

A BRAMATHERIUM SKULL (GIRAFFIDAE, MAMMALIA) FROM THE LATE MIOCENE OF KAVAKDERE (CENTRAL TURKEY). BIOGEOGRAPHIC AND PHYLOGENETIC IMPLICATIONS

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ABSTRACT.- A sub-adult skull from the Late Miocene of Kavakdere, described and referred to the Indian genus *Bramatherium*, increases the similarity between the Indian sub-continent and the Greco-Iranian province. The contents and subdivisions of the subfamily Sivatheriinae are reviewed, with 2 main groups being recognized, based upon the homologies and position of horns. They are perhaps both of western European origin.

Key words: Giraffidae, Mammalia, Upper Miocene, Turkey.

INTRODUCTION

Kavakdere is one of the many rich upper Miocene Mammal localities of Turkey. It is located close to the famous Sinap hill localities, North of Ankara. While Köhler (1987) doubtfully assigns the locality to zone MN 11, Sickenberg (1975) place it between the middle Vallesian and the early Turolian. The faunal list given by Ozansoy (1965) and Sickenberg (1975:81) includes *Helladotherium* and "Camelopardalis" as Giraffids. Ozansoy did not state, however, what was the basis for his determinations, nor did he describe any fossil. There are, however, on display in the MTA Museum, several complete Giraffid limb bones and an almost complete skull of unusual interest, since it is one of the very few Sivatheriine skulls known in the late Miocene from any where in the world.

DESCRIPTION

Genus : *Bramatherium* Falconer, 1845

Syn : ? *Helladotherium* Gaudry, 1860

Hydaspiatherium Lydekker, 1877

Type species: *B. perimense*, Perim Island, Dhok Pathan.

Other species: Several other species have been described from the Indian sub-continent.

These are *B. megacephalum* (Lydekker 1876), *B. grande* (Lydekker, 1880), and *B. magnum* (Pilgrim, 1910) (Pilgrim, 1911; Bohlin, 1926; Colbert, 1935). Some may be distinct from the type species, but this has yet to be demonstrated by more complete evidence. The difference in length of the pedicle of the anterior pair of horns, said by Lewis (1939) to distinguish *B. perimense* from *B. megacephalum* is probably of ontogenic or individual origin; the skull described by this author is that of a very old animal. *Bramatherium suchovi* Godina 1977 from the Turolian of Chimichlia in Moldavia, is not, in our opinion, referable to this genus, as explained below.

The skull from Kavakdere (Fig. 1-2), labelled 1947, is that of a young adult, with all milk premolars in use, M2 but slightly worn, and M3 not erupted yet. Of course, this young ontogenic age should not be overlooked when discussing features of the skull, especially the horns. The skull is complete, except for the premaxillae, tips of nasals and part of the lambdoid crest but only the horn bases are preserved; most of the sutures are indistinct.

The milk-teeth are much worn; the anterior lobe of DP3 is much longer than the posterior one, a primitive character found in all *Sivatheriines*. The permanent molars are only moderately hypsodont; they have a simple occlusal pattern, no entostyle,

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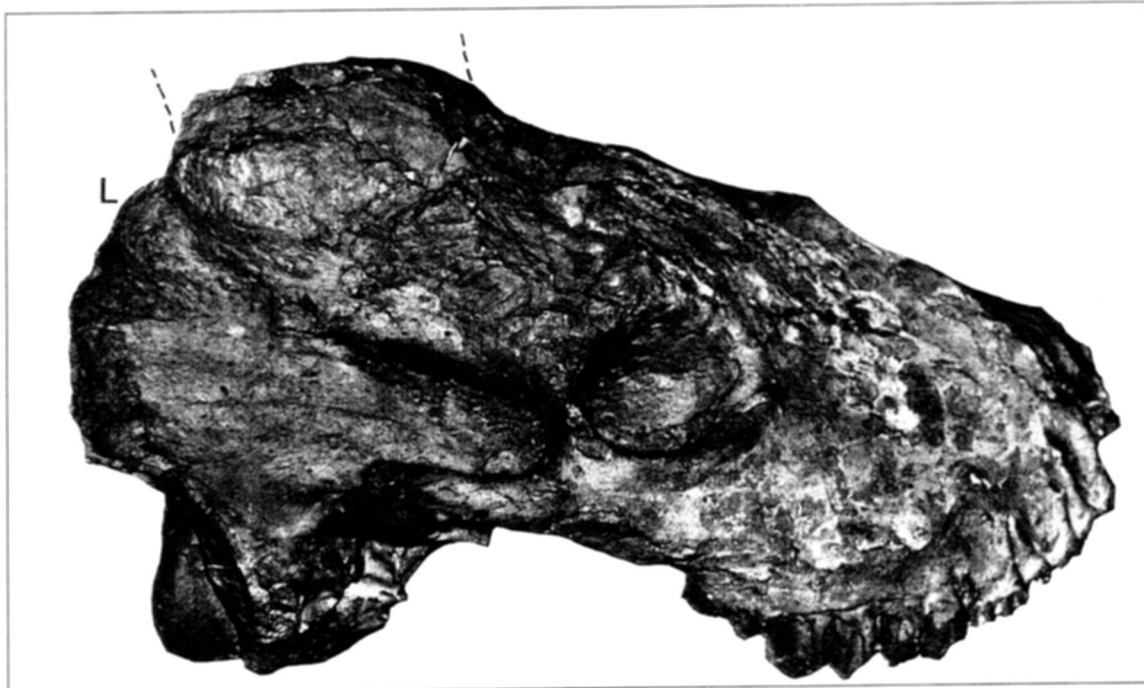


Fig. 1- The Kavakdere skull in lateral view. The broken line shows the approximative outline of the anterior horn.
L = lateral posterior horn. Scale = 15 cm.

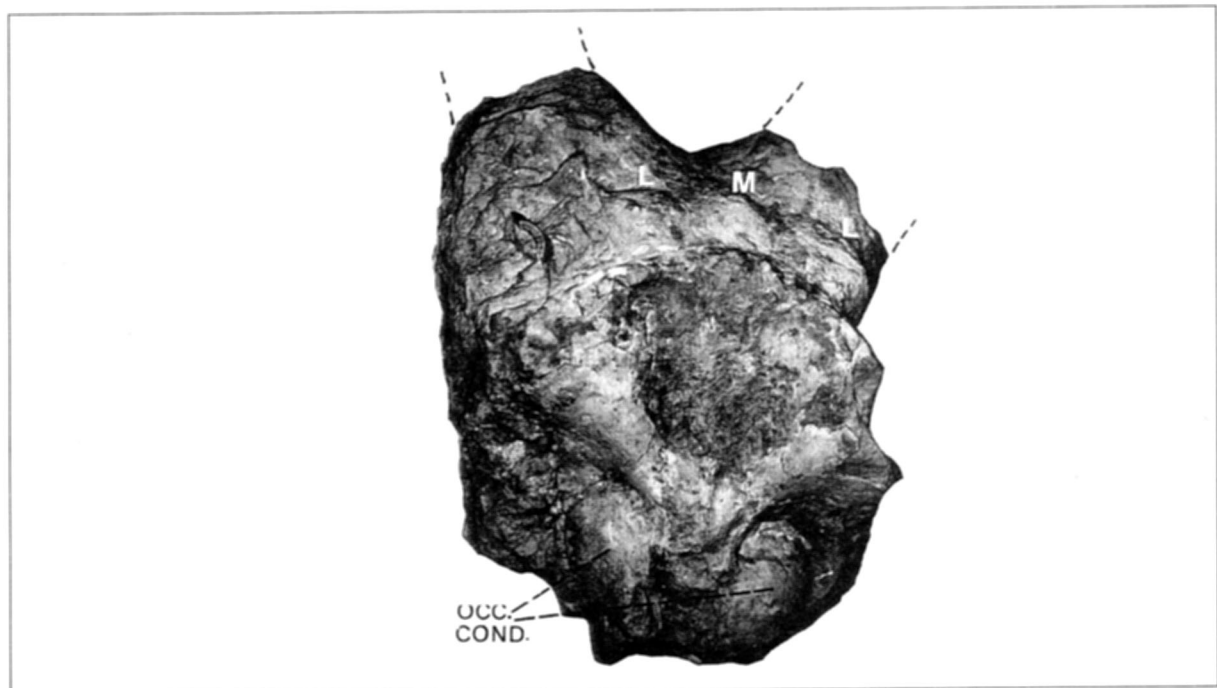


Fig. 2- The Kavakdere skull in posterior view. Occ.cond. = occipital condyles; L = lateral posterior horns;
M = median posterior horn.

weak external pillars but rather strong para- and mesostyles.

The skull can easily be referred to the *Sivatheriinae* by its large size, great height relative to its length and long post-orbital portion. The muzzle is very high above the tooth-row, and the profile of the nasals, whose tips are missing, was certainly slightly concave. A rather large ethmoidal fissure was probably present. The frontal roof was much higher than the orbitae, which look relatively small, with an elongate outline, a large lacrymal foramen inside them, and a rounded lower border (very different from the angular one found in *Palaeotragus* and related genera), which is still thicker than that of the adult *B. perimense* skull figured by Lewis (1939). The anterior border of the orbita is at the level of the middle of M3, and would certainly have been a little more posterior in the fully grown animal. This is again a difference with the skull figured by Lewis, in which the orbit is much more anteriorly placed, but this skull appears to have been partly reconstructed in plaster. The temporal fossae are deep anteriorly, being roofed over by lateral expansions of the frontal, which, however, disappear posteriorly. In other *Sivatheriines*, such as *Bramatherium* (including *Hydaspiatherium*) from the late Miocene of India (Colbert, 1935, fig. 174; Lewis, 1939, pl. 2), "Indrathierium" and *Sivatherium* from the Plio-Pleistocene of the same area (the skulls of which are in the British Museum of Natural History) and Africa (Harris, 1976; Geraads, 1985) and *Helladotherium* from the Turolian of Pikermi in Greece (Skull PIK 1500 in the Museum National d'Histoire Naturelle, Paris), the whole length of the temporal fossa assumes a groove-like shape, because these lateral expansions of the cranial roof extend backwards as far as the occipital crest: the young ontogenetic age of the Kavakdere specimen may well be responsible for this difference. This juvenile condition, and some crushing, may also account for the relatively narrow and rounded outline of the occipital, little expanded laterally. Its central part is deeply hollowed for insertion of extensor muscles and cervical ligament; lateral to this deep pit are strong buttresses diverging from above the foramen magnum, as in other Giraffids.

The occipital condyles are large, with their long axis almost vertical, in contrast to the Recent Giraffids, where they are oblique, allowing the skull to be extended in the same line as the neck; *Bramatherium*, on the contrary, like *Sivatherium* (Geraads, 1985), was certainly unable to lift the muzzle above the horizontal line, and was certainly not a browser.

The cranial basis resembles those of *Bramatherium perimense* (Colbert, 1935, fig. 176) and *Helladotherium* from Pikermi (PIK 1500, MNHN), but differs from those of *S. Gigonteum* from the upper Siwaliks (BM M15283) and from *S. maurusium* from Africa (Harris, 1976; Geraads, 1985) in that this region is not extremely shortened, with a still long auditory bulla and an auditory duct slightly inclined backwards, and not quite transversal as in *Sivatherium*.

There are 5 horns: a very large anterior pair, of which only the base is preserved, and 3 much smaller posterior horns, which are little more than swellings. The anterior pair arise in the frontal region, but wholly behind the orbits, their anterior border being at the level of the anterior end of the temporal fossa: they are thus more posterior than the anterior pair of *Sivatherium* or *Decennatherium* Crusafont, 1952, from the Vallesian of Spain (Morales, 1985) or than the median elevation of the Chimichlia skull (Godina, 1977). Although their bases are close together, the horns do not arise from a common base, but are separated on the skull roof. They are transversely compressed, but not flattened. Their length cannot be estimated, but the fact that they were broken near the base suggests that they were not very short. Their extensive pneumatization was, of course, responsible for their great fragility. Between this main pair of horns and the lambdoid crest are three transversely aligned bosses: a rounded median one (M in Fig. 2), and two antero-posteriorly elongated lateral ones (L in Figs. 1-2). Although not more than 2 cm high, these three bumps are quite distinct. Their surface is as smooth as the rest of the cranial roof, and nothing suggests that they might have been bases upon which true ossicones (i.e. isolated ossifications growing independently from the skull roof; see Geraads, 1991) would have

rested; it seems almost certain, on the contrary, that larger posterior horns would have developed, in the adult, from these incipient outgrowths of the skull roof.

Dimensions:

Height of occipital, from upper border of foramen magnum to lambdoid crest 139mm.

Minimum width across temporal lines 125mm.

Length from anterior border of DP2 to back of condyles 435mm.

Length DP2 - DP4 97.5mm.

Length from anterior border of foramen magnum to level of anterior border of glenoid fossa (in the sagittal plane) 120mm.

Length from anterior border of foramen magnum to back of M3 (id.) ~ 200

Bizygomatic width 2x112

Width from medial border of bulla to lateral border of the skull 84

Limb bones: There are some very large and massive Giraffid limb-bones in the MTA collection from Kavakdere; they certainly belong to *Bramatherium*. The dimensions of two of them are:

Radius:

anterior length = 640mm

proximal articular breadth = 147mm

Metatarsal:

length = 465mm

proximal breadth = 100mm

breadth of shaft = 61.5mm

distal breadth = 105mm

The metatarsal is thus longer than those of all other *Sivatheriines*, but stouter than those of comparable length, such as *Samotherium* (Geraads, 1986, Fig.6).

COMPARISONS

Among the *Sivatheriinae*, two main types may be distinguished. In one, exemplified by *Sivatherium* of the Plio-Pleistocene of Africa and the Indian sub-continent, there is a long pair of recurved posterior horns, arising from the rearmost part of the skull; a much smaller anterior pair of horns arise from above the orbits; they may even be absent in *S.hendeyi* from the early Pliocene of South Africa. Both pairs are laterally inserted, but the skull is not especially wide at the supra-orbital level (in contrast to the middle Miocene *Giraffokeryx* Pilgrim, 1910 and Palaeotragines). To the same type could be referred *Birgerbohlinia* Crusafont, 1952, from the Turolian of Spain, assuming that Montoya and Morales (1991) were correct in determining the position of the horns in this genus.

Another type of horn disposition can be found in *Decennatherium* from the Vallesian of Spain, and probably also of Greece (Geraads, 1979, 1989). It has two anterior horns, much closer together (Morales, 1985), which may be homologous with the median hump of "*Bramatherium*" *suchovi*. It is not known whether there was also a posterior pair of horns. *Decennatherium* is certainly not ancestral to *Sivatherium* since its anterior horns are more derived by being larger and less lateral, but it may well be ancestral to *Bramatherium*: the shape and position of the anterior horns of the Kavakdere skull are almost perfectly intermediate between those of the Spanish *Decennatherium*, and those of the Indian *Bramatherium*: they are still separate at the base, as in *Decennatherium*, but already shifted backwards, as in *Bramatherium*. The latter genus has horns of a type completely different from those of *Sivatherium*: the anterior pair, which is post-orbital, is much better developed than the posterior one. The Kavakdere skull shows that the anterior horns also appears earlier in ontogeny, and probably also in phylogeny. *Decennatherium* has no significant derived character in respect to *Bramatherium*, and could be close to its ancestor. *Helladotherium*, whose type-specimen of the type-species, from Pikermi, is evidently the female of some other genus, has more massive limb-bones than *Decennatherium*,

and a long grooved temporal fossa, a synapomorphy with *Bramatherium*, although this character is unknown in *Decennatherium*. It is accordingly provisionally included in the former genus.

The middle Miocene genera *Giraffokeryx* and *Injanatherium* Heintz, Brunet and Sen, 1981 share with the upper miocene *Palaeotragus* and *Samotherium* the following features: long conical supra-orbital horns, widely separated at the base; frontal much broader than the occipital; long and low skull; tendency to molarize P₃. They lack the following features of the *Sivatheriinae*: very large size; skull, and especially muzzle, short and high, with nasals concave in profile; lower border of orbit thickened; very large horns in males; axis of condyles almost vertical; cranial basis shortened, higher than the tooth-row; skull extremely pneumatized; premolars enlarged. These two genera being excluded, the history of the subfamily can be summarized as follows:

No undoubted Sivatheriine is known before the upper Miocene, where they appear in Spain with *Decennatherium*. Towards the end of this Mammalian stage, they are already known by similar or identical genera in Greece (at Ravin de la Pluie and Pentalophos: Geraads, 1979; 1989), perhaps Turkey ("*Samotherium*" *pamiri* Ozansoy, 1965 from Middle Sinap) and the Siwaliks (Flynn et al., 1995).

The Turolian is time of greater diversity, with the subfamily being present in almost all Eurasian sites of this period, south of the Himalaya, and even entering Africa. This expansion could be linked with that of open environments, since they were all mainly grazers. The fact that the earliest African Sivatheriine was found in Tunisia, and the similarity of the posterior horns of *Sivatherium hendeyi*, from the Mio-Pliocene of South Africa with those of *Birgerbohlinia* from the Turolian of Spain strongly suggests that the invasion of Africa followed an occidental route.

As discussed by Montoya and Morales (1991), the group wholly disappears, outside Africa and the Siwaliks, in the latest Miocene. This is also a period of decrease in diversity of Bovids, but of greater di-

versity of Cervids, testifying a return of greater wood cover.

BIOGEOGRAPHY

Although *Sivatheriines* were undoubtedly present in Africa in late Miocene times (in Tunisia at Douaria: Guérin, 1966; Geraads, 1985, and in the lower Oluka formation of Uganda: Geraads, 1994), *Bramatherium* seems absent from this continent, and this genus is known with certainty from Asia only. The Kavakdere skull is its westernmost undoubted representative, as long as *Helladotherium* cannot be demonstrated to be identical. The Kavakdere occurrence increases again the similarities between Indo-Siwalik faunas and those of the Greco-Iranian province, which are rather few: besides the Middle Miocene *Giraffokeryx*, late Miocene ruminants common to both realms include only *Miotragocerus* and *Nisidorcas* among Bovids.

AGE OF THE KAVAKDERE FAUNA

The Indian representatives of *Bramatherium*, with fully united horns, are mainly known in the Dhok Pathan, of late Turolian-equivalent age, while the more primitive *Decennatherium* and "*Bramatherium*" *suchovii* are Vallesian or early-middle Turolian. The Kavakdere skull being intermediate in morphology (and therefore not assigned to any species species), a middle Turolian age can be suggested on this basis, a conclusion not contradicted by the stratigraphic relations in the area (Ozansoy, 1965); a late Turolian age would perhaps even be more satisfactory, on the basis of the very large size of the limb-bones, but Kavakdere has the Bovid genus *Prostrepsiceros*, which is unknown after the middle Turolian (Bouvrain, 1982).

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