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Giraffidae from the middle Miocene hominoid locality of Çandır (Turkey).

1 figure, 2 plates

Denis GERAADS * and Fehmi ASLAN **

*UPR 2147 CNRS - 44 rue de l'Amiral Mouchez, 75014 PARIS, FRANCE
dgeraads@ivry.cnrs.fr

** MTA Genel Müdürlüğü, Jeoloji Etüdleri Dairesi, 06520 ANKARA, TURKEY

Abstract.- The site of Çandır has yielded one of the best collections of Giraffidae from the Middle Miocene of the Eastern Mediterranean. It is here referred to a single new species, whose comparison with other contemporaneous remains from this area and the Siwaliks raises some interesting phylogenetic problems.

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

Introduction

The Middle Miocene locality of Çandır (Ankara, Kalecik, Turkey) is well known for having yielded the hominoid primate *Griphopithecus alpani* (TEKKAYA, 1974). Çandır was excavated by the late I.TEKKAYA (collection in the MTA Museum, Ankara, labelled AÇ or MTA) and, from 1989 onwards, by E.GÜLEÇ (collection in the Department of Anthropology, Dil ve Tarih Cografya Fakültesi, Ankara, labelled ÇA). The present study is based upon both collections. E.GÜLEÇ's material is precisely registered, especially as to the exact provenance
from one of the several Çandır localities, but this is not always the case with TEKKAYA's, for which sometimes only the bone preservation and color can indicate something about a likely origin, usually with much doubt; this uncertainty is not of great consequence, however, since there does not seem to be any significant difference, neither in size nor in morphology, between the two main fossiliferous spots. These are Locality 1 mainly excavated by I.TEKKAYA, and Locality 3 mainly excavated by E.ĞULEÇ.

Materials and Methods

Systematic description

Giraffokeryx PILGRIM, 1910


Type-species: G.punjabiensis PILGRIM, 1910

Giraffokeryx anatoliensis n.sp.

Holotype : Rear part of a skull with the left post-orbital horn, N° ACHÜ-308, from Çandır locality 1, kept in the MTA Museum, Ankara (Pl.1, Fig. 1).

Derivatio nominis: from Anatolia.

Diagnosis: A species of Giraffokeryx which differs from the type-species by its shorter and less inclined horns, more salient occipital crest, and p3 always with oblique epicristid.

Hypodigm : All teeth of Giraffokeryx from Çandır, even isolated ones, can easily be identified, but this is not always the case for limb bones, which are only slightly larger, on average, than those of Palaeomeryx. For them, the identifications are only the most likely ones.
Description

a) Skull

On the holotype, the left horn is inserted above the post-orbital bar. No suture or line marks its limit from the hollowed frontal bone. Thus, the horn may either be an outgrowth of the frontal bone, or an originally independent bone, but fused because of the old age. It is very wide antero-posteriorly at the base, but rather compressed transversely; its lower part was strongly divergent from its counterpart, but the divergence lessens towards the tip, the horn being curved inwards. However, it is not inclined backwards, in contrast to *Giraffokeryx punjabiensis* from the Middle Miocene of Pakistan, which has also longer horns (COLBERT 1933). The tip is rounded rather than pointed, and there are some faint knobs, especially along the anterior border. Another difference with the Siwalik species is the backward protrusion of the supra-occipital crest, shelf-like at the base, but quickly becoming subdivided into two horn-like expansions, continuing the paired pillars of the occipital face. The occipital crest is always rather salient in giraffids, including *G. punjabiensis*, but never to this extent, which is reminiscent of *Ampelomeryx ginsburgi* DURANTHON & AL., 1995, from the early Miocene of Western Europe (see below). Given the importance of cranial appendages in Ruminant taxonomy, and the lack of evidence of intra-specific variability, we believe that these differences are sufficient to distinguish specifically the Turkish species from the South Asiatic one. Other characters of the skull are reminiscent of those of *G. punjabiensis*, or of other Middle Miocene Giraffids, such as *Injanatherium arabicum* MORALES & AL., 1987, from Saudi Arabia. The condyles are large, the bicondylar width being greater than the minimum width of the occipital, which is strongly constricted at mid-height; the basioccipital is rather wide anteriorly, but the anterior tuberosities are not more salient than in *I. arabicum*. A
primitive character, shared by *Canthumeryx* from the Middle Miocene of Jebel Zelten, Libya (HAMILTON 1973, 1978) but no longer present in later Giraffids, is that the mastoid still separates the post-tympanic apophysis of the squamosal from the paroccipital process of the occipital.

Dimensions:

<table>
<thead>
<tr>
<th></th>
<th><em>G. anatoliensis</em></th>
<th><em>I. arabicum</em></th>
<th><em>G. punjabiensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance from front of orbit to occipital condyle</td>
<td>230</td>
<td>205 ?</td>
<td>-</td>
</tr>
<tr>
<td>Maximum width across post-orbital horns</td>
<td>2 x 150</td>
<td>-</td>
<td>403</td>
</tr>
<tr>
<td>Width of braincase</td>
<td>98</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Minimum width across temporal lines</td>
<td>56</td>
<td>35</td>
<td>56</td>
</tr>
<tr>
<td>Bicondylar breadth</td>
<td>81</td>
<td>72</td>
<td>76</td>
</tr>
<tr>
<td>Distance between tips of paroccipital processes</td>
<td>84</td>
<td>±75</td>
<td>88</td>
</tr>
<tr>
<td>Maximum occipital width</td>
<td>133</td>
<td>128</td>
<td>144</td>
</tr>
<tr>
<td>Height of occip. (base of fo.magnum to occ.crest)</td>
<td>111</td>
<td>101</td>
<td>-</td>
</tr>
</tbody>
</table>

Another fragment of skull, AÇH-204, had no horn in front of the orbit, contrary to *G. punjabiensis*, which has 4 horns, but as it seems to have no supra-orbital horn either, it might be of a female, and no conclusion can be drawn as to the presence of ante-orbital horns in males.

b) Teeth

Upper teeth are little different from those of Upper Miocene *Palaeotragus*, but they are more brachyodont, and the anterior lobe of DP3 is longer. The premolars are not very large,
molars usually have no entostyle, almost no cingulum, and outer ribs and styles are moderate. Thus, they are rather different from those of *Canthumeryx*.

Dimensions:

- ÇA 91-78 (Loc.3)  DP2-DP4 = 58.5
- ÇA 93-69 (Loc.3)  DP4 length = 24
- ÇA 92-9 (Loc.3)   M1-M3 = 72.4
- ÇA 94-34 (Loc.3)  M1-M3 = 79
- ÇA 92-187 (Loc.3) P3-M2 = 82.8
- ÇA 90-30 (Loc.3)  M3 = 27 x 27
- AÇH-204          M1-M3 = 71

The lower incisors are present on an almost complete but imperfectly preserved mandible (ÇA 94-115). They are about as large as the isolated canines. There are 5 specimens of the latter tooth which all are clearly bilobed. The diastema is slightly shorter than the tooth row.

There are more than 30 lower premolars, many of them in mandibular fragments (Pl. 1, Fig. 2-3, and Pl. 2). They are variable, but not extremely so, and perhaps less so than at Paşalar. DE BONIS & al. (1997: 127) may have been right in suggesting that more than one species was present there. The p3 always has the paraconid well separated from the parastylid; they may tend to fuse lingually. On only 2 teeth out of 12 does the metaconid extend forwards, meeting the base of the paraconid, and the crest joining the protoconid to the metaconid (epicristid of VANDEBROEK’S nomenclature) is always oblique backwards. This oblique crest often incorporates the entoconid, leaving only a short intermediate crest (telocristid) between it and the rearmost one (posterior arm of the eocristid). On p4 (20 specimens), the metaconid
is always expanded into a lingual wall blocking the anterior valley, which may remain open
lingually at Paşalar (GENTRY 1990, fig.5C). The posterior end of the protoconid is always
bifurcated; its labial arm (eocristid) is interrupted before reaching the hypoconid on unworn
teeth; its lingual arm (epicristid) is always posterior and oblique.

Plate 2 about here

The limited range of variation of the premolars of *Giraffokeryx anatoliensis* strongly
suggests that the Siwalik premolars assigned to *G. punjabiensis* are too variable to be
accommodated within a single species. For instance, a p4 figured by PILGRIM (1911, pl.2,
fig.1) has a very large anterior lobe (paraconid + parastylid) closed lingually, while that of the
skull figured by COLBERT (1933, 1935) has no anterior lobe, as in Çandır. Similarly, the p3s
figured by PILGRIM (1911, pl.2, fig.2, 3) have transversal crests, while COLBERT (1935: 339)
states that: "the internal border of the third premolar may be closed or open."

The Çandır sample of lower premolars provides a new evidence of the normal
variability of giraffid premolars, which seems to confirm the previous hypothesis (GERAADS
1989) that apparent large variability may in some cases result from a mixing of taxa.

Lower molars display the same characters as at Paşalar (GENTRY 1990): weak or
absent ectostylids, no *Palaeomeryx*-fold, the third lobe of m3 forming a complete loop; the
latter looks larger than at Prebreza.

Dimensions:

<table>
<thead>
<tr>
<th>Sample</th>
<th>p2-m3</th>
<th>p2-p4</th>
<th>m1-m3</th>
</tr>
</thead>
<tbody>
<tr>
<td>AÇH-1290</td>
<td>137</td>
<td>57.5</td>
<td>80</td>
</tr>
<tr>
<td>ÇA 92-4 (Loc.1)</td>
<td>141.5</td>
<td>62.5</td>
<td>85</td>
</tr>
<tr>
<td>ÇA 94-115 (Loc.3)</td>
<td>78</td>
<td>i1-m3</td>
<td>306</td>
</tr>
</tbody>
</table>
AÇH-1295 64.5
MTA no N° 78.5
AÇH-2 77.5
AÇH-1287 89
MTA no N° 83 L base m3 = 38
ÇA 93-39 (Loc.3) 38.5
ÇA 93-3 (Loc.3) 36
AÇH-1 p3-p4 = 41.5
AÇH-7 41 80
ÇA 92-36 (Loc.3) L dp3 = 17.5 L dp4 = 28.3 L m1 = 24.4 dp2-dp4 = 61.8
ÇA 92-24 (Loc.3) 17.3 25.5 22.5
ÇA 92-28 (Loc.3) 27 24
AÇHU-1293 18.7 28.9
MTA no N° 17.8 27

Lower canines (lingual height x lingual width) : 15 x 10; 15 x 10.8; 16.7 x 11.9; - x 10.8.

c) Postcrania

They are seldom complete, sometimes hard to distinguish from those of *Palaeomeryx*, and do not contribute much to the systematic placement of the Çandır giraffid. The proximal metatarsal has 4 articular facets. Dimensions of the astragali are shown on Fig. 1. They differ from those of *Palaeomeryx* by their larger size and by the lack of expansion of the medial lip of the trochlea. Measurements of other bones are:

Distal humerus MTA 83-106: breadth = 72 minimum antero-posterior diameter = 33

MTA 83-109 71 36
MTA 83-141 69 33.5
<table>
<thead>
<tr>
<th>Sample Number</th>
<th>Location</th>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ÇA 93-32 (Loc.3)</td>
<td>75</td>
<td>33.2</td>
<td></td>
</tr>
<tr>
<td>ÇA 93-78 (Loc.1A)</td>
<td>75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Radius prox.</td>
<td>MTA 83-119: max.breadth</td>
<td>71.5</td>
<td></td>
</tr>
<tr>
<td>&quot; dist.</td>
<td>MTA 83-105</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>ÇA 92-16 (Loc.1)</td>
<td>69</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metacarpal</td>
<td>ÇA 91-85 (Loc.3): minimum breadth of shaft</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ÇA 91-116 (Loc.3)</td>
<td>28.5</td>
<td></td>
</tr>
<tr>
<td>Tibia</td>
<td>ÇA 92-13 (Loc.1): distal breadth</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>length</td>
<td>438</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ÇA 91-150 (Loc.3)</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>length</td>
<td>475</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MTA 83-101</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>Prox.metatarsal</td>
<td>ÇA 94-14 (Loc.3): max.breadth</td>
<td>46</td>
<td></td>
</tr>
</tbody>
</table>

Results and Discussion

Comparisons

Middle Miocene cranial remains of Giraffids are rare and fragmentary. *Injanatherium arabicum* is slightly smaller than *G. anatoliensis*. Only the very base of the post-orbital horn is preserved on the holotype, and not much can be said about its orientation; it may have been similar to that of the Çandır species. A clear difference, however, is that the occipital crest of the Arabian species is not more salient rearwards than in the Upper Miocene giraffids. It has also a more triangular basioccipital and extremely slender metapodials, and is certainly specifically distinct. It might be co-generic with the Çandır species, but is, in our opinion, more different from the type-species of *Injanatherium, I. hazimi* HEINTZ & AL., 1981, from the upper Miocene of Iraq, which is little distinct from *Samotherium*.

The premolars allow some comparisons with the poorly known species of the Eastern Mediterranean. On p4, the epicristid is never as transverse and anterior as it may be at Paşalar
The p4s from Inönü 1, a site which is probably younger, are similar to those of Çandır (Geraads & al. 1995). The premolars of the giraffid from Prebreza (Serbia), described by Pavlovic (1969) under the name of *G. punjabiensis*, are much more primitive, all crests having a transverse orientation. Slightly more primitive also is the p3 of *Georgiomeryx georgalasi* from the Middle Miocene of Chios (Paraskevaidis 1940; De Bonis & al. 1997): the metaconid extends less far backwards, and the talonid crests are more transverse. The same seems to be true of the p3 of *Injanatherium arabicum*, but its p4 is like the Çandır ones. Thus, the premolars suggest that Çandır is younger than Paşalar, Prebreza and Chios, but roughly contemporaneous with Inönü 1.

In Africa, *Canthumeryx* has very primitive premolars, even p4 being lingually open. From Fort Ternan, Churcher (1970) described *Palaeotragus primaevus* and *Samotherium africanum*: they might be co-specific (Gentry 1994) but remain poorly known; the premolars are very primitive by their great length and the transverse orientation of the cusps of p3. African Middle Miocene Giraffids are perhaps not closely related to the Asiatic ones. Hamilton (1978) described also as *P. primaevus* an incomplete skull from the younger Ngorora formation, but it is much more like the upper Miocene *Palaeotragus*, and certainly not of the same species as at Fort Ternan.

De Bonis & al. (1997) have included *Canthumeryx, Georgiomeryx, Injanatherium* and *Giraffokeryx* in the subfamily Canthumerycinae (a name whose author is Hamilton, 1978), defined by "flat and laterally directed supra-orbital horns". Of course, a clade based upon a single character is not falsifiable, and several of these genera or at least some of their species are closely related, but we are not convinced that this character is sufficient to define a monophyletic group. It is hard to believe that *I. hazimi* or the skull described as *Samotherium sinense* by Bohlin (1926, fig.137) are not closely connected to other *Samotherium*, from which they differ by this single character. Moreover, a skull of *Samotherium major* from
Samos (SAM 30 in Basel), also mentioned by BOH LIN (1926: 88) had its horns diverging by about 140°, and is therefore intermediate.

The most interesting point raised by the Çandır giraffid is that of its relationships with primitive Ruminants such as Ampelomeryx from the lower Miocene of Western Europe. The latter has long occipital expansions, reminiscent of the protruding occipital shelf of G. anatoliensis n.sp., and supra-orbital horns of similar shape, said to be unfused with the frontal bone in the juveniles, but it also has the non-giraffid characters of a large upper canine, double lachrymal foramina (as in Canthumeryx), and closed anterior gully on metatarsal. If the independent nature of the Ampelomeryx horns is confirmed, it might be that the acquisition of this character predates those believed to be of familial value in latter giraffids, such as the upward shift of the mastoid exposure, reduction of lachrymal foramen, and perhaps bilobed canine.

Cladistic analysis of these large Ruminants must await full description of taxa such as Ampelomeryx or Palaeomeryx. In the meantime, we take the conservative view of including the Turkish species in Giraffokeryx, although it shares no obvious derived character with PILGRIM’S type-species; the orientation and shape of the main horns, and the morphology of the teeth support this identification.

Acknowledgements

We are especially grateful to Prof. ERK SIN GÜLEÇ, who invited us to work on the Çandır Giraffids from her own excavations, to the late Prof. I. TEKK AY A, to SEVIM YILDIRIM, and to ZIYA GÖZLER, general Director of the MTA, who kindly allowed us to study material in MTA. We also thank H. THOMAS for allowing D.G. to examine the material of both species of Injanatherium. The missions of D.G. in Turkey were funded by the "Programme
Paléoenvironnement, évolution des Hominidés" of the Centre National de la Recherche Scientifique.

References


Captions to plates:

Plate 1

Fig. 1 - *Giraffokeryx anatoliensis*, holotype. a: antero-supero-lateral view; b: postero-infero-lateral view. Fig. 2: right tooth-row, AÇHÜ-1292. Fig. 3: right tooth-row, AÇHÜ-1290. Scale = 10 cm.

Plate 2

Variation of the occlusal pattern of lower premolars (p3 and p4) of *Giraffokeryx anatoliensis* n.sp. (R = right, L = left). Fig. 1: Rp3-p4, AÇHÜ-1292; Fig. 2: Rp3-p4, AÇHÜ-5; Fig. 3: Rp3-p4, AÇH-1; Fig. 4: Lp3-p4, AÇH-7; Fig. 5: Rp3, no N°; Fig. 6: Lp3, AÇH-12; Fig. 7: Lp3, AÇH-14; Fig. 8: Lp3, AÇH-1060; Fig. 9: Rp3, no N°; Fig. 10: Rp4, AÇHÜ-1282; Fig. 11: Rp4, AÇHÜ-1288; Fig. 12: Rp4, no N°; Fig. 13: Lp4, AÇH-1593; Fig. 14: Rp4, no N°; Fig. 15: Rp4, AÇH-13; Fig. 16: Rp4, AÇHÜ-1284; Fig. 17: Rp4, AÇHÜ-948; Fig. 18: Rp4, AÇHÜ-1287; Fig. 19: Rp4, AÇHÜ-693; Fig. 20: Lp4: AÇH-1277. Scale = 4 cm.

Caption to figure

Fig. 1 - Plot of medial height versus distal width of the tali of the large Ruminants of Çandır and Inönü.