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## A new species of *Criotherium* (Bovidae, Mammalia) from the late Miocene of Bulgaria

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**ABSTRACT:** We describe here a new species of the bovid *Criotherium*, from the late Miocene of Bulgaria. The genus was previously known to definitely occur only in Samos (Greece) and Kemiklitepe (Western Turkey), with the single species *C. argalioides*. The new species, *C. nikolovi*, is more primitive than the latter, although both are probably contemporaneous, suggesting the occurrence of two lineages in the Eastern Mediterranean. Hypotheses concerning the inclusion of *Criotherium* in the tribe Ovibovini are discussed.

**Key-words:** Mammalia, Bovidae, Ovibovini, late Miocene, Bulgaria, Balkan peninsula.

### INTRODUCTION

*Criotherium* is a strange late Miocene bovid, best known from Samos but quite rare elsewhere, and usually referred to the Ovibovini. The contents of this tribe are disputed, but it is usually meant to include the living *Ovibos* and perhaps *Budorcas*, together with several late Miocene to Pleistocene mainly holarctic forms. Up to now, *Criotherium* has been known by a single species, *C. argalioides*. We describe here a skull of a more primitive form, from Bulgaria.

The skull was discovered by the late Ivan Nikolov in the course of his investigations in the sixties and seventies, when he made field researches in the late Miocene of S-W Bulgaria and excavated several localities, especially Kalimantsi-1 and Hadjidimovo. Unfortunately, after his death, the skull remained in the collections of the National Museum of Natural History, Sofia, unlabeled and without data about its origin. However, it is almost certain that it comes from Kalimantsi, because:

- \* the surface of the fossil is covered by large irregular ferro- or ferri-oxide and manganese black stains; of all Bulgarian late Miocene localities this condition is known only at Kalimantsi, and the overall aspect of the skull is that of the Kalimantsi fossils.
- \* the sediment filling the brain-case has the same mineral composition as the Kalimantsi sediments (mostly quartz, with some feldspar, magnetite, very small amphibolite or mica fragments).
- \* the granulometry is indicative of alluvial deposits and also similar to the Kalimantsi one, being irregular in vertical and lateral direction.
- \* the localities of Kalimantsi, and especially Kalimantsi-1, are those which yielded the greatest number of fossils to I. Nikolov.

Thus, we assume that the skull is from Kalimantsi, and probably from Kalimantsi-1.

#### The fossiliferous site of Kalimantsi: location, fauna and biochronology:

The large fossiliferous area around the Kalimantsi village, in the Middle Struma basin, includes more than 10 late Miocene mammal localities. The locality of Kalimantsi-1, belonging to the newly established Gradishte lithocomplex, yielded a fauna which is probably of early Turolian age, while other Kalimantsi faunas (referred to the Strumyani genetic lithocomplex) belong to the middle Turolian (SPASSOV *et al.*, 2006). Preliminary identifications of the fauna collected during our new excavations at Kalimantsi-1 on the river bank (2002-2003) are: Proboscidea indet., *Hipparion* gr. *macedonicum*, *Hipparion* cf. *brachypus*, *Bohlinia* sp., *Helladotherium duvernoyi*, *Gazella* sp., *Tragoportax* sp. (see SPASSOV & GERAADS 2004, for the taxonomy of this genus), *Mesopithecus* sp.. The *Mesopithecus* material is insufficient for a definite conclusion about the affinities of the Kalimantsi-1 sample, which lie either with the earlier *M. delsoni* or with the later and smaller *M. pentelicus*, but partial male and female remains (coll. D. KOVACHEV) consist of relatively robust individuals. In addition, *Deinotherium gigantissimum* (see MARKOV, 2004), *Ancylotherium pentelicum* and *Acerorhinus* sp. were identified after revision of the old collections from the same level.

Above Kalimantsi-1, the middle Turolian fauna of Kalimantsi is represented by ca. 10 different localities, where *Gazella* sp., *Hipparion mediterraneum* and *H. brachypus* predominate. *Tragoportax* cf. *amalthea*, *Palaeoreas lindermayeri*, *Helladotherium duvernoyi*, *Bohlinia attica*, *Adcrocuta eximia* and *Mesopithecus pentelicus* are also common. Detailed comparisons (KOSTOPOULOS *et al.*, 2001; GERAADS *et al.*, 2003, 2005, 2006; KOUFOS *et al.*, 2003; HRISTOVA & KOVACHEV, 2005; SPASSOV *et al.*, 2006) suggest that these faunas have

an age close to that of Pikermi or slightly older, most probably in the first part of the middle Turolian.

#### Abbreviations

BMNH: Natural History Museum, London

MCGL: Musée Cantonal de Géologie, Lausanne

NMNH: National Museum of Natural History, Sofia

KAL: Kalimantsi, Bulgaria

KTD: Kemiklitepe-D, Turkey

#### SYSTEMATICS

Genus *Criotherium* F. MAJOR, 1891

*Type-species: Criotherium argalioides* F. MAJOR, 1891.

*Diagnosis:* a bovid of large size. Horn-cores short and stout, moderately divergent, not spiralled but with a strong heteronymous torsion, a strong postero-lateral keel, and at least a weaker antero-medial one, inserted behind the orbits, their caudal side not very far from the occipital. Frontal bone extensively hollowed, elevated far above the orbits and much bent, with a post-cornual part in the same plane as the parietal. Braincase quite short and broad, dorsal part almost in the same plane as the occipital. Occipital low and broad. Occipital condyles with articular surfaces extending far anteriorly onto the posterior tuberosities of the basioccipital, and supplementary articulations medial to the paroccipital processes. Cranial flexure weak (basicranium making a wide angle with the palate). No ethmoidal fissure. Infra-orbital foramen above P2.

The genus *Criotherium* was previously known only by its type-species:

*Criotherium argalioides* F. MAJOR, 1892

*Type:* BMNH M-4199, designated by PILGRIM & HOPWOOD (1928).

*Diagnosis:* a *Criotherium* of large size. Horn-cores uprightly inserted, close to the occipital, with very strong keels, ridges and grooves, perhaps with a tendency to curve forwards in their upper part, and a hint of median rugosities on the frontals. Braincase extremely shortened; muzzle high and narrow, premaxillae not contacting the nasals. Teeth hypsodont, no entostyle, paracone and metacone ribs present on upper molars, styles moderate, premolar row not much shortened.

*Type-locality:* Samos, precise locality unknown.

Outside Samos (SCHLOSSER, 1904; SOLOUNIAS, 1981), the species has been described only from Kemiklitepe-D, Turkey (BOUVRAIN, 1994), but a few fragmentary remains from Sinap were referred to ?*Criotherium* sp. by GENTRY (2003), and the genus might also be present in the Turolian of Thermopigi, Northern Greece (E. TSOUKALA, pers. comm.).

*Criotherium nikolovi* n. sp.

*Type*: FM-1740 (Pl.1A-D; Fig. 1), NMNH, Sofia, Bulgaria.

*Diagnosis*: differs from the type-species by its smaller size. Horn-cores less upright and inserted less caudally, longer, without such a sharp postero-lateral keel and no accessory grooves and ridges, braincase longer, parietal less steeply inclined in side view, basioccipital less flattened, no pre-orbital fossa, muzzle less lengthened and broader. All these features are probably primitive.

*Type-locality*: probably Kalimantsi-1 (see above).

*Derivatio nominis*: dedicated to the late Ivan NIKOLOV, who found the type-specimen.

*Description*: the skull is relatively complete and not deformed but lacks the tip of the muzzle with the premaxillae, the zygomatic arches, the rostral part of the basioccipital, the tip of the right horn-core, and all teeth, but their roots show that it was fully adult. Besides this, the surface is much weathered, especially that of the muzzle. The outlines of many sutures are no longer traceable.

The muzzle is not particularly high and narrow, and the face has a concave dorsal profile in lateral view, especially above the orbits. It is very unlikely that the missing premaxillae had any contact with the nasals, which are widest at the level of the rostral tip of the frontals, but narrow markedly rostrally. The maxillae are poorly preserved; the position of the infra-orbital foramen is uncertain, but was not very posterior. The facial part of the jugal bone may have been bilobed, as in *C. argalioides*. There is no ethmoidal fissure, and no pre-orbital fossa.

The most obvious and remarkable feature is the strongly elevated frontal, which rises between the horns, far higher than the orbits. The bone is strongly bent, as the supra-orbital and post-cornual parts, in the sagittal plane, make an angle of about 90° (Fig. 1A). The mid-frontal suture is quite complex, and elevated as a sagittal ridge, at least in the supra-orbital area, but perhaps not between the horn-cores. The bone is strongly pneumatized above the orbits, but we do not know whether a sinus extended into the horn-core. The supra-orbital foramina are small, not sunken, and very far from the horn-cores. There is no post-cornual

fossa. The orbit is not much elevated above or behind the tooth-row; its anterior border is above the back of M3.

In front view, the horn-cores diverge by an angle of about  $35^\circ$ , and the left one is perfectly preserved. In lateral view, its anterior border is in the same plane as that of the facial part of the frontal, while the caudal border makes an angle of about  $140^\circ$  with the brain-case. It is thus strongly inclined backwards. Because of the highly elevated frontal bone, it is inserted far from the orbits, but there is no true pedicle demarcating the frontal from the horn-core. It is slightly compressed transversely at the base, and very short relative to its basal diameter. It is not curved but strongly twisted on its axis, as it describes a complete clockwise whirl. There is a very strong postero-lateral keel, starting above the post-orbital process, and a weaker, but still conspicuous, medial keel (Fig. 1B). Between them is a broad groove, which is posterior at the base; the rest of the surface is finely ornamented. The tip of the horn-core, which is not broken and at most slightly weathered, is blunt, and not pointed as most bovid horn-cores.

The parietal is short, not at all convex between the widely separated temporal lines, or between the frontal and occipital, but with two shallow depressions on either side of the midline. The supra-occipital is low and broad. The occipital proper is almost in the same plane as the dorsal part of the parietal. It is also low and broad, with well-marked muscular ridges and tubercles. The mastoid exposure is long, and probably contacted the parietal, but is not very broad; its postero-dorsal part passes gradually into the latero-medial part. As the cranial base is not perfectly preserved, there is no definite evidence of supplementary articular atlantoid facets, but the condyles pass smoothly, almost without a notch, to the base of the paroccipital processes, which are flattened. This morphology is similar to that found in *C. argalioides*, and it is therefore likely that the extra articular facets present in this species were also present in *C. nikolovi*. The basioccipital has large rounded posterior tuberosities, far forward of the foramen magnum, connected by broad low ridges to the anterior ones, which are incomplete but were certainly also broad and low. A broad groove runs along the bone, and reaches the foramen magnum. Remarkably, although the upper profile of the brain-case makes a strong angle with the face, the basioccipital makes an angle of no more than  $10^\circ$  with the palate (the skull is not deformed). The tympanic bullae are well inflated, oval, with their main axis at an angle of about  $30^\circ$  with the sagittal line. The *foramen ovale* is not preserved. The choanae almost reach the level of the posterior border of M3.

*Comparisons:* Skull FM-1740 differs from *Criotherium argalioides* in the following features:

- it is slightly smaller (Table 1). Virtually all measurements fall well below the minimum values for Samos and Kemiklitepe.
- the backward shift of the horn-cores has not proceeded so far, and the brain-case is not so extremely shortened. At Kalimantsi, the horn-core remains about 5 cm above the nuchal crest, whereas they are closer in the Samos and Kemiklitepe specimens, and may even almost come into contact (S58 in MCGL).
- the horn-cores are still inclined backwards, as in *Palaeoreas*. Although it is common for bovid horn-cores to become more inclined in the course of evolution, the upright insertion of those of *C. argalioides* is clearly a specialized feature linked with their very posterior insertion.
- although quite massive, the horn-cores still assume the shape of normal bovid horn-cores; by contrast, those of *C. argalioides* are more stocky, with an extremely salient postero-lateral keel which ends abruptly at the upper end, giving the tip the shape of a saddle rather than that of a point. Furthermore, the rugose ridges which run parallel to the main keel in *C. argalioides* are absent in FM-1740.
- the auditory bullae have a slightly more antero-posterior orientation than in the Samos specimens of *C. argalioides* (30° in respect to the sagittal line instead of 40° in AMNH 22802: D. KOSTOPOULOS, pers. comm.), probably in relation with the less extreme shortening of the brain-case; however their orientation in the Kemiklitepe skull is similar to that of FM-1740.
- the muzzle is not so elongated. The orbit is not so far above the tooth-row, and the lacrymal bone reaches the level of M1, whereas it remains above M2 at Samos and KTD. The shallow ante-orbital fossa of *C. argalioides* is absent in FM-1740.
- the rostral border of the choanae reach the level of the (missing) M3s, whereas they are more caudal in *C. argalioides*.

All these features of *C. nikolovi* are more primitive than those found in *C. argalioides*, and they bring the Bulgarian form closer to *Palaeoreas lindermayeri*, a Turolian bovid from the Aegean region (BOUVRAIN, 1980; GERAADS *et al.*, 2003, and references therein), and FM-1740 is indeed intermediate in the inclination, divergence and shortening of the horn-cores, strength of their keels, and inclination of the brain-case roof. GENTRY (1971) advocated a close relationship between these genera, and his opinion was recently (GENTRY, 2003) strengthened by the recognition of some similarities of *Palaeoreas zouavei* BOUVRAIN, 1980, from the early Turolian of Greece, with *Criotherium*. *Palaeoreas lindermayeri* indeed has the caudal face of the occipital condyles in the same plane as the occipital itself, as in

*Criotherium*. However, *Palaeoreas* is clearly distinct from both species of *Criotherium* by its smaller size, long nasals and contact between them and premaxillae, lack of frontal sinuses (hence depressed supra-orbital foramina), presence of a post-cornual fossa, cranial basis not shortened, lack of lateral extra facets for the atlas, and more loosely twisted horn-cores. Most of these features are primitive and could be expected in an ancestor of *Criotherium* but the fusion of the interfrontal suture in both species of *Palaeoreas* is apomorphic and not found in *Criotherium*. Evidence for a close relationship between these two genera can be retained as a working hypothesis, but is still weak.

*Plesiaddax simplex* KÖHLER, 1987 is based upon a skull fragment from Kayadibi (Turkey) that is too incomplete to be usefully compared, but the generic identification is probably correct.

From Garkin in western Turkey, ERDBRINK (1978) described as *Plesiaddax inundatus* a large sample of skulls and post-cranials, but unfortunately he poorly illustrated them. BOUVRAIN *et al.* (1995) questioned the generic attribution, suggesting that the Garkin ovibovine might be close to *Criotherium* although, according to them, it cannot be included in this genus because of the horn-core torsion (Erbrink mentions "a barely discernible homonymous curvature", whereas it is heteronymous, and strong, in *Criotherium*). "*Plesiaddax*" *inundatus* resembles *Plesiaddax depereti* from China (BOHLIN, 1935b) in the very broad horn-core bases, the short distance between them and the nuchal crest, and the flattening of the posterior side of the posterior tuberosities of the basioccipital, which act as a stop facet for the atlas. This latter feature, brought to an extreme in *Urmiatherium polaki* from Maragha (MECQUENEM, 1924-25), and in *U. intermedium* and *P. depereti* from China (BOHLIN, 1935b), is absent in *Criotherium*. However, "*Plesiaddax*" *inundatus* resembles FM-1740 rather than *P. depereti* in that the skull is rather long and narrow, the frontal between the horn-cores much higher than the nasals, the choanae are not far behind M3, there are no large lateral extra facets for the atlas, the premolars are not much reduced, and we agree with BOUVRAIN *et al.* (1995) that the Turkish form is clearly less derived than the *P. depereti*-*Urmiatherium*-*Parurmiatherium* group.

## CONCLUSION: EVOLUTION AND RELATIONSHIPS

SOLOUNIAS (1981) listed *Criotherium argalioides* from several quarries in Samos: Q1, Q2, Q6 and quarry A. The fossils were excavated by several parties and are kept in various institutions, but according to BOUVRAIN *et al.* (1995) and D. KOSTOPOULOS (pers. comm.), all the definitely identifiable material belongs to the lower Turolian faunas, and this is also true



of Kemiklitepe-D. Since it is very unlikely that even the lowermost level of Kalimantsi is earlier than the Turolian, we must admit the existence of two lineages in *Criotherium*, with two roughly contemporaneous species, one in Samos and western Turkey, the other in Bulgaria (and perhaps Northern Greece).

The tribal affinities of *Criotherium* are still disputed. It had long been included in the Ovibovini (e.g. BOUVRAIN & BONIS, 1984: Fig. 3A), but GENTRY (1996) and GENTRY *et al.* (1999) pointed out the difficulties of including all genera commonly referred to this tribe in the same group (Fig. 3B), and recent parsimony analyses of living forms further weakened the Ovibovini concept. Cladistic analyses based upon behavioral and morphological characters place *Ovibos* close to *Budorcas* and separate from *Ovis* and *Capra* (GENTRY, 1992; VRBA & SCHALLER, 2000: Fig. 3C), but others based upon RNA/DNA sequences show either *Budorcas* to be closer to *Capra* than is *Ovis*, and *Ovibos* still more distant (LALUEZA-FOX *et al.*, 2005: Fig. 3E), or the opposite, i.e. *Ovibos* closer to *Capra* than is *Ovis*, and *Budorcas* more distant (ROPIQUET & HASSANIN, 2005: Fig. 3D). Molecular genetics clearly fails to provide the final answer for modern forms, but it does not support the hypothesis of a close relationship between them.

Among morphologists, the strengthening of the atlanto-cranial joint, including development of extra articular facets and changes in basioccipital morphology, plays an important role in "ovibovine" systematics. The most extreme cases of reinforcement are found in those taxa with short stocky horn-cores with an expanded basis, clearly used for "Rammkampf": *Urmiatherium*, *Parurmiatherium*, *Plesiaddax*, *Tsaidamotherium* (from the late Miocene of China: BOHLIN, 1935c), *Ovibos*. The horn-cores are slender in *Mesembriacerus* from the Vallesian of Greece (BOUVRAIN & BONIS, 1984) but their strong backward inclination frees the forehead, and head to head clash is also very likely in males of this genus. If this is used as a major synapomorphy, these upper Miocene forms and *Ovibos*, to the exclusion of *Budorcas*, form a tribe Ovibovini, which might even be remote from other Bovids (GENTRY, 1996: Fig. 3B). However, and although strengthening of the atlanto-cranial joint does not occur in *Connochaetes* and *Syncerus*, which also practice "Rammkampf", this morpho-functional specialisation is certainly linked to this agonistic behaviour, and is therefore likely to occur in parallel. Recently, GENTRY (2003) grouped *Criotherium* together with *Palaeoreas* in the Antilopini, and suggested close relationship between *Urmiatherium* and *Oioceros*. The most conservative view would be to relate only the Plio-Pleistocene ovibovines to *Ovibos*, but molecular analyses show that it is unlikely that they stand far apart from the caprines.

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Caption to plate:

*Criotherium nikolovi* n. sp., holotype skull FM-1740 in A: right lateral, B: antero-dorsal, and C: occipital views. D: stereo pair of the cranial base.

Captions to figures:

Figure 1. *Criotherium nikolovi* n. sp. A: sagittal skull profile, and B: cross section of the left horn-core at base and about 5 cm above it (front is towards the top of the page, midline is to the right).

Figure 2. Various cladograms of the Ovibovini and related forms.

Table 1 Comparative measurements of *C. nikolovi* and *C. argalioides*

	FM-1740	KTD	Samos**
Length foramen magnum - P2	~ 235	270*	246-275
Foramen magnum-front of choanae	128	142	137-149
Braincase width	96	102*	96-113
Bi-mastoid width	109	123.5*	122-125
Height from alveolar border to orbital roof	85	111	?95-130
Post-orbital width	132	158	156-167
Occipital height	48	50	55-57
Length M1-M3	60 ?	66*	62.5-75

\* from BOUVRAIN, 1994; \*\* from BOHLIN, 1935a