

***Palaeoreas lindermayeri* (Wagner, 1848)
(Mammalia, Bovidae)
from the upper Miocene of Bulgaria,
and a revision of the species**

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ABSTRACT

Palaeoreas lindermayeri (Wagner, 1848) is represented in the upper Miocene of Hadjidimovo-1 (Bulgaria) by what may be the largest known sample of a fossil Bovid species from a single locality. The size of the animals is on the average larger than at the type locality, Pikermi, but the biochronological usefulness of size and other inter-population differences remain, in our opinion, doubtful, in spite of the restricted geographic range of the species. *P. lindermayeri* was probably a gregarious and territorial Bovid, perhaps similar to the blackbuck in its ecology and behavior, but it cannot be referred to any modern tribe.

KEY WORDS

Mammalia,
Bovidae,
Palaeoreas lindermayeri,
upper Miocene,
Bulgaria,
revision.

RÉSUMÉ

Palaeoreas lindermayeri (Wagner, 1848) (Mammalia, Bovidae) du Miocène supérieur de Bulgarie et une révision de l'espèce.

Palaeoreas lindermayeri (Wagner, 1848) est représenté dans le Miocène supérieur de Hadjidimovo-1 (Bulgarie) par ce qui pourrait bien être le plus important échantillon connu d'une espèce de bovidé fossile d'une même localité. C'est un animal d'une taille en moyenne un peu supérieure à celle du spécimen de la localité type, Pikermi, mais l'utilité biochronologique des différences inter-populationnelles métriques et morphologiques demeure, à notre avis, douteuse, malgré la faible étendue géographique du domaine de répartition de l'espèce. *P. lindermayeri* était probablement un animal grégaire et territorial, peut-être semblable à l'antilope cervicapre par son écologie et son comportement, mais il ne saurait être rattaché à une tribu moderne.

MOTS CLÉS

Mammalia,
Bovidae,
Palaeoreas lindermayeri,
Miocène supérieur,
Bulgarie,
révision.

INTRODUCTION

THE LOCALITY HADJIDIMOVO-1: LOCATION, FAUNA AND BIOCHRONOLOGICAL POSITION

The Hadjidimovo fossiliferous area is situated in the Mesta river valley near the town of Hadjidimovo and the Bulgarian-Greek border; it is a late Miocene fossil site with four localities of vertebrate fauna. The sediments (light clay sands) belong to the Nevrokop formation (Vatsev 1980). The site was first mentioned by Nikolov (1973, 1985) but its richness was only fully acknowledged after the excavations of one of us, the site discoverer (DK), between 1985 and 1998.

More than 19000 bone remains from Hadjidimovo (DK collection) are presently stored in the Assenovgrad Museum, Sofia – a palaeontological division of the National Museum of Natural History. This huge collection, which comes mainly from the locality Hadjidimovo-1 (Hadjidimovo-Girizite) and is still unpublished, makes it the richest upper Miocene site of Bulgaria and among the richest of the Eastern Mediterranean. This exceptional abundance of fossils at Hadjidimovo-1 prompted one of us (NS) to start a research program upon this site, which will hopefully become a reference locality of the late Neogene of Eurasia.

The preliminary faunal list of the locality Hadjidimovo-1 includes at least 29 mammal species (Spassov 2002). The faunal complex of Hadjidimovo-1 shows similarities in taxonomic composition and global features of the faunal assemblage with several localities with *Hipparion* fauna of the Balkano-Iranian region, including the territory North of the Black Sea, indicating a middle/late Maeotian (middle Turolian) age. Most probably the locality could be placed at the beginning of MN12. This conclusion on the biochronological and faunistic similarity of Hadjidimovo-1 has also been tested after the Poisson criterion of sample similarities by comparison with the faunal check-lists of various localities (Spassov 2002).

Only the Chalicotheriidae from the locality have been studied in detail (Geraads *et al.* 2001). The present paper is devoted to *Palaeoreas lindermayeri* (Wagner, 1848), the most abundant large

mammal of Hadjidimovo-1. It will be compared with the much smaller sample from Kalimantsi, a SE Bulgarian locality not far from Hadjidimovo (Nikolov 1985; Spassov 2002), with the reference material from the type locality of the species, Pikermi, and with that from some other minor sites.

SYSTEMATICS

Family BOVIDAE Gray, 1821

Genus *Palaeoreas* Gaudry, 1861

TYPE SPECIES. — *Antilope lindermayeri* Wagner, 1848.

DIAGNOSIS. — See Bouvrain 1992: 57.

Palaeoreas lindermayeri (Wagner, 1848)

HOLOTYPE. — Horn-core fragment (Wagner 1848: pl. 12, fig. 5) (No. 520, Institute of Paleontology, Munich).

TYPE LOCALITY. — Pikermi (Greece).

DESCRIPTION

Cranial material prevail among the material from Hadjidimovo-1. We have counted 184 fairly complete horn cores, 95 frontlets, 65 skulls and skull fragments with horn cores and 20 neurocranials. This amounts to a total of 369 skull fragments and skulls, possibly representing the largest known sample of a single bovid species from a single locality. The material includes also many mandibles. Limb bones are less common, at least in the Assenovgrad collections, and we have not tried to sort them out. In contrast to the Pikermi material, that of Hadjidimovo-1 is usually not crushed, and the bone surface is not polished as it is so often the case at Pikermi, allowing observation of more details. *Palaeoreas lindermayeri* has already been described by several authors (Gaudry 1861; Gentry 1971; Bouvrain 1980, 1992; Geraads & Güleç 1999). Nevertheless, the very rich and well preserved material permits us not only to repeat the main characters of the species, but also to revise and confirm them in a very large sample and to insist upon some other poorly known features.

profile, but none is complete anteriorly (Fig. 1). Only one specimen has an ethmoidal fissure, but most specimens do not have any. The ante-orbital depression is variable in size and depth, but is always present. The infra-orbital foramen opens above P2 or P2-P3; there are often two or several of them. The anterior border of the choanae is usually at the level of the middle of M3.

The frontal is strongly bent between the horn-cores, with its anterior and posterior parts at an angle of about 90°-100°. The supra-orbital foramina are small, and located in deep and wide depressions. The analysis of male skulls of different individual age leads to the conclusion that the supra-orbital foramina decrease in size with age from subadult to adult individuals and migrate to the upper edge of the frontal pit. This must be born in mind in taxonomic interpretations. The inter-frontal suture is always closed, and often elevated behind the horns. The fronto-parietal suture is also almost always closed. None of the frontals show any evidence of sinuses. There is a large and deep post-cornual fossa, extending onto the post-orbital bar.

The brain-case is of regular width. The temporal lines are weak, but the squamoso-parietal suture is often raised as a well defined ridge.

The occipital is rather low and broad, with both sides facing mostly posteriorly, separated by a broad raised area. The paroccipital processes are curved forwards. The mastoid exposure is of moderate width, its lower part faces laterally, and sometimes produces a small mastoid apophysis. In one case at least, the mastoid is fused with the squamosal in the post-tympanic area. This is of course a component, together with the lack of frontal sinuses, fusion of frontal sutures, and thickening of supra-otic ridges, of a general trend towards strengthening of the brain-case.

The basi-occipital is rather long, and much narrower anteriorly than posteriorly, but the anterior tuberosities are prominent (Fig. 1C). All specimens have a central depression, all the way from the foramen magnum to the presphenoid.

The bulla commonly bears a rounded longitudinal ridge, stronger anteriorly along the medial border of the tympano-hyal. The foramen ovale is small and rounded.

The horn-cores diverge by an angle of about 40-45°. They are usually twisted on their axis, with rarely a tendency towards some slight spiralling. The posterior keel is constant, but variably expressed. There is no anterior keel, but there may be a ridge instead, which usually becomes sharper upwards. The pedicle is always made of compact bone, without sinuses.

Dentition (Fig. 2)

All medium-size dentitions from Hadjidimovo must be referred to *Palaeoreas*, there being no other Bovid of similar size. Their main features agree with those given by Gentry (1971) except that the front and back edges of p3 and p4 are rarely transversal, and that there is usually (but not always) a deep labial groove between protoconid and hypoconid on p4. The metaconid of p4 is more transversal than that of p3, and it may be anteriorly expanded so as to close the middle lingual valley on worn teeth.

Female skulls

Three crushed adult skulls from Hadjidimovo-1 (HD-3454, HD-5134 and HD-unnumbered) are of the same size as the horned skulls described above, but are hornless. Their dentitions are identical, in size and morphology, with those of the horned *P. lindermayeri* skulls, but these skulls differ from them, besides their hornless condition, by their weaker basicranial angle, weaker anterior tuberosities of basioccipital, and less advanced fusion of the inter-frontal suture.

Female skulls of *Palaeoreas* were previously (Gentry 1971; Bouvrain 1980, 1992) thought to bear smaller horns than males, but neither the bivariate plot of basal horn-core diameters (Fig. 3), nor the principal component analysis on the most complete skulls (Fig. 4) show any clear distinction between two groups. Furthermore, these three skulls cannot be referred to any other taxon (the remaining Bovid fauna consists of Boselaphines, Antilopines, and very few cf. *Protoryx*). Therefore, it must be concluded that the female of *P. lindermayeri* was hornless (see part Taphonomy, ecology, ethology and relationships).

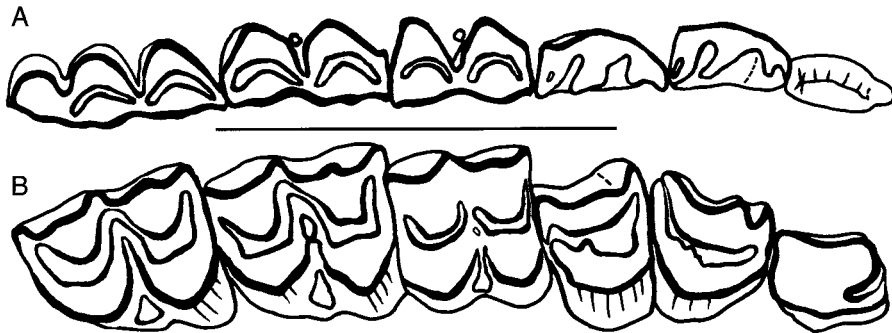


FIG. 2. — *Palaeoreas lindermayeri* (Wagner, 1848) from Hadjidimovo-1; **A**, lower tooth row (HD-2443); **B**, upper tooth row (HD-3664). Scale bar: 5 cm.

DISCUSSION

Variation in Palaeoreas

P. lindermayeri is by far the best known species of the genus. It is mainly known from Pikermi, but also from Samos (Gentry 1971), Halmyropotamos (Melentis 1967), Vathylakkos 1 and 3, Ditiko 1 and 2, Prohoma (Bouvrain 1992) and Kemiklitepe (Geraads & Güleç 1999). It is also present in Kalimantsi. Other reports from Turkey are either based on teeth alone, and are therefore unreliable, or on incorrectly identified horn-cores (such as those from Gülpınar, see Tekkaya 1973). A skull from Titov Veles in Macedonia was referred by Ciric (1957) to this species, but this is also incorrect, because the outline of the horn cores is concave laterally in front view, whereas it is always convex in *P. lindermayeri*. Therefore, the geographic range of this species is quite restricted: Greece, southern Bulgaria and westernmost Turkey. Thus, interestingly, this species, which is among the dominant ones in the rich Turolian sites of South Bulgaria (see below), has quite a limited range and has not been reported, e.g., from the Northern Pontic region where numerous rich localities are known.

By almost all its dimensions, the *P. lindermayeri* from Hadjidimovo-1 is larger than that of Pikermi. This is especially true of teeth and horn dimensions, and brain case size (Table 1; Figs 3-5).

However, there does not seem to be any difference in proportions, the Hadjidimovo-1 fossils looking just like larger versions of the Pikermi

ones, which are quite similar to the specimens from Kalimantsi. However, a few specimens from the Assenovgrad Museum collection, of which the only measurable one is HD-3155, have a different facies, and are slightly smaller and more similar to those from Pikermi. According to one of us (DK), they most probably come from another Hadjidimovo locality, Hadjidimovo-Tumbichkite, that is from deposits several tens of meters higher than the level of Hadjidimovo-1; they could be contemporaneous with Pikermi. The single specimen from Halmyropotamos cannot be distinguished from the Pikermi sample. A specimen from the latest Miocene of Ditiko (Bouvrain 1980) differs from the Pikermi sample by its larger size, relatively smaller horns, smaller post-cornual fossa, more waisted basi-occipital, and more inflated bulla. Bouvrain (1980) considered that these differences do not warrant specific distinction. On the contrary, she recognised as *P. zouavei* Bouvrain, 1980 a skull from the early Turolian of Ravin des Zouaves n° 5 (RZO), which shares with the Ditiko specimen a larger size and relatively smaller horns as compared with the Pikermi material. Its supra-orbital foramina are larger than in *P. lindermayeri*, but other differences look weak and were perhaps accentuated by deformation. For example the infra-orbital foramina are only very slightly more posterior than at Hadjidimovo-1, the orbit is rather less prominent than in the latter sample, and its relative position to the tooth row is the same. Table 2

TABLE 1. — Comparative measurements of the skulls of *Palaeoreas lindermayeri* (Wagner, 1848) from Pikermi, Kalimantsi and Hadjidimovo-1. Highly significant *t*-tests between Pikermi and Hadjidimovo-1 are noted *. Measurements used for the Principal component analysis (Fig. 5) are in bold.

Measurements	Pikermi				Kalimantsi mean	Hadjidimovo-1			
	mean	N	min	max		mean	N	min	max
Antero-posterior diameter of horn-core*	43.1	12	36.7	49.7	45.7	52.4	34	43.7	61
Transverse diameter of horn-core*	37.7	14	33.5	41.3	37.8	42.5	33	34.6	48
Length of horn-core (straight line)	180	6	150	210		190	11	180	230
Width over lateral borders of pedicles*	86	13	80.3	96	92	97.5	23	91	107.5
Width over lateral borders of supra-orbital foramina	34	12	30	43.5		34	12	29	40.7
Minimum width of brain-case*	62	6	55.7	66	64.8	72	25	67	83
Maximum occipital width*	73.5	2	73	74		84	18	77	91
Bi condylar width*	47.5	2	47.3	47.6	46	54	14	50.6	57.4
Occipital height*	30	2	28.8	32	34	36	17	32.7	40
Width over posterior tuberosities of basioccipital*	28	3	26	29.5		37	18	32	40
Width over anterior tuberosities of basioccipital	23	1				22	16	16	26.5
Length of bulla						28	13	24.5	31.5
Width of bulla						20	12	17.5	22
Length from supra-orbital foramina to top of occipital*	95	3	87	100	100	115	23	100	131
Ditto. to occipital condyle	109	1				136	17	125	146
Length from basion to M3						99	16	78	120.5
Length from basion to P2						161	8	141	182.5
Length from occipital condyle to P2	163	1			166				
Length M1-M3*	39	7	38	40	39	43	27	40.8	45.4
L P2-P4*	27	4	25.5	28.5	25	30	13	28.3	32
L P2-M3*	64	6	62	67	66	72	13	68.9	75.8

lists the most significant differences among of the various *Palaeoreas* populations; it shows that their classification is not straightforward. The material from Kalimantsi and Kemiklitepe does not differ from the typical Pikermi population. That of Hadjidimovo-1 is characterised by a large body size combined with large horn-cores and small supraorbital pits but we do not think that

this warrants specific distinction. The materials from other localities are too poor, at the present time, for their taxonomic positions to be definitely settled, but we believe that the differences between the various samples reflect the intraspecific population variability in time and space, at no more than subspecific level. We think it would be unwise to draw biochronological conclu-

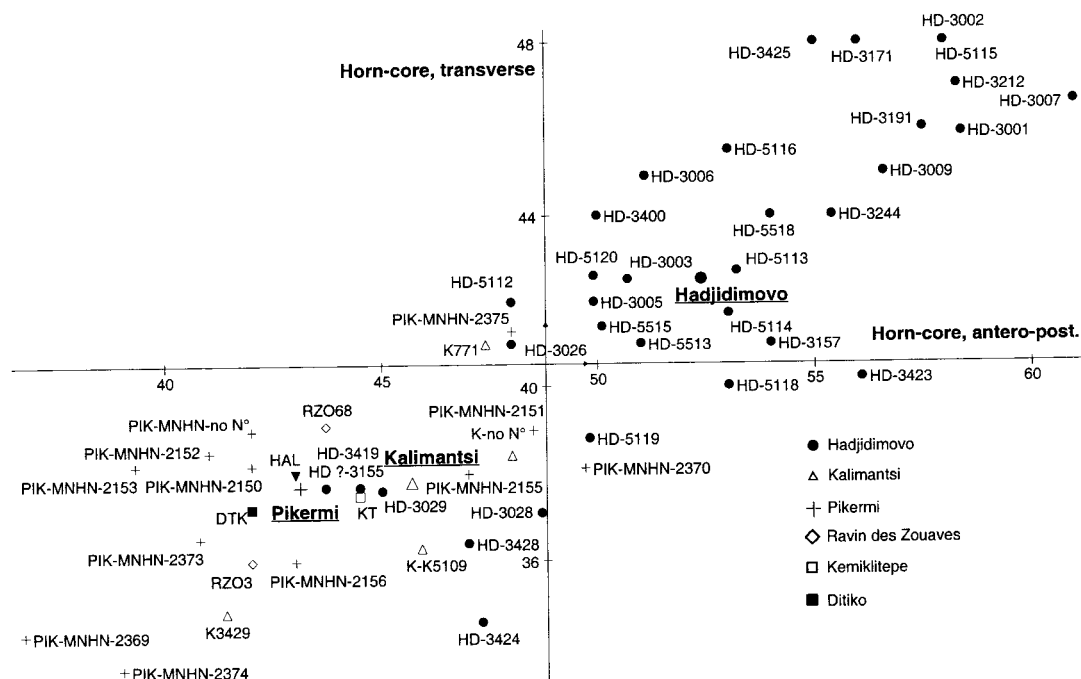


FIG. 3. — Plot of antero-posterior vs. transverse diameters of *Palaeoreas lindermayeri* (Wagner, 1848) horn-cores. Mean measurements for each site are underlined. They include also those specimens where only one measurement can be taken.

TABLE 2. — Character distribution in some populations of *Palaeoreas* Gaudry, 1861. Abbreviation: **RZO**, Ravin des Zouaves.

	<u>Pikermi</u>	<u>Kalimantsi</u>	<u>Hadjidimovo</u>	<u>Ditiko</u>	<u>RZO</u>	<u>Kemiklitepe</u>	<u>Samos</u>
Size	small	small	large	large	large	small	large?
Relative size of horns	large	large	large	small	small	large	small?
Supra-orbital pits	small	small	small	small	large	small	small
Basi-occipital tuberosities	small	?	large	large	large	?	?

sions from the inter-populational variations of this species.

The Turkish species *Palaeoreas elegans* Ozansoy, 1965 and *P. brachyceras* Ozansoy, 1965 have spiralled (instead of twisted) horn-cores, unfused inter-frontal suture, and supra-orbital foramina of normal shape, and there is no reason to include them in the genus *Palaeoreas*. *P. asiaticus* from Garkin (Köhler 1987) was considered by Gentry & Heizmann (1996: 383) as “doubtfully separate from *P. lindermayeri*”, but it is smaller than the latter species, the inter-frontal suture is visible, and the posterior keel is almost straight, instead

of spiralled. These are all similarities with “*P.*” *elegans*, and we think it is closer to this species than to *P. lindermayeri*, even though the tight spiralling recalls that of the latter species.

Taphonomy, ecology, ethology and relationships

The large number of frontlets and horn-cores in the taphocoenosis provide the opportunity to calculate the minimum number of individuals at about 260. They were concentrated in isolated rock lenses with an area of tens of square meters and a maximum thickness of less than 1 m. The very high male/female ratio can be explained by

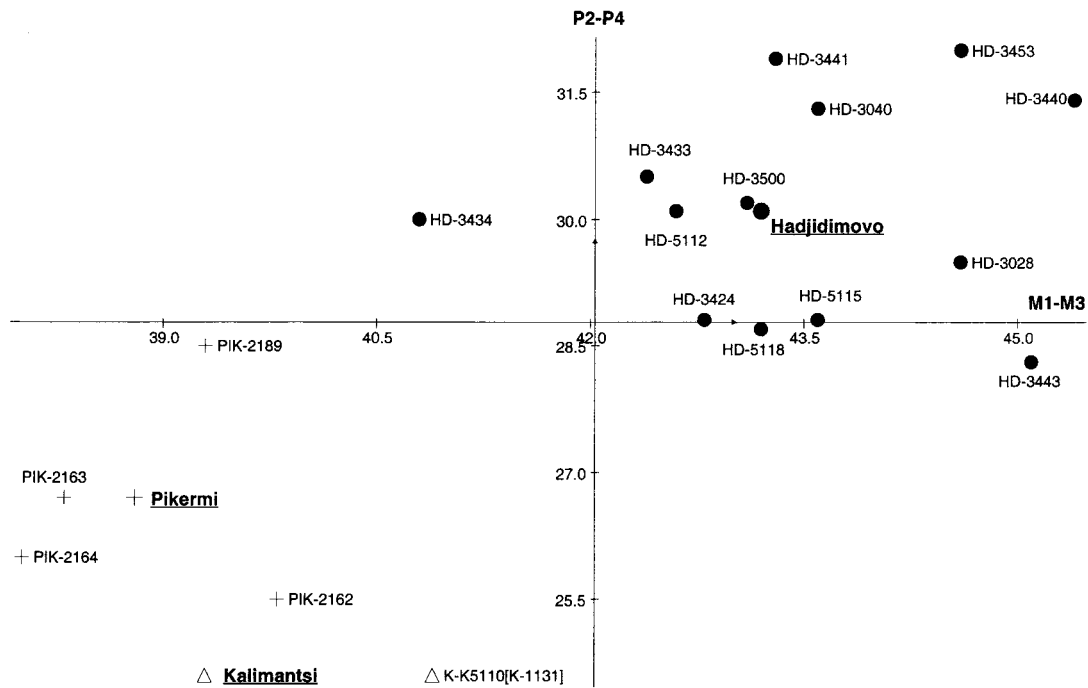


FIG. 4. — Plot of upper premolar vs. upper molar length of *Palaeoreas lindermayeri* (Wagner, 1848). Means and symbols as for Fig. 3.

differential preservation, the male skulls with their very thick braincases being far more robust than female ones. The same bias presumably acted against juvenile specimens. Similarly biased sex-ratios are found, for the same reason, in *Tragoportax*, both in Pikermi and Hadjidimovo-1. However, it is unlikely that taphonomic bias was the sole factor for this concentration of the remains of hundreds of male individuals, and it is likely that in the thanatocoenosis there were mainly herds of males.

Palaeoreas lindermayeri is the dominant species of Hadjidimovo-1 among 29 taxa (Spassov 2002). Such antelopes of medium to large size living in relatively large herds are usually mixed feeders or grazers (groups 3-5 of Gagnon & Chew 2000) living in open landscapes. According to Solounias *et al.* (1999) this species was mostly a browser. However, some of its morphological features fit better those of a grazer. Its teeth, although not hypsodont by modern standards, are clearly not brachyodont. Furthermore, although no skull is

perfectly preserved in this area, some of the best specimens show that the premaxillae are wide, and that they are inclined downwards, with their anterior tip below the occlusal plane. These two features denote grass-feeding, according to Spencer (1995). It is clear, in any case, that *Palaeoreas* did not inhabit a forest-like, tree-dense woodland.

The taphonomic data as well as the frontal morphology and sexual dimorphism in horns could also suggest a social structure close to that of some Reduncini (*Kobus kob*) including territorially dominant males as well as both male and female herds. Territoriality in *Palaeoreas* is shown by the presence of an ante-orbital depression, hence of a pre-orbital gland. The horns probably played an important role in display and intra-specific tournaments. The development of such a socialization usually takes place in Bovids inhabiting spaces open enough, living in herds and having a high degree of visual communication. It is found neither in the low-social inhabitants of dense woods, nor in the super-social Bovids of

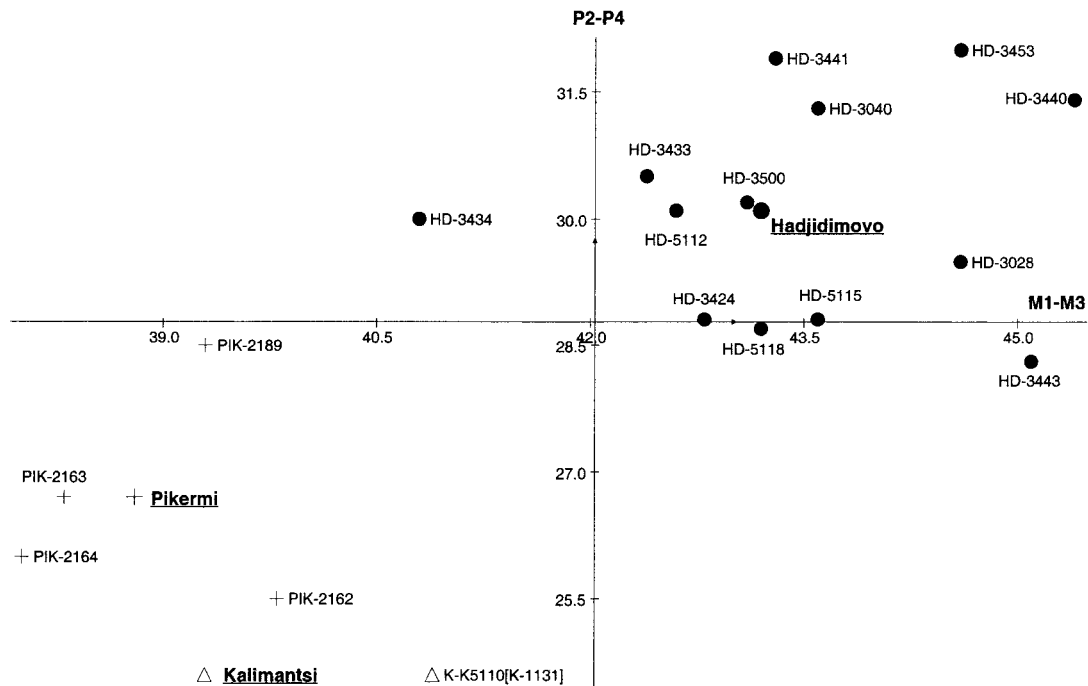


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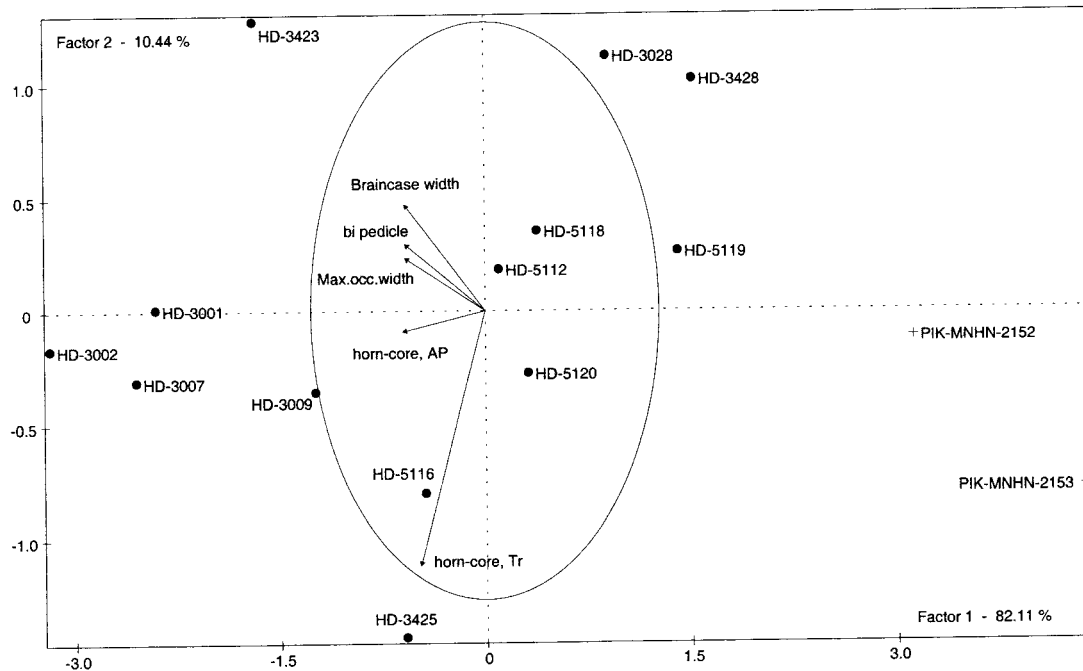


Fig. 5. — Principal component analysis on the most complete skulls. Symbols as for Fig. 3. Abbreviations: **Braincase width**, minimum width of braincase; **bi pedicle**, width over lateral borders of pedicles; **Max.occ.width**, maximum occipital width; **horn-core, AP**, antero-posterior diameter of horn-core; **horn-core, Tr**, transverse diameter of horn-core.

the fully open spaces (see Geist 1974; Janis 1986). The best Recent analogue is perhaps *Antilope cervicapra*, a species where the horns are highly evolved and specialized, with an important social function (Geist 1966). They usually gather in herds of 20-30 to several hundreds, living in open plains covered with scrub; they penetrate open forests, but avoid dense forests (Prater 1971). This agrees with the environment that we have suggested above for *Palaeoreas* (Spassov 2002).

The lack of sinuses in the frontal bone, pedicle, and horn-core, as well as the lack of horns in females, provide a few more clues about social structure and “agonistic” behaviour. These morphological features are strongly correlated in modern Bovids. Species with hornless females usually lack any frontal sinus (the main exception being *Aepyceros*), and in the species lacking frontal sinus the horns are small or absent in females (the main exceptions being *Tragelaphus*

euryceros and, less clearly, *Taurotragus*). Therefore, absence of horns in female *Palaeoreas* is not unexpected. According to Roberts (1996), it denotes a low level of competition among females.

The thickness of horn-cores and overall robustness of the rear part of the cranium suggest intensive use of horns in intra-specific fighting. This is in contrast with modern Tragelaphines, which share with *Palaeoreas* the fused frontal suture and spiralled horns, but which use their large horns primarily for display. Another behaviour that can be definitely ruled out is violent frontal clashing (“Rammkampf”) such as performed by some Caprines and Bovines, because it is always associated with extensive frontal and cornual sinuses. Lack of sinuses and torsion of horn-cores in *P. lindermayeri* are again similarities with *Antilope*, although the overall shape of the skull is more derived than in this genus. Overall, the cranio-cornual morphology of *Palaeoreas* has no

modern equivalent, and it is hard to draw definitive conclusions about its fighting behaviour. We could suggest at least that its horns had an active display role and also were used in tournament fights of frontal pressure type, similar to *Antilope* (Geist 1966).

This has certainly no bearing on the systematic position of *Palaeoreas*, whose skull is quite distinct from that of *Antilope*. Reduncines could be a modern equivalent for the social structure, but their forwardly directed horn tips and related very prominent anterior tuberosities of basioccipital, typical for the tribe, are missing here. It is more reasonable not to refer *Palaeoreas* to any modern tribe.

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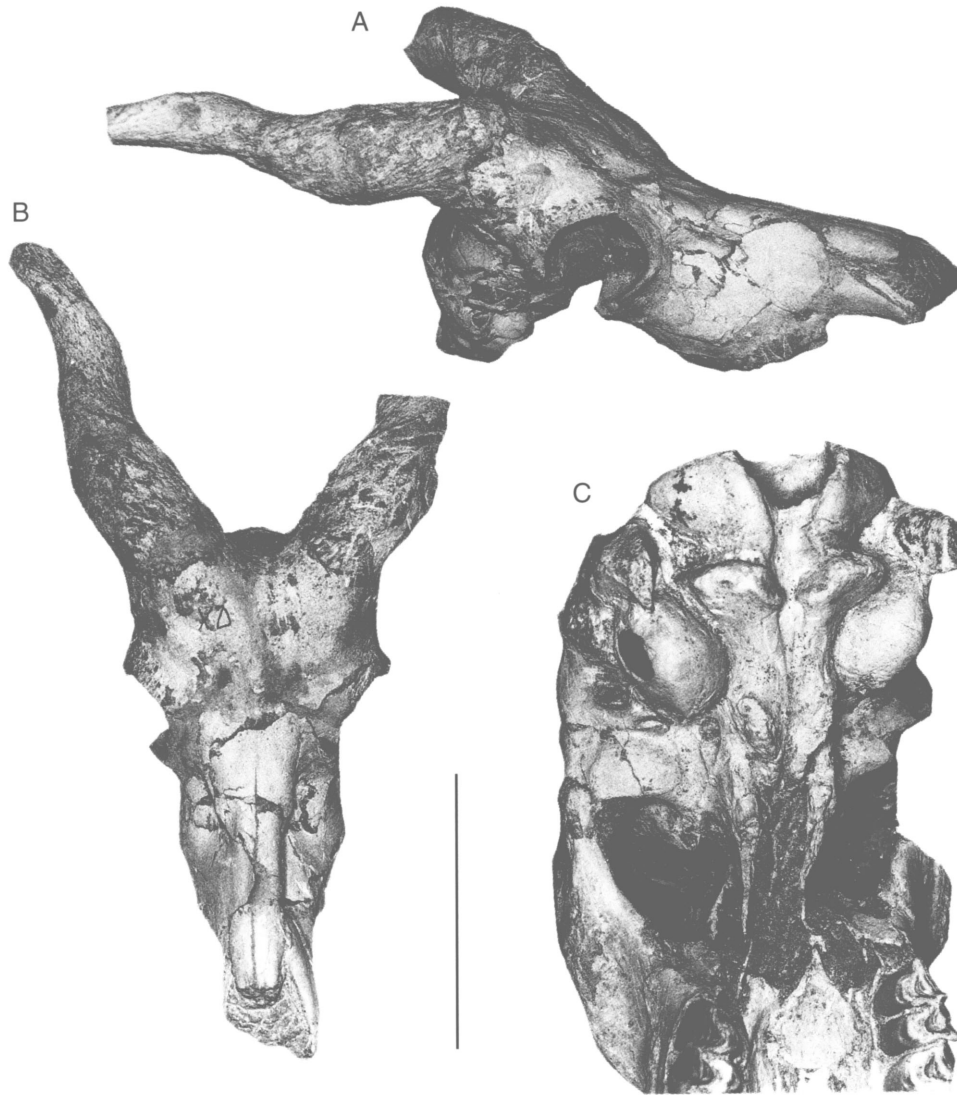


FIG. 1. — *Palaeoreas lindermayeri* (Wagner, 1848), Hadjidimovo-1; **A**, skull HD- 5112, oblique antero-lateral view; **B**, same specimen, front view; **C**, skull HD-5120, oblique latero-ventral view of the cranial base. Scale bar: A, B, 10 cm; C, 5 cm.

Skull (Fig. 1)

The face is long, with the rear border of M3 at the level of, or slightly behind, the front edge of the orbit. The face is also low, the fronto-nasal profile being deeply concave. In lateral view, the upper nasal line intersects the orbit, as in

Pikermi. It is probably in the belief that the Pikermi skulls are deformed that Bouvain (1992: fig. 7) reconstructed the face higher than it really was, with too straight a facial profile.

The premaxillary-nasal contact is moderately long. The nasals have a slightly convex upper