfactorily be put in any modern tribe or even subfamily, and they may all belong to extinct groups.

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#### Captions to plates

##### Plate 1

Fig.1 : *Heteroprox anatoliensis*, right "antler" AÇHÜ-311 in anterior (1A) and lateral (1B) views. Fig.2 : *Heteroprox anatoliensis*, left "antler" AÇHÜ-310 in lateral (2A) and anterior (2B) views. Fig.3 : *Tethytragus koehlerae*, skull fragment AÇH-263, basal view (same specimen as Pl.3, Fig.2). Scale = 100 mm for Figs.1-2, 75 mm for Fig.3.

## Plate 2

Fig.1 : *Turcocerus gracilis*, left horn-core ÇA 91-102 in lateral (1A), anterior (1B) and medial (1C) views. Fig.2 : *Tethytragus koehlerae*, mandible ÇA 91-102. Scale 75 mm for Fig.1, 100 mm for Fig.2.

## Plate 3

Fig.1 : *Tethytragus koehlerae*, frontlet ÇA 91-197 in lateral (1A) and anterior (1B) views.  
 Fig.2 : *Tethytragus koehlerae*, skull fragment AÇH-263, lateral view (same specimen as Pl.1, Fig.3). Fig.3 : *Tethytragus koehlerae*, skull fragment. Fig.4 : *Hypsodontus ? pronaticornis*, juvenile mandible ÇA 91-54. Scale = 50 mm for Fig.2, 100 mm for Fig.1, 3, 4.

## Captions to figures

Fig.1 - *Micromeryx* aff. *flourensianus*, p3 and p4, p4. Scale = 10 mm.

Fig.2 - Plot of medial height vs. distal width of the smaller Ruminant tali from Çandır.

Fig.3 - *Heteroprox anatoliensis* n.sp., lower tooth series, ÇA 92-7. Scale = 20 mm

Fig.4 - *Turcocerus gracilis*, plot of antero-posterior vs. transverse diameters of horn-cores.

Fig. 5 - *Turcocerus gracilis*, lower tooth series, ÇA 92-88. Scale = 20 mm.

Fig.6 - *Hypsodontus ? pronaticornis*, plot of antero-posterior vs. transverse diameters of horn-cores.

Fig.7 - *Tethytragus koehlerae*, plot of antero-posterior vs. transverse diameters of horn-cores.

Fig.8 - *Tethytragus koehlerae*, plot of premolar length vs. molar length.

Fig.9 - *Tethytragus koehlerae*, lower tooth series MTA 5107. Scale = 20 mm.