

Tragoportax Pilgrim, 1937 and *Miotragocerus* (*Pikermicetus*) Kretzoi, 1941 (Mammalia, Bovidae) from the Turolian of Bulgaria

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Н. Спасов, Д. Жераадс, Д. Ковачев – *Tragoportax* Pilgrim 1937 and *Miotragocerus* (*Pikermicetus*) Kretzoi, 1941 (Mammalia, Bovidae) из туролия Болгарии. Работа посвящена распространению и находкам trib. Boselaphini (Bovidae) в Болгарии. Приведено описание очень богатого материала, найденного в позднемiocеновых породах района г. Хаджидимово (ЮЗ Болгария), а также — находок около с. Кочериново. Род *Tragoportax* s. lato уже известен по району Калиманцы. Новые находки дают возможность сделать ревизию всех фоссильных находок в этом районе. Там, в более поздних отложениях видимо присутствует *T. amalthea*, который отличается от *T. rugosifrons* более близкостоящими рогами. Один из наличных ископаемых черепов отличается особенностями, сходными с вторым из упомянутых двух видов. Его наличие можно объяснить различием в пространственной приуроченности разных находок. В районе Хаджидимово установлены: *Tragoportax rugosifrons* (Schlosser) и *Miotragocerus* (*Pikermicetus*) *gaudryi* (Kretzoi). Эти таксоны описываются впервые на территории Болгарии. Материал из Хаджидимово отличается очень хорошей сохранностью. Этот факт, в сочетании с богатством материала, дает возможность критически пересмотреть диагностические особенности родов *Tragoportax* и *Miotragocerus*. Эти два рода хорошо различаются по морфологии черепа в его части, находящейся за рогами (у рода *Tragoportax* эта область вогнута) и по базикокипитальной поверхности (у рода *Tragoportax* через нее проходит продольная бороздка). В эволюции Bovidae эти особенности отличаются стабильностью в связи с консервативностью неврочраниума. Они дают возможность подтвердить родовый ранг *Miotragocerus* и уточнить таксоны видовой группы в рамках рода *Tragoportax*. Один из черепов *M. (P.) gaudryi* был определен как череп женского индивида. Благодаря ему установлены новые данные о наличии выраженного полового диморфизма у представителей р. *Miotragocerus*. На основании морфофункциональных особенностей

Abstract. The present paper is focused on the occurrence and taxonomy of the Boselaphini (Bovidae) in Bulgaria. The very rich material from the Upper Miocene localities at the town of Hadjidimovo is described as well as the finding at Kocherinovo. Up to now, the genus *Tragoportax* s. lato has been known from the occurrences near the village of Kalimantsi. New finds from the latter localities allow for a revision also on the remains in this fossil-bearing area. It seems that near Kalimantsi the upper levels of the section contain *T. amalthea* that differs from *T. rugosifrons* in its more massive horns and small intercornual frontal surface. One of the skulls has features more similar to the second species mentioned that could be due to provenance from a different locality in the area. The material from Hadjidimovo contains *Tragoportax rugosifrons* (Schlosser) and *Miotragocerus* (*Pikermicetus*) *gaudryi* (Kretzoi). These taxa are here described for the first time from Bulgaria. The very good state of the fossil material from Hadjidimovo and its richness make possible a revision of the diagnostic features of the genera *Tragoportax* and *Miotragocerus*. The two genera are well discernible after the post-hornual morphology (the presence of a fronto-parietal post-cornual depression in *Tragoportax*) and the relief of the basioccipital surface (presence of a longitudinal groove in *Tragoportax*). These features allow to confirm the generic rank of *Miotragocerus* and to specify the taxa of the species group within *Tragoportax*. A skull of *M. (P.) gaudryi* determined as a female individuum supplies new evidence for the presence of a strong sexual dimorphism in the representatives of the genus *Miotragocerus*. Based on the morphofunctional features of *Tragoportax rugosifrons* and *Miotragocerus gaudryi* a conclusion is made that these two species have occupied different ecological niches in the palaeozoocenosis.

Tragoportax rugosifrons и *Miotragocerus gaudryi*, сделан вывод о том, что они занимали разные экологические ниши палеозооценоза.

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Key words: *Tragoportax*; *Miotragocerus*; *M. (Pikermicetus)*; Late Miocene; Bulgaria.

Introduction

The Bovids included in recent times in the genus *Tragoportax* Pilgrim, 1937, were among the most widespread in Oriental and South-eastern Europe, as well as in Western Asia (the "Balkano-Iranian" province), in the Late Miocene. Numerous European, Asiatic, and even African sites, have yielded remains of various taxa linked to *Tragoportax*, that were described during the last 150 years. These remains, unfortunately often incomplete or poorly preserved, are now stored in many scientific collections. The opinions expressed by authors are often incomplete or contradictory, and numerous taxonomic and nomenclatorial problems remain unsolved. In spite of the wealth of scientific papers on the subject, recent revisions do not provide a satisfactory frame of the taxonomy of this group of fossil Boselaphines.

We describe here the rich and well-preserved sample of boselaphines from the Turolian site of Hadjidimovo-1 (South-western Bulgaria) as well as from other Bulgarian localities (Kocherinovo and Kalimantsi) using our new conceptions on the taxonomic frame of the "*Tragoportax*-*Miotragocerus* complex" (Spassov, Geraads, in press).

The Boselaphini from the locality Hadjidimovo-1

Hadjidimovo-1. Location, fauna and biochronology

The Hadjidimovo fossiliferous area is situated in the Mesta river valley near the Hadjidimovo town (Gotse Delchev district) and the Bulgarian-Greek border; it is a Upper Miocene fossil site with 4 localities of vertebrate fauna. The sediments (light clayey 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 inventor (D. K.), between 1985 and 1998.

More than 19,000 bone remains from Hadjidimovo (D. K. collection) are presently stored in the Assenovgrad Museum — a paleontological branch of the National Museum of Natural History (NMNH) — Sofia. This huge collection, which comes mainly from the locality Hadjidimovo-1 (Hadjidimovo-Girizite) and is still mostly unpublished, makes it the richest Upper Miocene site of Bulgaria and among the richest of the Eastern Mediterranean. Intensive investigations of the fauna and especially of the ungulates of the locality have started recently (Spassov, Ginsburg, 1999; Geraads et al., 2001, 2003; Kostopoulos et al., 2001; Hristova et al., 2002). The faunal list of the locality Hadjidimovo-1 includes about 30 mammal species. The faunal complex of Hadjidimovo-1 shows similarities in taxonomic composition and faunal associations with several *Hipparion* localities of the Balkano-Iranian region, and of the Northern Paratethys, indicating a Middle/ Late Maeotian (Middle Turolian) age. Hadjidimovo is somewhat earlier than Pikermi and it could be placed at the MN11/12 boundary (Spassov, 2002).

Systematic description

Order Artiodactyla Owen, 1848
Family Bovidae Gray, 1821
Subfamily Bovinae Gray, 1821
Tribe Boselaphini Simpson, 1945
Genus *Tragoportax* Pilgrim, 1937

Synonyms. *Tragocerus* Gaudry, 1861 (non *Tragocerus* de Jean, 1821); *Pontoportax* Kretzoi, 1941; ?*Gazelloportax* Kretzoi, 1941; ?*Mirabilocerus* Hadjiev, 1961; *Tragoceridus* Kretzoi, 1968; *Mesembriportax* Gentry, 1974; ?*Mesotragocerus* Korotkevich, 1982

Type-species. *Tragoportax salmontanus* Pilgrim, 1937

Included species. *Tragoportax amalthea* (Roth & Wagner, 1854) (*Capra amalthea* Roth & Wagner, 1854). Pikermi, most probably also Samos and Halmyropotamos (Greece); = ?*T. frolovi* (M. Pavlow) — Chobruchi (Moldova);



Fig. 1. Post-cornual frontoparietal area in *Tragoportax* and *Miotragocerus*. Left : *Tragoportax rugosifrons* No HD 5125; right : *M. (Pikermicetus) gaudryi* No HD 5126. Hadjidimovo, coll. of the Assenovgrad Museum (Paleontological Branch of the N.M.N.H. — Sofia) (drawings — V. Simeonovsky)

from the end (?) of the Early Turolian to the beginning of the Late Turolian.

Tragoportax rugosifrons (Schlosser, 1904) [= *T. parvidens* (Schlosser, 1904); = *T. recticornis* (Andree, 1926); = *T. punjabicus* (Pilgrim, 1910); = ? *T. aiyengari* (Pilgrim, 1939); = ? *T. ensicornis* (Kretzoi, 1941)]. Samos (lower levels?), Prochoma, Ravin des Zouaves, Vathylakkos-Ravin C (Greece), Hadjidimovo (Bulgaria), Vele-Karaslari (Republic of Macedonia), Tudorovo (Moldova) ?, Novoukrainka (Ukraine), Siwaliks (Pakistan) and possibly in: Vathylakkos 2, Nikiti 2 (Greece), Maragha (Iran); from the Vallesian/Turolian boundary to the Middle/Late Turolian boundary.

?*Tragoportax curvicornis* Andree, 1926. Samos (= *T. browni* Pilgrim, 1937, Siwaliks, Pakistan, Turolian).

Tragoportax salmontanus Pilgrim, 1937. Siwaliks (Pakistan). (Some investigations indicate for the type an age of ~ 8.1 — 7.9 Ma but this absolute date is doubtful: Barry et al., 2002).

Tragoportax maius Meladze, 1967. Bazaleti. Perhaps a synonym of *Tragoportax eldaricus* (Gabashvili, 1956), type-species of the genus *Mirabilocerus* Hadjiev, 1961. Eldar, Georgia: late Vallesian to Early/Middle Turolian ?

?*Tragoportax cyrenaicus* Thomas, 1979, Sahabi (Libya: probably Late Miocene).

Tragoportax acrae (Gentry, 1974). Langebaanweg (South Africa), Mio-Pliocene.

Tragoportax macedoniensis Bouvrain, 1988. Ditiko (Greece; MN13).

Stratigraphic and geographic distribution. From the Vallesian/Turolian boundary (or Late Vallesian ?) to the end of the Turolian, perhaps earliest Pliocene in Africa. From South-Eastern Europe and the Northern Paratethys region through Asia Minor and the Middle East to Africa and the northern part of the Indian Subcontinent (and possibly central Asia).

Revised diagnosis. Size generally large, approximately that of European *Cervus elaphus*. The postcornual fronto-parietal surface is a flat or slightly concave well-defined depressed area, usually bordered laterally by well marked temporal ridges and caudally by a step leading to a slightly raised plateau (Fig. 1). The basi-occipital has a longitudinal groove between the anterior and the posterior tuberosities, in the bottom of which often runs a weak sagittal crest (Fig. 2). Adult male horn-cores are long and slender, usually curved backwards, with a triangular to subtriangular cross-section, well marked postero-lateral keel and flattened lateral sides, but are less compressed than in *Miotragocerus*. Anterior rugosities growing downwards from the anterior keel at the basis of horn-cores are absent or weak, and usually do not extend onto the frontal. Demarcations (steps) on the anterior keel are often found, but are few when present. Horn-cores have a heteronymous torsion (anticlockwise on the right horn), so that the anterior keels first diverge in anterior view, but they re-approach towards the tips. The interco-

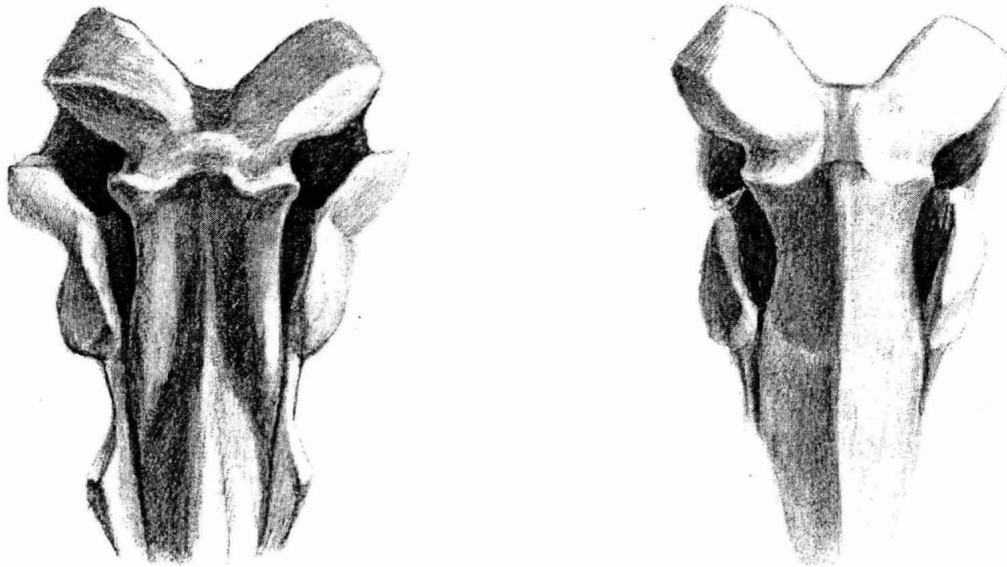


Fig. 2. Basi-occipital area in *Tragoportax* and *Miotragocerus* (*Pikermicerus*). Left: *Tragoportax rugosifrons* No HD 5125; right : *M. (Pikermicerus) gaudryi* No HD 5126 and 2010. Hadjidimovo (drawings — V. Simeonovsky)

rnual plateau is rather short antero-posteriorly, broad and almost rectangular between the horn-cores. The occipital is not much broader ventrally than dorsally, giving it a trapezoid (rather than triangular) outline.

Teeth rather hypsodont; labial walls of upper teeth, and lingual ones of lower teeth with less accentuated ribs and styles than in *Miotragocerus*. Premolars relatively shorter than in *Miotragocerus*. P2 short relatively to P3, especially its anterior part, and parastyle curved backwards. P3 with linguallly inflated hypcone. Metaconid of p3-p4 larger than in *Miotragocerus*, splayed linguallly and T-shaped on p4, with an open anterior valley.

***Tragoportax rugosifrons* (Schlosser, 1904)**

Tragoportax sp. I (large form): Spassov, 2002

Holotype. skull (Schlosser: 1904, taf. XII [IX], fig. 6)

Type-locality. Samos

Diagnosis. *Tragoportax* of large size. The fronto-parietal postcornual depression is as a rule distinctly surrounded by a continuous torus, formed laterally by the temporal ridges and caudally by a transverse ridge connecting the temporal ridges (Fig. 1). The intercornual plateau is wide. The male horn cores are usually nearly straight with a moderately convex anterior outline in lateral view, and a slightly concave posterior one. The anterior keel is as a rule regularly curved, with at most a slight tendency to form a demarcation. The tip of the horn core is not distinct from the general shape and direction of the horn core (in con-

trast to *T. amalthea*). The anterior keel is almost straight to slightly twisted in front view.

Description. The Hadjidimovo Material (Pl. 1, 2). The *Tragoportax* sample from Hadjidimovo is more abundant than that of *Miotragocerus* and is the third more abundant form of the site, together with *Gazella*, after *Palaeoreas* and *Hipparion*. It is represented mainly by mandibles (159 mandibles and mandibular fragments), more than 40 skulls and skull fragments, upper tooth rows and a lot of isolated teeth, several isolated horn cores, several tens of metapodials and metapodial fragments, (see inventory numbers of the skull, mandibular and metapodial material in tables 1-4: Collection of the Assenovgrad Paleontological Branch of National Museum of Natural History — Sofia).

Skull. It is larger than that of *Miotragocerus* (Tables 1, 2). There is probably a contact between the premaxilla and the nasal. There is a wide and deep lachrymal fossa. The infra-orbital foramen opens above P2. The anterior border of orbit remains behind the level of M3. The frontals and pedicles are hollowed. The horn-cores are long, and the best preserved skulls suggest that they were inclined backwards. Their antero-posterior diameter is greater than in most other species of the genus. They are usually strongly divergent (about 40-60°), but the divergence decreases towards the tips. They are but slightly curved backwards, and the posterior border is almost straight. In lateral view, the anterior border forms a regular curve, the tip not being dis-

Table 1

Skull dimensions and morphologic features of *Tragoportax rugosifrons* and *Miotragocerus (Pikermicerus) gaudryi* from Hadjidimovo (HD), and the fossil Boselaphini from Kalimantsi ((K) and Kocherinovo (coll. of the Assenovgrad Paleont. Museum and N.M.N.H. – Sofia), *Tragoportax amalthea* and *M. (Pikermicerus) gaudryi* from Pikermi (PIK) (MNHN -Paris, University of Athens) and *Tragoportax* from Samos (NHM_Wien; Pal. Inst.Univ. Munster).

Species and localities	HORN-CORES							BRAIN-CASE															
	Max. A-P diameter (oblique)	A-P diameter (perpendicular)	Transverse diameter	Length (straight line)	Width over pedicles	Distance between internal sides	Width over supra-orbital pits	Min. post-orbital width	Max. occipital width	Bi-condylar width	Occipital height	Width over post. tuberosities of basioccipital	Width over ant. tuberosities of basioccipital	Min. distance between temporal lines	L from supra-orbital pits to top of occipital	L from front of horn-cores to top of occipital	L from front of horn-cores to occip. condyle	L from basion to M3	L from basion to P2	L from occipital condyle to P2	L M1-M3	L P2-P4	L P2-M3
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>M. (P.) gaudryi</i>																							
HD - 2007, ♂	64	60	27	-	107	38	-	76	84+	60	43	36	25	22	162	142	163	-	-	-	-	-	-
HD - 2039, ♂	30,3	64	33	-	106	38	46	82	94	57	44	-	-	-	192	164	178	-	-	-	-	-	-
HD - 5519, ♂	78	67	33	145+	-	-	-	-	-	-	43	-	-	-	-	152	169	110	-	-	-	-	-
HD - 2010, ♂	73,1	64	31,7	175+	99	34	41,6	74	90	57	42	33	24,5	29	191	171	182	-	-	-	-	-	-
HD 3704																					53		
HD, mean, ♂	72	62	31	168	104	38	44	79	91	58	43	35	25	21	182	159	173	110	-	-	-	-	-
HD 55611 ♀, sub ad.		31-32	21													120					54		97-98
HD ♀?																					50,7	44	
MNHN - PIK - 2439	-	-	-	-	-	-	-	-	93	58	45	-	-	-	-	-	-	-	-	-	52	-	-
MNHN - PIK - 2366, ♂	88	70	27+	-	-	-	-	-	-	-	-	37,5	-	-	-	155	-	-	159	-	52	-	99
MNHN-PIK 2439																					52		
Kalimantsi (K3761)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50,3	39	-
Kalimantsi (K3730)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	53	42,2	-
Kalimantsi (K3772)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	52,3	41,8	-
Kalimantsi (K553)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50,8	-	-
Kalimantsi (K757)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50,3	-	-

Continuation of table 1

<i>T. amalthea</i>																						
MNHN - PIK - 2285	80	70	33,4	240+	-	-	-	-	-	-	57	-	-	-	157	-	-	-	-	-	-	-
MNHN - PIK - 2286 ♂	90	76	33+	-	-	38	-	78,4	98,5	57	50	-	28,5	42	174	-	-	-	-	-	-	-
MNHN - PIK - 2287	79,2	70,1	45,5	-	123	37	-	82,7	110	-	50	-	-	-	-	164	-	-	-	-	-	-
MNHN - PIK - 2288,	88,8	63	30	-	-	-	-	-	95+	59+	53	-	-	-	179	-	-	-	-	-	-	-
MNHN - PIK - 2376	-	-	-	-	-	-	-	-	105	64	46	38	36	-	-	-	-	-	-	-	-	-
MNHN - PIK - 2379	-	-	-	-	-	-	-	-	100	58	45	34	26	40	-	-	-	-	-	-	60	-
PIK - Athens	83	63,5	49	285	127	-	47	-	97,5	-	-	-	-	-	-	-	-	-	-	-	47	-
PIK, mean ♂	80	67	39	274	118	38	45	82	102	60	50	35	29	41	170	164	-	-	-	-	-	-
<i>T. cf. amalthea</i>																						
Kalimantsi (K759),	75-76	64,8	39,3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kalimantsi, (K55601)	82	74	45	-	-	-	-	-	~108	-	-	-	-	-	-	-	-	-	-	-	-	-
Kalimantsi (K3725)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	~62	43,4	-
Kalimantsi (K3768)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	59,5	41,8	-
Kalimantsi (K3727)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	66,9	-	-
Kalimantsi (K3731)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	61,5	-	-
Kalimantsi (K3742)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	62	-	-
Kalimantsi (K3728) ♂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	44,8	-
<i>T. amalthea</i> ?																						
NHMW-SAM-V,12,	73,5	68,5	33	325	105	-	37	82	102	-	41+	-	-	-	165	147	170	-	-	-	-	-
<i>T. amalthea</i>																						
PIM-SAM-66	-	-	-	-	110	-	42	82	-	58	-	32,3	23,7	-	148	-	-	-	-	-	-	-

Continuation of table 1

<i>T. nuginifrons</i>																						
HD-5140, ♀ ? ♂	-	34,4	32,4	-	-	48	-	77	85+	-	47	-	-	-	-	-	-	-	-	-	-	-
HD-3034, ♀ ?	-	35,5	33,8	-	-	-	-	79	96	-	-	-	36,3	37	155	139	-	-	-	-	-	-
HD-2011, ♂	76	68	43	235+	-	-	-	81	-	-	-	-	-	35	-	156	-	-	-	-	-	-
HD-2327, ♀ ?	-	37	30	-	107	42,5	42	81	99	66,6	41,6	41	29	37	159	135	154	-	-	-	-	-
HD-2322, ♀ ?	37?	34,4	29,5	-	108,6	42	-	82	-	-	40	36	28	37	-	122	-	-	-	-	-	-
HD-2006, ♂	60	51	38	-	116	50	-	83	103	68	46	42	25	37	-	-	-	-	-	-	-	-
HD-2027, ♂	61	56	35	210+	127	61	-	83	105	72	50	44	25	38	165	153	183	-	-	-	-	-
HD-2326, ♀ ?	-	31	30	-	108,4	50	-	83	-	-	-	-	-	26	-	119	-	-	-	-	-	-
HD-5130, ♀	-	37	32	-	-	-	-	84	-	-	-	-	-	37	145	137	-	-	-	-	61	42,7
HD-2023, ♂	79	-	36	-	-	61	-	86	115	-	48	42	26	42	-	161	-	-	-	-	-	-
HD-2001, ♂	71	64	44	-	123	-	-	88	-	-	-	-	-	44	171	156	-	-	-	-	62,5	42
HD-5129, ♂	67	56	38	200+	117	-	36	88	-	-	47	46	27	-	173	165	-	139	-	-	-	-
HD-5132, ♂	73	62	42	-	128	-	54	89	110	71	45	43	30	42	173	166	187	135	243	260	65,5	46
HD-5125, ♂	70	60	35	-	123	-	56	91	109	68	45	41	24	35	169	155	177	132	236	256	66,3	-
HD-5127, ♂	58	55	34	285	-	-	-	-	110	72	41	39	23	43	-	145	183	134	232	-	-	44,3
HD-2306, ♂	-	-	-	-	-	-	-	-	107	69	42	43	28	-	-	-	-	-	-	-	-	-
HD, mean, ♂	68	59	38	243	122	59	49	87	108	70	46	43	26	40	170	157	183	135	237	258	-	-
HD 2339 ♀		35	29																			
HD 2340 ♀		34,5	30																			
HD 2377 ♀		39	29,5																			
HD 2375 ♀		36	30																			
<i>Tragopontax</i> sp.																						
Kocherimovo-1, ?	-	31	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 2
Mandibular teeth dimensions of *Tragoportax rugosifrons* and *M. (Pikermicerus) gaudryi* from Hadjidimovo

Measurements No	p2-m3	m3	m1-m3	p2-p4
<i>Tragoportax rugosifrons</i>				
HD 2506	-	27,7	67,9	-
HD 2511	-	-	-	-
HD 2513	-	-	69,2	-
HD 3834	-	-	72,9	-
HD 2521	-	-	77,8	-
HD 3824	-	-	69,7	-
HD 2443	110,2	-	66,4	43,4
HD 2484	-	-	70,7	-
HD 2518	-	-	68	-
HD 2489	-	-	68,2	-
HD 2519	-	27,7	67,9	-
HD 2524	-	-	70,3	-
HD 3896	-	-	69,1	-
HD 2527	110,1	30	72,4	41,8
HD 2480	-	-	71,7	-
HD 2484	-	-	70,5	-
HD 2489	-	-	68,2	-
HD 2440	121	31	73,6	47
HD 2518	-	-	68,6	-
HD 2524	-	-	70,5	-
HD 2497	-	-	-	-
HD 2445	-	27,5	65,4	-
HD 2501	-	-	67,1	-
HD 2468	-	-	-	-
HD 2565	-	-	66,9	-
HD 2493	-	-	68,7	-
HD 2520	-	-	68,7	-
HD	114,5	28,2	67,4	48,2
HD	108,5	27,7	65,3	43,3
<i>M. (Pikermicerus) gaudryi</i>				
HD 3893	-	25,6	-	-
HD	-	23,5	-	-
HD 3839	102	-	59,2	46,2
HD 3825	101	-	57,7	45
HD 3894	-	-	57,4	-
HD 3895	96	-	59,4	40,1
HD 2499	93,5	-	52,8	39,8
HD 3590	-	-	55,4	-
HD 3828	-	-	53,8	-

inct from the base. The anterior keel is not stepped, and continuous. Torsion is always weak, and normal (heteronymous). The basal cross-section in adult males is triangular, with flattened lateral, medial, and posterior faces. There are usually no posterior grooves. The cross-section is more oval in juveniles, because the postero-lateral keel is less marked, and almost rounded in females (see below). The anterior keel is the strongest; it can bear, especially in old males, rugose bony outgrowths, but they do not normally extend onto the frontal, except in rare exceptions. The inter-cornual plateau is rectangular, short antero-posteriorly, but wide, the horn-cores being inserted rather far apart, with their medial borders parallel to each other. The fronto-parietal post-cornual area is de-

pressed in adult males, often rugose, and surrounded by a strong ridge. The occipital surface is rectangular, its dorsal part being broad. From the occipital foramen to the sphenoid, a continuous groove runs along the basioccipital, often with a weak sagittal keel in its middle. The choanae open well behind M3. The basicranial angle is quite open.

Female and sub-adult skulls. There is no large Bovid hornless skull in Hadjidimovo. However, there are at least two skulls that we interpret as females of *T. rugosifrons*, HD 5130 and 5138. Their teeth are well preserved, and they are both fully adults. Their size and morphology is identical to those of the male skulls, and there is no doubt that they belong to the same species. However, their horn-cores are much smaller, with a rounded oval basal cross-section, but with a postero-lateral keel in one of them (HD 5130), without anterior keels or flattening of the surfaces. Several separate horn cores (HD 2337; 2339; 2340, 2375) with suboval cross-section, slightly flattened anterior surface and similar dimensions (some of them with rudiments of postero-lateral keel) must also belong to female individuals (Table 1).

We interpret as sub-adult male skulls a few frontlets and brain cases (HD 3034, 2327, 5137, 5140), with horn-cores smaller than in adult males, but with a triangular basal cross-section and flattened surfaces, with well expressed anterior keel.

Teeth. Premolars and molars are large (Table 2) and rather hypsodont with relatively less accentuated relief of the posttrite walls than in *Miotragocerus (Pikermicerus)* from the same locality. The premolar row is relatively short. P2 is short relatively to P3, with a distally sloping parastyle. Its parastyle-paracone portion is short. P3 has a lingually inflated hypocone. The metaconid of p3-p4 is well developed, especially that of p4 which is T-shaped in occlusal view. The anterior valley of p4 in all observed specimens is open, without the small cuspids that form a kind of cingulum in this region in *M. (Pikermicerus)*.

Metapodials. The metapodials are large (Tables 3, 4), with a cervid-like appearance, being slender and transversally compressed, but are relatively robust by comparison with the metapodials of the smaller Boselaphini from Hadjidimovo, *Miotragocerus*. The widening from diaphysis to epiphysis is smooth, without abrupt change of width. The trochlear keels are neither very prominent nor very sharp.

Table 3

Metacarpal dimensions of Tragoportax rugosifrons from Hadjidimovo

No	Transversal diameter prox.	Antero-posterior diameter prox.	Transversal diameter dist.	Antero-posterior diameter dist.	Diaphysal transv. diameter	Length
38001	40,5	29,1	41,5	30,8	25,1	254
38059	-	-	39,8	30	24,4	-
38061	-	-	42,3	30,3	23,9	-
38010	-	-	42,7	30,7	23,4	-
38039	-	-	44,7	30,9	25	-
38374	41,6	28,7	-	-	24	-
38035	-	-	38,4	30	23,1	-
38022	-	-	41	29,6	24	-
38030	-	-	41,2	30,6	-	-
38034	-	-	41,5	29,5	-	-
38026	-	-	42	28,5	-	-
38071	-	-	42	28,3	-	-
38023	-	-	41,8	30	-	-
38047	-	-	41,2	29	-	-
38041	-	-	40,3	29,8	-	-

Table 4

Metatarsal dimensions of Tragoportax rugosifrons and M. (Pikermicrus) gaudryi from Hadjidimovo

No	Transversal diameter prox.	Antero-posterior diameter prox.	Transversal diameter dist.	Antero-posterior diameter dist.	Diaphysal transv. diameter	Length
<i>Tragoportax rugosifrons</i>						
38002	36	38,7	42,7	30,4	24,5	258
32004	35,7	36	40,8	29,8	24,3	265
38003	39	39,6	43,6	30	24,9	257
38043	-	-	-	28,5	23,5	-
38042	-	-	41,2	29,5	-	-
-	-	-	42,9	28,9	24	-
38060	-	-	-	27,8	24,3	-
38036	-	-	41,2	30	-	-
38076	-	-	43,5	30,1	-	-
38057	-	-	43,2	30,2	-	-
38006	-	-	38,6	28,5	-	-
38055	-	-	39,6	27,8	-	-
38029	-	-	41,2	30	-	-
<i>M. (Pikermicrus) gaudryi</i>						
38370	32	29,7	-	-	19	220?
38007	-	-	31,5	23	17,7?	-
-	-	-	31,7	25,8	-	-
38015	-	-	33,8	24,6	-	-
38053	-	-	33,5	25,3	-	-

Comparison

There are many differences between the two Boselaphines from Hadjidimovo. *Tragoportax rugosifrons* differs from *Miotragocerus* mainly by: the larger size; the broad rectangular intercornual plateau; the presence of a fronto-parietal postcornual depression; the shape of the basioccipital (with longitudinal groove often with a thin sagittal crest); the long horn cores with a relatively small antero-posterior

diameter; their triangular cross-section and normal torsion; the hypsodont teeth; the relative length and morphology of the premolars (fig. 1-6, tab. 1-4).

The *Tragoportax* from Hadjidimovo has similarities with *T. amalthea* (Roth & Wagner) in its main features and general aspect, but also differs clearly by: the greater intercornual distance, the less robust horn cores (fig. 7), lesser development of the rugosities on the anterior horn-core keel, lesser concavity of the

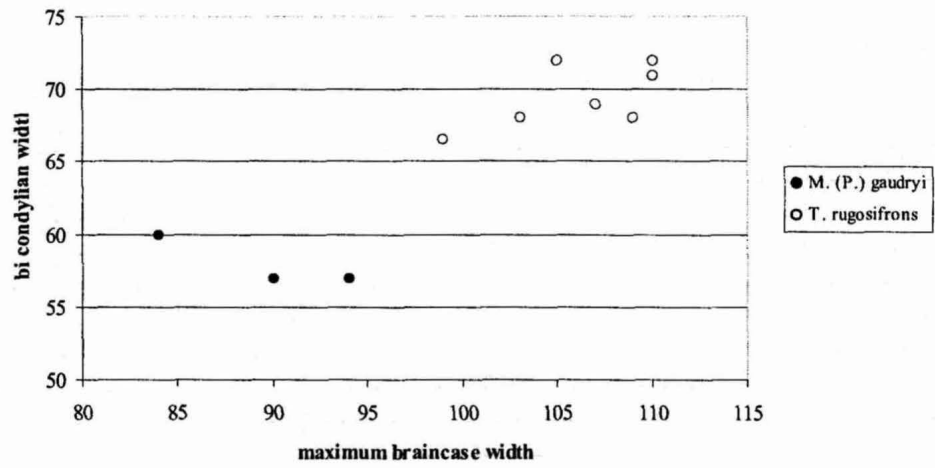


Fig. 3. Neurocranial dimensions in *Tragoportax rugosifrons* and *M. (Pikermicerus) gaudryi* from Hadjidimovo

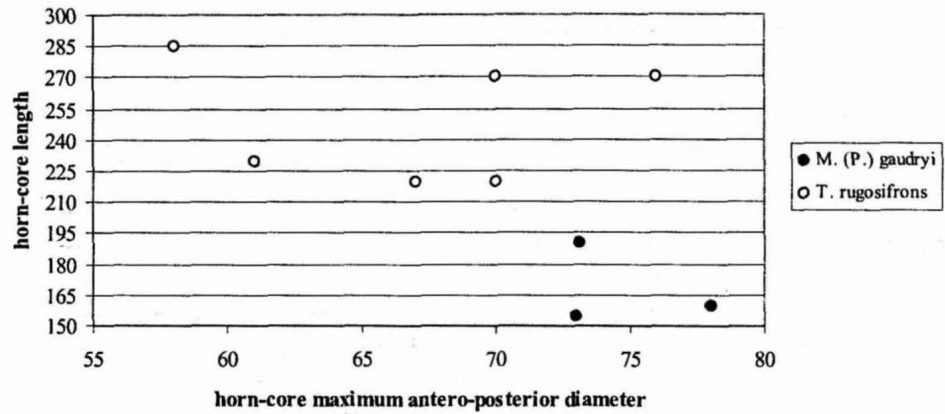


Fig. 4. Horn-core proportions and length in *Tragoportax rugosifrons* and *M. (Pikermicerus) gaudryi* from Hadjidimovo

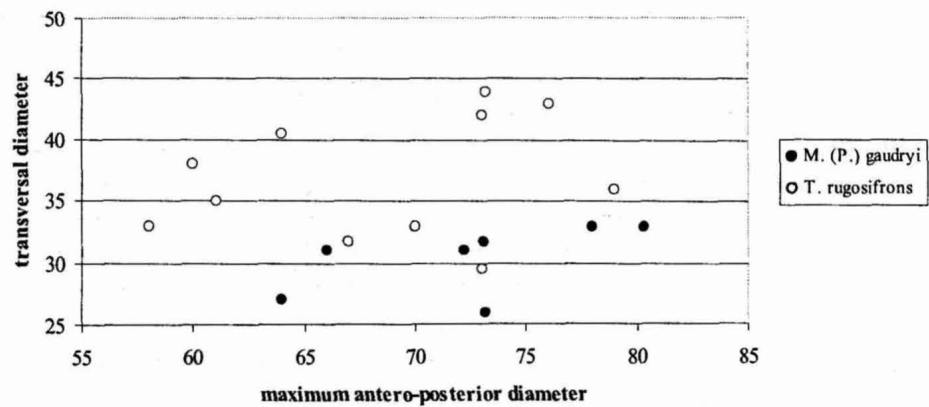


Fig. 5. Basal horn-core diameters in *Tragoportax rugosifrons* and *M. (Pikermicerus) gaudryi* from Hadjidimovo

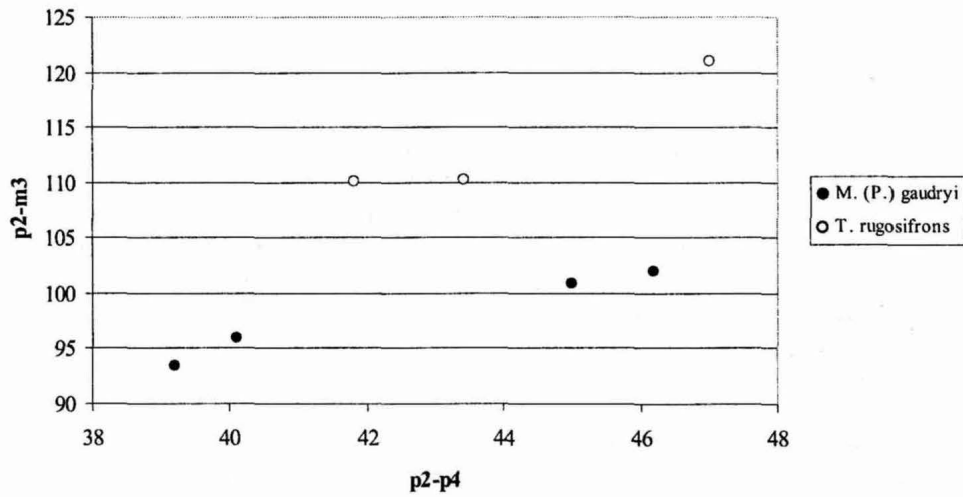


Fig. 6. Mandibular teeth proportions in *Tragoportax rugosifrons* and *M. (Pikermicrus) gaudryi* from Hadjidimovo

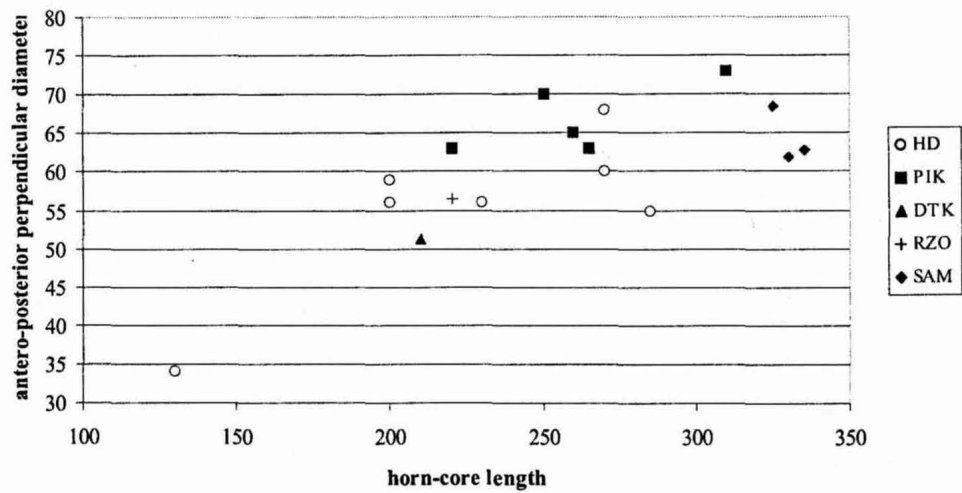


Fig. 7. Horn-core proportions in various *Tragoportax* taxa from various localities (HD — Hadjidimovo, PIK — Pikermi, DTK — Ditiko, RZO — Ravin des Zouaves, SAM — Samos)

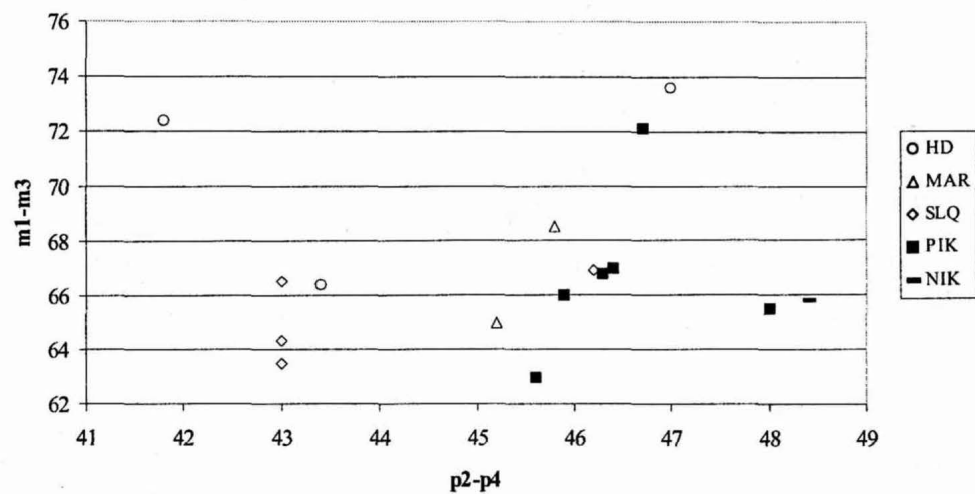


Fig. 8. Teeth proportions and size in *Tragoportax* from various localities. (SLQ — "Thessaloniki", Arambourg's collection; other abbreviations as in fig. 7)

caudal face of the horn core in lateral view, usually weaker torsion of the horn-core anterior keel, as well as by the virtual lack of steps (demarcations) on the keel. The tip of the horn-core is usually not distinct from the general outline of the horn core, or at least less so than in the Pikermi *T. amalthea*, where this tip is demarcated by a marked concavity of the anterior edge in lateral view. The cheek-teeth sample from Hadjidimovo show also some differences, having somewhat shorter premolar row in relation of the molars (fig. 8).

From the specimens described as *T. curvicornis* (Andree, 1926: Pl. XI-6,7 and Solounias, 1981: fig. 30-H) the sample from Hadjidimovo differs by the very slight backward curve of the horn core (reflected in the very slight concavity of the posterior border of the horn core in lateral view).

"*Miotragocerus*" *cyrenaicus* Thomas, from Sahabi (Libya) differs by its curved and divergent horn-cores, but the species is illustrated by a single specimen.

The single specimen from Novaya Emetovka (type of *Mesotragocerus citus* (Korotkevich)) that could be referred to *Tragoportax* shows more twisted and more inclined horn cores than the Hadjidimovo form.

From *T. ("Mirabilocerus") maius* Meladze, of which we have seen good photos kindly provided by A. Vekua and D. Lordkipanidze (see also Meladze, 1967: Pl. XXVII), the sample from Hadjidimovo differs by the larger and more quadrangular inter-cornual surface, the much stronger temporal lines and torus that surrounds the fronto-parietal postcornual depression, lesser inclination of the horn core and the totally different profile of the horn core, with the antero-posterior diameter decreasing gradually, in contrast of the abrupt diminishing in "*Mirabilocerus maius*" above the first half of the horn core, with a change of curve in its second half, thus forming a sinusoidal contour. "*M.*" *maius* is perhaps a junior synonym of *T. ("Mirabilocerus") eldaricus* (Gabashvili, 1956), the type of which is an isolated horn-core.

The horn cores of the specimens from Hadjidimovo differ by the same features from those of *T. acrae* (Gentry, 1974, 1980). The latter differ also by their convex posterior profile (instead of concave in the Hadjidimovo sample).

The *Tragoportax* from Hadjidimovo is much larger than *T. macedoniensis* (Bouvrain, 1988), and has straighter and more robust horns in males, more rectangular inter-cornual surface and more rectangular (wider) occipital surface.

Compared with *T. salmontanus* from Siwaliks (type-species of the genus) the horns of the Hadjidimovo *Tragoportax* are longer, less inclined and not so twisted. There are less rugosities on the fronto-parietal postcornual surface (see Pilgrim 1937, 1939). The horn-cores of the poorly known *T. perimensis* from the Middle Siwaliks (Pilgrim, 1939) are much shorter. Another poorly known species from Siwaliks, *T. islami* (a possible synonym of *T. salmontanus*), has also more rugosities on the fronto-parietal postcornual surface, which extends farther back than in the Hadjidimovo form.

The sample of *Tragoportax* skulls from Hadjidimovo show all the main features of the *Tragoportax rugosifrons* morphology, by comparison with the type specimen and the other Samos specimens figured and described by Schlosser (1904). A small sample of *Tragoportax* skulls from Veles-Karaslari from the Skopje Museum of Natural History (R. of Macedonia) is identical with the skulls from Hadjidimovo and represent the same species. The skulls from Hadjidimovo are similar to the preserved skulls with horn cores of *T. rugosifrons* from Prochoma (Spasov, Geraads, in press).

Genus *Miotragocerus* Stromer, 1928

Synonyms. *Pikermicetus* Kretzoi, 1941; ?*Indotragus* Kretzoi, 1941; *Dystychoceras* Kretzoi, 1941

Type species. *Miotragocerus monacensis* Stromer, 1928

Included sub-genera. *Miotragocerus* (*Miotragocerus*) Stromer, 1928; *Miotragocerus* (*Pikermicetus*) Kretzoi, 1941

Included species. *Miotragocerus* (*Miotragocerus*) *monacensis* Stromer, 1928 — Oberföhring (Austria); ?*Hostalets*, ? *Ballestar* (Spain); approx. MN8/9.

?*Miotragocerus* (*Miotragocerus*) *pannoniae* Kretzoi, 1941 — Sopron (Hungary); Altmannsdorf, Mistelbach, Inzersdorf (Austria); most possibly also Eppelsheim and Höwenegg (Germany). The species has also been listed in several localities from the Vallesian of Spain (Morales et al., 1999), from Kalfa in Moldavia (Pevzner and Vangengeim, 1993) and Grizev in Ukraine (Korotkevich, 1988); Late Middle Miocene-Vallesian.

Miotragocerus (*Pikermicetus*) *gaudryi* (Kretzoi, 1941) with three subspecies (see below). Mostly at: Pikermi, Samos, Halmyropotamos, Nikiti 1 (Greece, Turolian); Hadjidimovo (Bulgaria, Early/Middle Turolian); Veles — Karaslari (R. of Macedonia), Le Coiron (France,

early Turolian); possibly at Belka (Ukraine, Turolian); Piera, Early Turolian and Venta del Moro, Late Turolian (Spain); Mt Lubéron (France, Middle/Late Turolian); ? Maragha (Iran, ?E. Turolian), Nikiti-2 (Greece, early Turolian), Maramena (Greece, Turolian/Ruscinian boundary), Kalimantsi (see below). The presence of the species at Nikiti-1 (Greece, end of Vallesian?) is uncertain.

Possibly also a fourth species: see "*Tragoportax* (*Pikermicerus*) aff. *gaudryi*": Moyá-Solá, 1983 (see Discussion). Spain, France, Late Vallesian.

Stratigraphic and geographic distribution. From MN8/9 to MN13 of Europe and possibly the Middle East (from W.E. Europe to C. Asia).

Revised diagnosis. (The shape of horn-cores and those of associated structures are those of adult males). Size small (about that of fallow deer). The post-cornual area of the skull is not depressed or raised as a low plateau (Fig. 1). Basioccipital without median longitudinal groove, but with a faint sagittal keel (Fig. 2). Strong temporal crests in early forms (*Miotragocerus*), weaker in more recent ones (*Pikermicerus*). Horn-cores short, medio-laterally compressed, with flattened lateral and medial surfaces. Sharp anterior keel, but postero-lateral keel absent or poorly marked, and posterior face not well delimited. The section is therefore sub-elliptic. Anterior rugosities at base of horn-cores usually strong, extending onto the frontal along the keel, which often has several demarcations (steps) along its course. In front view, due to a slight torsion of the horn-cores bases, the keels are often slightly convergent upwards in the basal portion, then diverge towards the tips. The inter-cornual area is much longer than broad, especially narrow anteriorly. The occipital surface is high, much broader basally than at its top. Teeth brachyodont, with strongly folded walls. Compared to *Tragoportax*, well documented forms have a long premolar row, with especially long P2 compared to P3, due to lengthening of its anterior part. Hypocone of P3 poorly expanded lingually. Metaconid of p3-p4 weak, anterior valley with incipient lingual wall (Spassov, Geraads, in press).

Subgenus *Miotragocerus* (*Pikermicerus*) Kretzoi, 1941

Type species. *Pikermicerus gaudryi* Kretzoi, 1941: 342.

Diagnosis. Cranial features as for genus (fig. 2). Weak temporal lines. Compared to *M. (Miotragocerus)*, the horn-cores are relatively

short and massive, with a concave caudal edge. Long premolar row. Metapodials of the size of the fallow deer, without lateral longitudinal groove; abrupt widening from diaphysis to epiphysis.

Stratigraphic and geographic distribution. Whole Turolian; possibly late Vallesian. Europe and perhaps Middle East (see above the distribution of the Genus)

Miotragocerus (Pikermicerus) gaudryi (Kretzoi, 1941)

Pikermicerus gaudryi Kretzoi, 1941

Miotragocerus monacensis: Solounias, 1981-pars

Tragoportax gaudryi: Moyá-Solá, 1983

Holotype. skull illustrated in Gaudry (1865, Pl. 49, fig. 1)

Type-locality. Pikermi

Diagnosis. That of the subgenus

M. (Pikermicerus) gaudryi gaudryi (Kretzoi, 1941)

Tragoportax sp. II: Spassov, 2002

Holotype. skull illustrated in Gaudry (1865, Pl. 49, Fig. 1)

Type-locality. Pikermi

Diagnosis. A subspecies of *M. (P.) gaudryi* with horn cores straighter than in *M. (P.) gaudryi andancensis* from the Early Turolian of France, larger than *M. (P.) gaudryi crusafonti* from the Early Turolian of Spain and France, teeth smaller than those of *M. (P.) gaudryi leberonensis* from the Late Turolian of the same area.

Description. The Hadjidimovo material (pl. 1-3). (Coll. of the Assenovgrad paleontological branch of the N.M.N.H. — Sofia): complete and partial skulls (HD 2007, 2010, 2015-2016, 2019, 2039, 2325, 3704, 5519); several identified mandibles and metapodials (see inventory numbers in tables 2-4).

Skull. It is larger than those of *M. monacensis*, but smaller than those of *Tragoportax* from Hadjidimovo (Fig. 3). The ante-orbital fossa is small and shallow. The anterior border of orbit does not reach the level of M3 (one specimen observed). The frontals, and probably also the pedicles, are hollowed. The horn-cores are short, slightly inclined backwards, and very compressed transversally. They look stout and massive in lateral view: their antero-posterior diameter is greater than in other species of the genus (Fig. 9) and this dimension is greater relatively to the length of the horn-core than in *Tragoportax* from the same locality. Horn-cores are only slightly divergent. In lat-

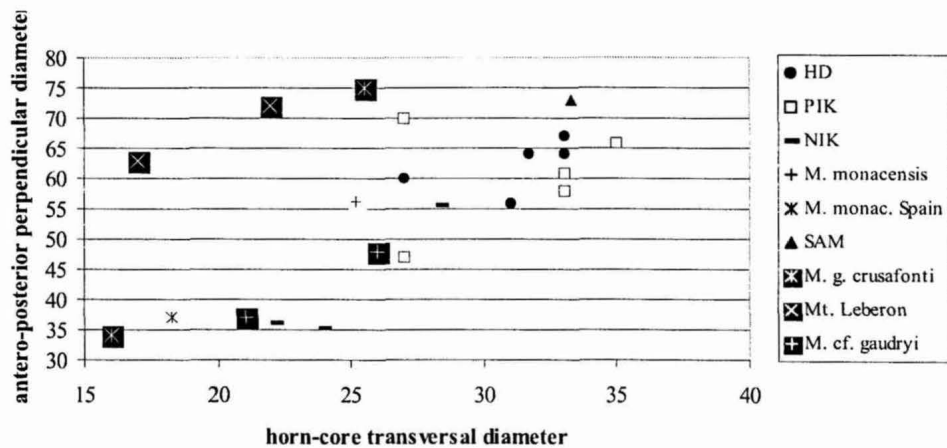


Fig. 9. Horn-cores' proportions and dimensions in various taxa of *Miotragocerus*

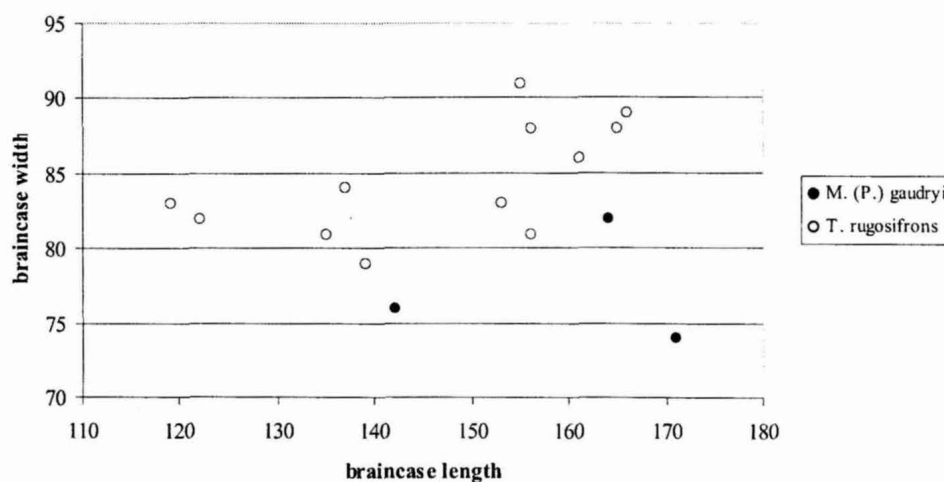


Fig. 10. Neurocranial proportions of *Tragoportax* and *M. (Pikermicetus)* from Hadjidimovo. Length of brain-case from front of horn-cores to top of occipital

eral view the anterior contour is strongly curved, but the posterior one is only slightly curved backwards. The demarcations are well represented along the anterior keel. The keel torsion is weak (in some specimens almost absent) and homonymous: in front view the keels are often slightly convergent upwards at base, then diverge towards the tips. The basal cross-section in adult specimens of both sexes is subtriangular, less triangular than in *Tragoportax* from the same locality, with a rounded posterior face, without longitudinal groove, nor postero-lateral keel (only very weakly distinct in a few specimens). The anterior keel between the demarcations is well marked. The rugosities on the anterior keel are more common than in *Tragoportax* from the same locality and in most cases they extend onto the frontal. The inter-cornual plateau is usually long, narrow and triangular. The neu-

rocranium is long compared to *Tragoportax* (Fig. 10). The fronto-parietal post-cornual area is not depressed, and shows rugosities in one specimen. The occipital surface is subtriangular, its dorsal part being relatively narrow with bulging top. The basioccipital has no median longitudinal groove, but bears a faint sagittal keel (Fig. 2). The basicranial angle (one specimen observed) is quite well marked (but less than in *Palaeoreas*).

Teeth. Premolars and molars are relatively small and brachyodont with pronounced relief of the posttrite walls. The premolar row is relatively long. P2 is long relatively to P3, due to lengthening of its anterior part. Its parastyle is straight, not curved distally. P3 has a narrow parastyle, not protruding labially. The metaconid of p3-p4 is weak, the anterior valley has an incipient lingual wall. Length M1-M3 (53 mm) falls within the size range of *Pikermi* (48.6

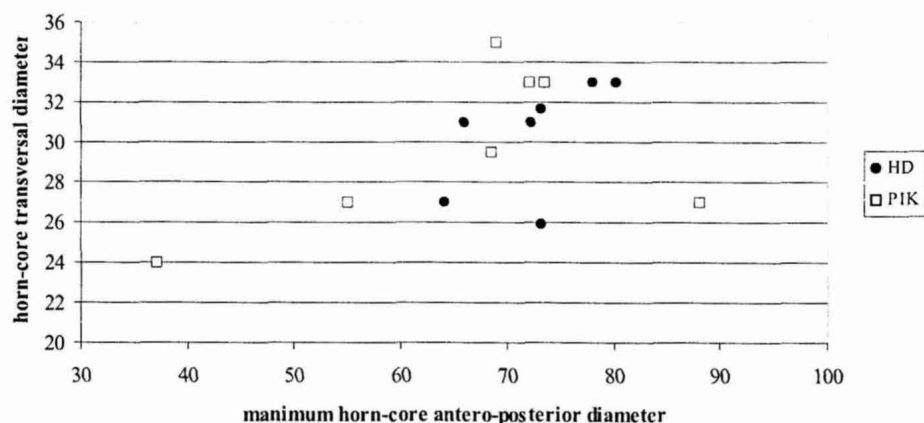


Fig. 11. Comparison of the horn-cores' proportions and dimensions of *M. (Pikermicerus)* from Hadjidimovo and Pikermi

— 53.9 mm), it is slightly smaller than at Nikiti (55.1 mm), but much larger than at Piera (45 mm).

Female skull. HD 55611 (Pl. 3.1, Table 1). The skull is of a subadult animal (dP3-dP4 present, frontal suture visible). It is well preserved, (except horn cores) incl. the rostral bones, but it is crushed laterally (incl. the frontals anteriorly to the horn core bases). The mandible, which is still attached, is also well preserved except the angular processes. The basioccipital surface is damaged. The skull is smaller than a *Tragoportax* skull (total length about 305 mm) and the fronto-parietal postcornual area is not depressed. The angle between the splanchnocranium and the neurocranium is large (about 150°) — a condition typical for the Boselaphini. The P2 (length about 15 mm) and the premolar row are very long. The P2 parastyle is high and not curved backward. The labial relief of the upper teeth is strong, the m1-m2 have strong ectostylids. All these features as well as the tooth row length are the same as in *M. (P.) gaudryi*. The anterior border of the orbits are above M2. The praemaxillae are slender, not at all broadened anteriorly. The upper profile of the splanchnocranium is convex but this is possibly somewhat exaggerated because of the transverse crushing. The mandibular corpus is strongly convex ventrally. The frontals under the horn cores are pneumatized. The preserved horn core bases are small. The horn core shape in spite of some deformation suggest a nearly oval cross-section, wider and more rounded posteriorly and more angular anteriorly.

Metapodials. The metapodials, of the size of the fallow deer, are relatively small compared with *Tragoportax* from the same locality (see tab. 4) and slender. The widening from diaphysis to epiphysis is clearly bovid-like with

abrupt change of width. The trochlear keels are prominent and sharp. The lateral longitudinal **groove** specific to the metapodials of *?M. pannoniae* is absent here.

Comparisons

Comparison with the ante-Turolian forms. The horn core of the type of *M. (Miotragocerus) monacensis* from the Astaracian/Vallesian (Stromer, 1928) is smaller than the horn cores of the sample from Hadjidimovo, and the temporal lines are stronger (Fig. 9). The comparison with *M. pannoniae* is difficult because the type-material is scarce, and moreover belongs to a subadult individual, and because referral of material from other localities is uncertain. The differences of the *M. (Pikermicerus) gaudryi* sample from Hadjidimovo with the graceful horn-cores of the type of *M. (P.) monacensis* are clear. From the horn-core from Inzersdorf supposed to represent an adult male of this species (Thenius, 1948) it differs mainly by the less straight posterior edge of the horn-core and probably by the smaller number of demarcations. From the Höwenegg sample described as *M. pannoniae* by Romaggi (1987) the Hadjidimovo skull material differs also by the curved (no straight) surface of the posterior horn core wall as well as by the shorter horn cores. The metatarsals of the *M. (Pikermicerus)* from Hadjidimovo lack the proximal lateral (and in some cases lateral and medial — at Höwenegg) longitudinal depression described for some Vallesian bones referred to *M. pannoniae* (see below). The comparison with the material of *M. (Pikermicerus)* “cf. *gaudryi*” from the Late Vallesian of La Croix Rousse in France (data in Moyá-Solá, 1983: 166) shows that both the metapodials and

PLATE I

1. *M.(Pikermicerus) gaudryi*, lower tooth-row, no N°. 2. *Tragoportax rugosifrons*, lower tooth-row, HD-2443. 3. *Tragoportax rugosifrons*, upper tooth-row, HD-3664. 4. *M.(Pikermicerus) gaudryi*, upper tooth-row (P2 missing), HD-3672. 5. *Tragoportax rugosifrons*, skull HD-2040, lateral view. 6. Same specimen, front view. 7. *Tragoportax rugosifrons*, skull, HD-5127, lateral view. 8. *M.(Pikermicerus) gaudryi*, frontlet HD-2010, front view. 9. *M.(Pikermicerus) gaudryi*, braincase with horn-cores, HD-5519, lateral view. Scale = 5 cm for Figs. 1-4, 15 cm for Figs. 5-6, 8-9, 20 cm for Fig. 7.

PLATE II

1. *Tragoportax rugosifrons*, occipital, HD-5132. 2. *M.(Pikermicerus) gaudryi*, occipital, HD-2039. 3. *Tragoportax rugosifrons*, female skull, HD-5138. 4. *Tragoportax* sp., female skull from Kocherinovo (FM 2024). 5. *M.(Pikermicerus) gaudryi*, basi-occipital, HD-2007 (stereo). 6. *Tragoportax rugosifrons*, occipital, no N° (stereo). Scale = 10 cm for Figs. 1, 2, 4-6; 15 cm for Fig. 3.

PLATE III

1. *M. (Pikermicerus) gaudryi*, female subadult skull from Hadjidimovo (HD 55611), lateral view. 2. Same specimen, dorsal view of neurocranium. 3. *Tragoportax* cf. *amalthea*, frontlet from Kalimantsi, K-759, antero-dorsal view. 4. *T. ? rugosifrons*, dorsal view of skull from Kalimantsi, K 55603. 5. *Tragoportax* cf. *amalthea*, incomplete skull from Kalimantsi, K-55601. Scale = 6 cm for Fig. 2, 10 cm for all others.

horn cores of the Hadjidimovo material are clearly larger.

Comparison with the Turolian samples. *M. gaudryi* — The differences between the three accepted forms of *M. gaudryi* are also mostly metrical. So, *M. (P.) gaudryi* (= *Tragoportax gaudryi* sensu Moyá-Solá, 1983 and Bouvrain, 1988) generally increase in size from Early to Late Turolian (Moyá-Solá, 1983; Bouvrain, 1988). The metrical data of the metapodials (tab. 4) as well as those of the mandibular/maxillar teeth and horn-cores (Tab. 2, Fig. 9, 11) show that the Hadjidimovo sample has larger body and teeth than *M. gaudryi crusafonti* from Piera (MN11, Spain; Moyá-Solá, 1983: 137-138). This locality has yielded a large number of Boselaphine crania. However, some details of Moyá-Solá's description and figures suggest that the sample might not be homogeneous, and perhaps include some *Tragoportax*. On the other hand, the lower teeth from Hadjidimovo (Tab. 2) are smaller than the latest as well as largest known form, *M. g. leberonensis* from Mt Lubéron (MN 12–13, France) and Venta del Moro (MN13 of Spain) (data in Moyá-Solá, 1983: 161). The horn cores from Hadjidimovo differ from those from Le Coiron, France, described by Romaggi (1987) as *Graecoryx andancensis* by the lack of a strong curve backward, especially in females. The Hadjidimovo material is very close in skull and horn-core morphology as well as in dimensions to the material from the Middle Turolian of the type-locality, Pikermi (Tab. 1, Fig. 15, 17). The Greek material from Samos (Solounias 1981), as well as two undescribed frontlets from Veles-Karaslari could be included in the same form, *M. (P.) gaudryi gaudryi*.

Skull No. 55611 deserves special attention. The combination of features such as face/neurocranium angle, tooth dimensions, proportions and morphology as well as the post-cornual morphology fit the Boselaphini, especially *Miotragocerus (Pikermicerus) gaudryi*. The facial bones of the genus and the species are very poorly known, but the shape of the mandible and of the splanchnocranial contour resemble the skulls determined by Romaggi (1987) as *Miotragocerus pannoniae* and *Graecoryx andancensis* (i.e. *M. (P.) gaudryi andancensis* in our meaning). The small horn core cross-section could correspond to a female specimen. The dimensions are somewhat smaller than in the female of *Graecoryx andancensis* (see Romaggi, 1987) (i.e. of *M. (P.) gaudryi andancensis*) but it could be explained by the subadult age of the Hadjidimovo specimen. These dimensions (31-32 × 21) are not very far from the horn cores dimensions (35.3-38.7 × 22.2-24) of the skulls noted as females from the Nikiti-1 *M. (Pikermicerus)* (see Kostopoulos & Koufos (1996). The presence of only one female skull of *M. (Pikermicerus)* in the Hadjidimovo taphocoenosis is not so astonishing having in mind the difference in the thickness of the female and male bones of the skull dome. We have also found only one female skull in a very large sample of male skulls in the *Palaeoreas* collection from Hadjidimovo as well (Geraads et al., 2003).

Discussion

The Hadjidimovo material and the taxonomy of "Tragoportax" and the Late Miocene Boselaphini. Today, most authors agree that there are

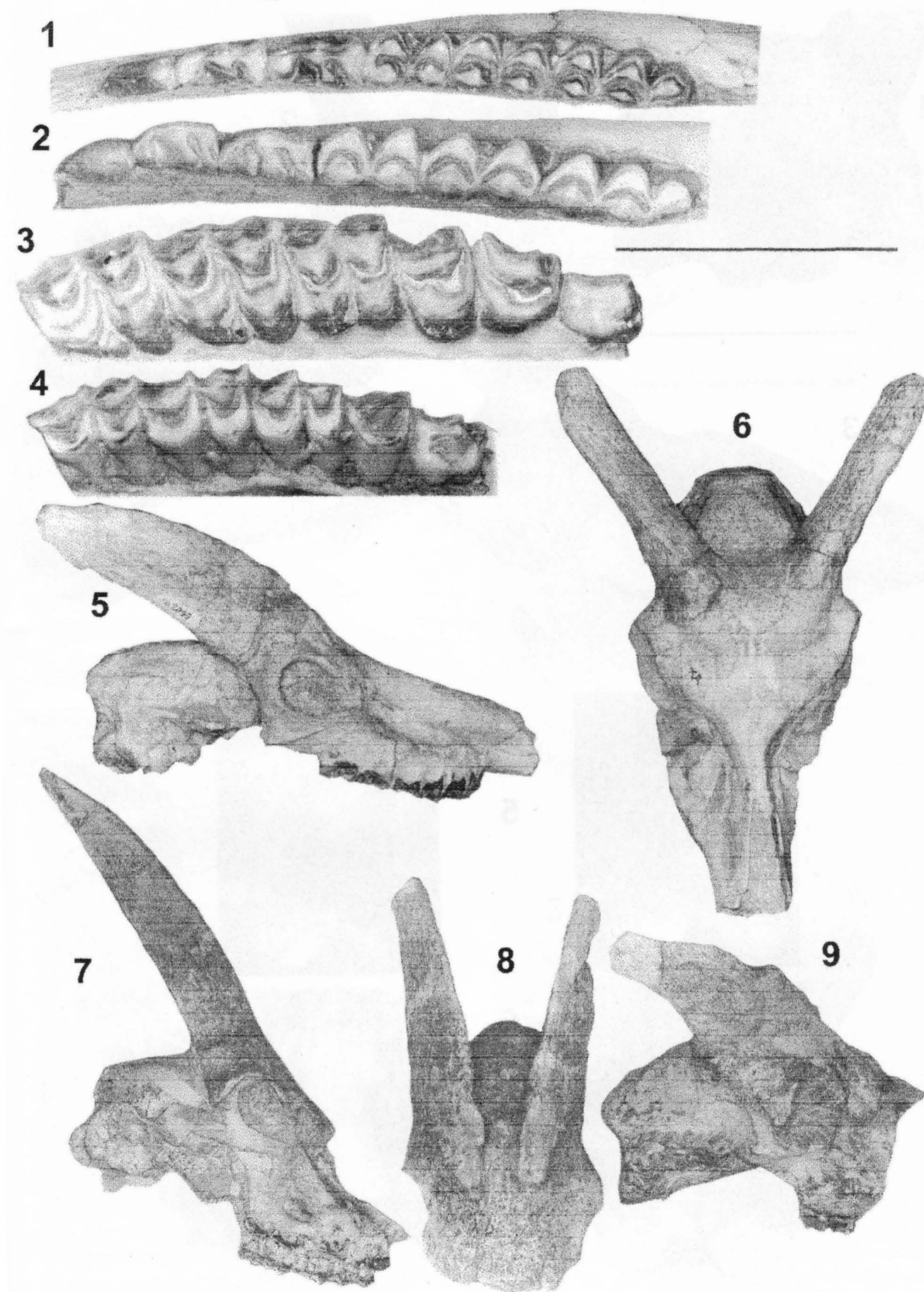


PLATE II

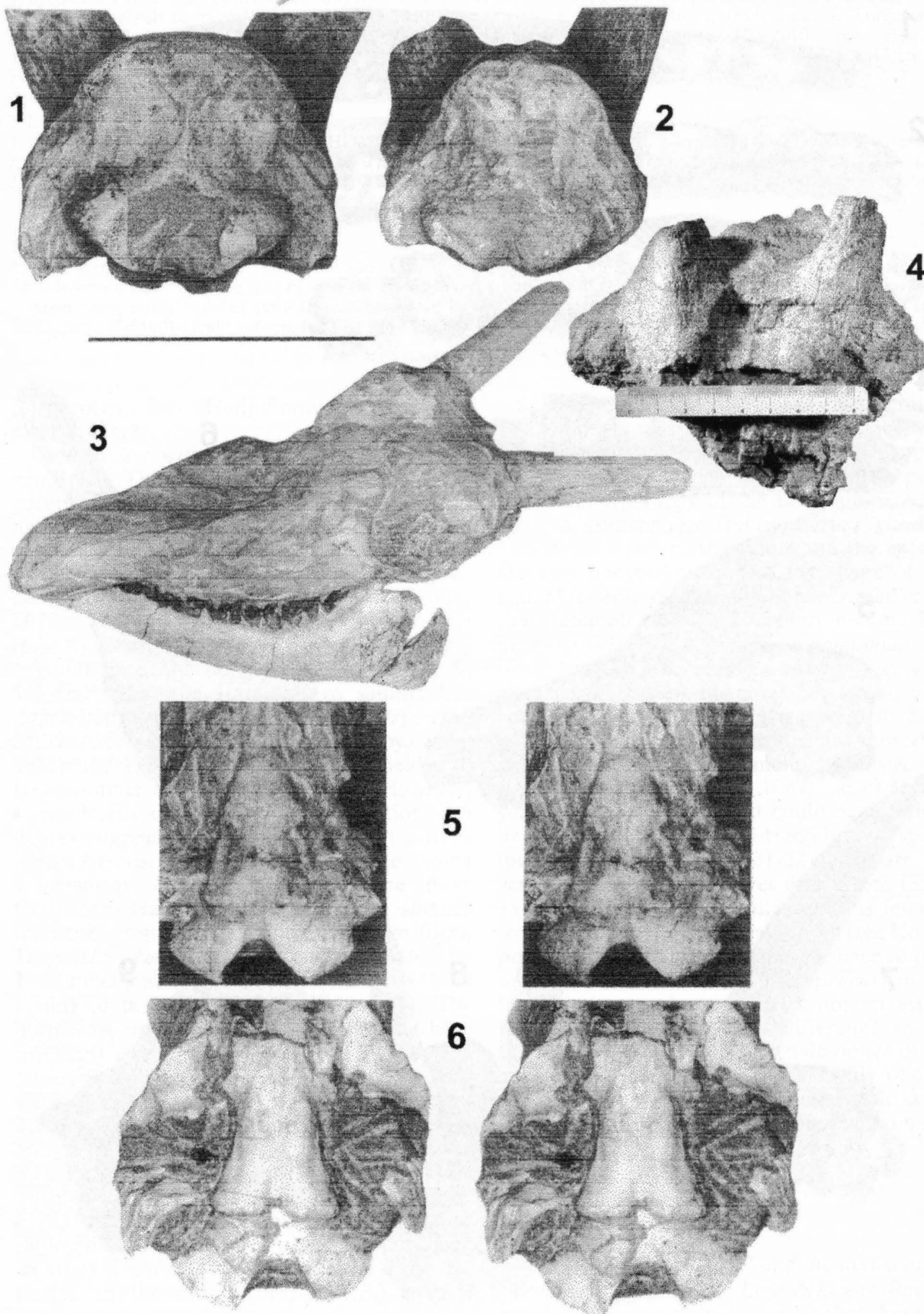
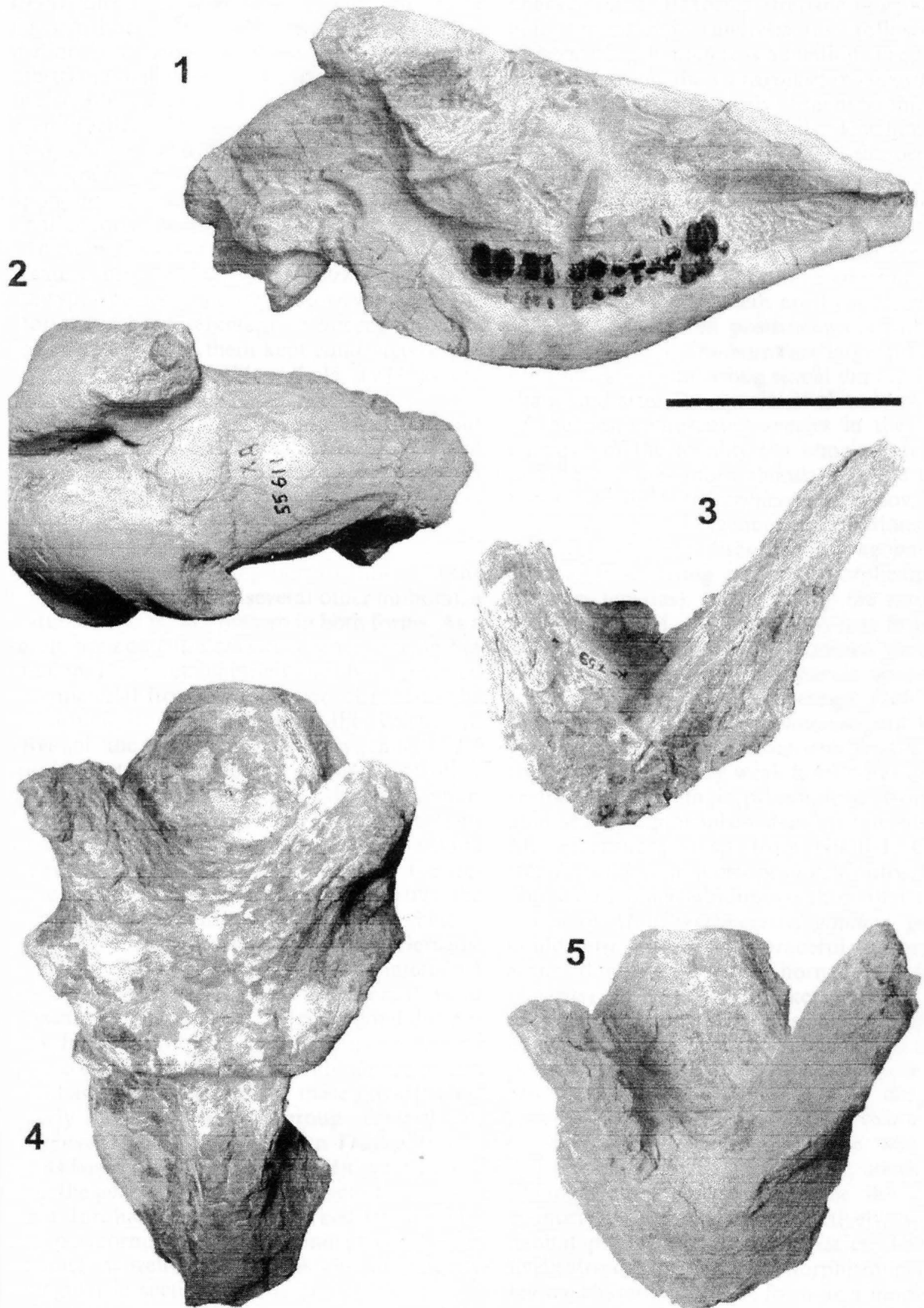


PLATE III



two clearly distinct forms at Pikermi (Solounias, 1981; Moyá-Solá, 1983; Bouvrain, 1994), one is smaller with shorter and more massive horn-cores, with an elliptical cross-section, the other is larger with horn-cores sub-triangular in section (Moyá-Solá, 1983). The smaller species — *T. gaudryi* Kretzoi — has been recognized in other European sites (Moyá-Solá, 1983; Bouvrain, 1988; Kostopoulos, Koufos, 1996). Kretzoi (1941) insisted upon the very characteristic morphology of the smaller form, based upon a Pikermi skull described by Gaudry (1865), which led Kretzoi to create a new genus for it, *Pikermicerus*, with the type-species *P. gaudryi*. However, later authors have been reluctant to accept this new genus, and most of them kept *gaudryi* as a species of *Tragoportax* (Moyá-Solá, 1983; Bouvrain, 1988, 1994).

Solounias (1981) had divided, correctly in our opinion, the “*Tragoportax*” complex into two distinct genera: *Miotragocerus* Stromer (where he places the type of “*Pikermicerus*” *gaudryi* Kretzoi) and *Tragoportax* Pilgrim. However, he used an unsuitable criterion for the separation of the two genera, the “demarcation” of the horn core (“steps” after several other authors), a feature that is in fact present in both forms. As a result, the contents of his two genera are, in our opinion, incorrect. The rich and well-preserved new material from Hadjidimovo offered us the opportunity to confirm most of the typical features of the small form usually called “*T.*” *gaudryi* but also to identify a number of other morphological features setting this form apart from *Tragoportax* s.str. Some of them are located in the most conservative part of the skull, the neurocranium, and this supports the generic distinction proposed by Kretzoi. Thus, the forms usually included in *Tragoportax* belong in fact to two distinct genera (Spassov, Geraads, in press). As noted above, the type material of the type-species of *M. (Miotragocerus)* is at present too incomplete to permit a good distinction from *M. (Pikermicerus)*. Both subgenera have compressed horn-cores with a more or less oval basal cross-section. All these bovids stand clearly apart from the group centred on *Tragoportax amalthea*, i.e. from *Tragoportax*, a genus based on *T. salmantinus*. In our conception, the genus *Tragoportax* includes the usually large Turolian forms with marked fronto-parietal postcornual depression and grooved basioccipital as well as with horns long and clearly triangular in section (Fig. 1, 2).

Morphofunctional characteristics, sexual dimorphism and ecology of Miotragocerus (Piker-

micerus) gaudryi and Tragoportax rugosifrons from the Hadjidimovo taphocoenosis. We could characterize both forms after the morphologic and taphonomic analysis as follows: *M. (Pikermicerus) gaudryi* is a medium sized bovid (clearly smaller than *Tragoportax rugosifrons*). The teeth are relatively brachyodont, with strongly folded posttrite walls. The horns are relatively short with clear sexual dimorphism. The species is clearly less abundant in the taphocoenosis of the locality than *Tragoportax rugosifrons*.

Tragoportax rugosifrons is a large bovid (its weight reaches 200 kg, as estimated from its metapodials). Its cheek-teeth are hypsodont for a Miocene bovid, with posttrite walls with relatively weak relief. The horns are large, present in both sexes but with strong sexual dimorphism in shape and size. The species is abundant — one of the best represented species in the taphocoenosis of the locality (its remains are more than three times more abundant in the taphocoenosis than *M. (Pikermicerus)* Spassov, 2002).

According to the general conceptions existing till the recent discoveries, *Tragoportax* s. str. has very strong sexual dimorphism (with hornless females), stronger than the sexual dimorphism in *M. (Pikermicerus)* (see Bouvrain, 1994). Our data from Hadjidimovo show that at least in one of the *Tragoportax* species the females possess horns. Romaggi (1987) has demonstrated that in *M. pannoniae* and *M. (P.) gaudryi andancensis* (= *Graecoryx andancensis*) the females have very weak horn cores and the sexual dimorphism is pronounced. Considerable sexual dimorphism demonstrate also the *M. (Pikermicerus)* sp. from Nikiti-1, Greece (see *T. gaudryi* in: Kostopoulos, Koufos, 1996). Our data from Hadjidimovo show that the females of *M. (Pikermicerus) gaudryi gaudryi* could also have very graceful horns. The sexual dimorphism in the horns of *M. (Pikermicerus)* is probably weaker than in some *Tragoportax* species (hornless female individuals are known at least from Samos) but clearly pronounced, and more expressed than in modern highly gregarious animal of the open spaces (see Janis, 1986). This particularity of *M. (Pikermicerus)* in combination with relatively small (medium) body size, tooth morphology and relative rarity in the taphocoenosis could indicate relatively wooded habitat preferences for this species. The relatively strong horn sexual dimorphism in *Tragoportax* characterizes this form as a moderately gregarious (Geist, 1974) and partially territorial animal with developed visual display sig-

nals, probable one-male dominance in the herds, and possible herds of male individuals. The combination of all above mentioned features of this bovid indicates, following the Jarman principle (Janis, 1986) that *Tragoportax* ecological niche was related to more open spaces than the *M. (Pikermicerus)* habitats in probable mosaic landscapes. In this respect, it is comparable to modern *Hippotragus*.

The Boselaphini from Kocherinovo-1

The site of Kocherinovo-1

The site is discovered by I. Nikolov in the early 70s in the green clays of Gradishte region between the villages of Kocherinovo and Mursalevo (SW Bulgaria). The very recent investigations consider the sites Kocherinovo 1 and 2 as localities of the newly established Gradishte lithocomplex (Gradishte bench- mark group of strata) (Tzankov et al., in press). The proposed age of both localities is early Turolian (Spasov et al., 2004; Спасов et al., in press).

Tragoportax sp.

Material, description and comparison. A skull fragment (FM 2024 N.M.N.H.- Sofia) with part of the postcornual fronto-parietal surface, part of the left maxillary and the bases of horn-cores as well as fragments of attached left and right mandible, probably from the same adult specimen (Pl. 2.4). The preserved part of the postcornual surface indicate similarities with the characteristic morphology of *Tragoportax* (see the diagnosis of the genus). The dimensions of the horn core cross-section at the base are close to the female specimens of *T. rugosifrons* from Hadjidimovo (Table 4a). As we have noted, the females of this species, possibly in contrast to some other *Tragoportax* species (see discussion in Spasov and Geraads, in press) were not hornless. However, the dimensions of the preserved teeth (L m3 = 23-24 mm) are clearly smaller than the dimensions of the males of *T. rugosifrons*.

The Boselaphini from Kalimantsi

The site of Kalimantsi

The fossiliferous site of the Kalimantsi village is the richest one in the basin of Middle Struma river and the best known of the Bulgarian Up-

per Miocene localities of vertebrate fauna. In fact under the name Kalimantsi refers to a large area (~ 6 km²) of Upper Miocene fossiliferous deposits with more than 10 known points (localities) of fossil mammalian fauna. This fauna is best known by the classic monograph of Bakalov and Nikolov (Бакалов, Николов, 1962). The biochronology of the fauna from the localities was based until recently mostly on the latest papers of Nikolov (Nikolov, 1985) related to the analyses of the data known till the 80s from the "classic" localities of the Kalimantsi area as: Kalimantsi 1 (the old excavations at the river bank), Kalimantsi 2 (Peshternik), Kalimantsi 3 (Prehvarloka) and Kalimantsi 4 (Beliovski pat) (Цанков et al., in press). The excavations in the late 70s and the 80s organized by one of us (D.K.) led to the discovery of a rich fossil material as well as new Kalimantsi (KAL) localities as KAL-Pehtsata, KAL-Bukovets, KAL-Bardovski pat, KAL-point "Atso" etc.

An opinion prevailed until recently (Kojumdjieva et al., 1982) that the lower fossiliferous level in the Kalimantsi area (KAL-1) is of Vallesian age. The very recent revision of the biostratigraphy of the Kalimantsi localities demonstrate that all Kalimantsi sites (localized in more than 100 m thick deposits) are of Turolian age and that there is no evidence of any Vallesian fauna in the Kalimantsi area. KAL-1, which seems to belong to the newly established Gradishte genetic lithocomplex, is more likely to yield a fauna of early Turolian age, while other Kalimantsi faunas (referred to the Strumyani lithocomplex) are probably of Middle Turolian age. (Цанков et al., in press; Spasov et al., in press; Spasov et al., 2004).

Tragoportax Pilgrim, 1937

Bakalov and Nikolov (1962) (Бакалов, Николов, 1962) have described from Kalimantsi and Gorna Sushitsa (without mentioning which part of the material belongs to G. Sushitsa site) some maxillary and mandibular fragments with teeth and postcranial remains (partially stored in the Univ. of Sofia) as *Tragoportax amalthea*. Nikolov (1985) notes the presence of the species at Kalimantsi-Peshternik without description of the material. At least part of this material could indeed belong to *Tragoportax* (sensu our taxonomic concept — Spasov, Geraads, in press), from the tooth dimensions and premolar morphology (see Бакалов, Николов, 1962, Pl. XXXIV-1 and XXXV-1; and p. 80, specimens 1-2, 4). On the other hand, it will be hardly

possible, because of the scarcity of the material, to determine the species with certainty.

New Kalimantsi material in the Assenovgrad Paleontological Museum. Several skulls and skull fragments in poor condition of fossilization: K 759, 55601, 55602, 55604, 55605, 55606, 55610, 55603 (Pl. 3; Table 1), maxillary fragments with teeth: K 3725, 3727, 3728, 3731, 3742, 3768 (Table 1): All the material is most probably from the MN12 zone of the Kalimantsi fossiliferous area; exact localities unknown.

Description and discussion. All skulls display *Tragoportax* features such as triangular horn core shape, depressed fronto-parietal postcornual region, and (when preserved) basioccipital with longitudinal groove (fig. 1-2) and almost rectangular intercornual frontal surface. Compared to *T. rugosifrons* and *T. amalthea* almost all skulls have (if we could judge after the poorly preserved material): generally large horn core cross-section; relatively small intercornual frontal surface; in most of the skulls well expressed rugosities of the anterior horn core crest, reaching in some cases the frontal bone in front of the horns (Pl. 3.3, 3.5). These characters are closer to the *T. amalthea* conditions and we could refer all these material to *Tragoportax* cf. *amalthea*. One of the skulls (No. K 55603) (Pl. 3.4) has relatively large intercornual distance at the base of the horns and demonstrate more affinity with *T. rugosifrons*. This similarity might be related to individual variations. On the other hand, we need to note again that the exact localities of the noted Kalimantsi *Tragoportax* material is not known. Most probably the skulls were found in different local fossiliferous points. The last mentioned skull (that we refer to *T. ?rugosifrons*) could originate from a separate (lower?) local site.

Miotragocerus (Pikermicrus)
gaudryi cf. *M. (P.)*
gaudryi gaudryi Kretzoi, 1941

Material, description and comparison. (coll. of the Assenovgrad Paleontological Museum). Maxillaries with teeth: K 3730, 3745, 3748, 3753, 3757, 3761, 3772; two frontlets (K 55608, K 55609) belong probably to juv.-subad. individuals of this species.

The tooth features and measurements (see Table 1) correspond to the noted description of *M. gaudryi* from Hadjidimovo (see above) morphology and dimensions.

General conclusions

At present, at least three Bulgarian Upper Miocene localities document the genus *Tragoportax*: Hadjidimovo-1 (MN11/12 boundary) — *T. rugosifrons*, Kocherinovo-1 (MN11) — *Tragoportax* sp. and Kalimantsi fossiliferous area (the Kalimantsi sites from the MN12 zone) — most possibly *T. amalthea*. In the latter sites, it coexists with *M. (Pikermicrus) gaudryi*. The presence of *T. rugosifrons* is probable in one of the MN12 zone Kalimantsi localities.

Our conclusions on the ecology and distribution of *Tragoportax rugosifrons* and *M. (Pikermicrus) gaudryi* confirm those of Bouvrain (1994) that *T. rugosifrons* is mostly a grazer (or perhaps a mixed feeder; Solounias et al., 1999), and in any case a species of more open environment than *M. (P.) gaudryi* which inhabits more woody biotopes. However, the occurrence of both species at Hadjidimovo (and possibly in Kalimantsi) demonstrate, in contrast to previous opinions, that *Tragoportax* and *M. (Pikermicrus)* can co-exist in East Europe, where both genera were present. It is likely, therefore, that they co-existed also in Pikermi, as they did in Halmyropotamos, Veles — Karaslari, Maraga and probably Nikiti — 2 and Maramena (Spasov & Geraads, in press). After Solounias et al. (1999) the Turolian Pikermian biome of the "Greco-Iranian" province were dominated by relatively homogenous woodlands. According to another recently expressed opinion, the Pikermian biome and especially the landscape from Hadjidimovo was rather represented by forest-savanna-like (in terms of physiognomy of the landscape) biotopes and not by hardly penetrable dense thickets and woods (Spasov, 2002). The above mentioned ethological interpretations of the morphological characteristics of *M. (P.) gaudryi* and *T. rugosifrons* support mostly the second opinion. If the occurrence of the two discussed bovids in one and the same stratigraphic level is not proven in Pikermi (Bouvrain, 1994) it is not the case in Hadjidimovo, where they are both elements of the same taphocoenosis. They co-existed in the Hadjidimovo zoocoenosis occupying different niches: more woody habitats for *M. (P.) gaudryi* and more open habitats for *T. rugosifrons* in a mosaic landscape. In both forms females possess horns, but demonstrate clear sexual dimorphism.

One of the latest representatives of *Tragoportax*, *T. macedoniensis*, could be a relic form of the wooded habitats, or probably documents

a neotenic reversal. Living in woody local conditions (Bonis et al., 1992), it reverted to some adaptations to forest environment: relative brachyodonty and long premolar row, as well as relatively small body and horn size (see Bouvrain, 1988).

References

- Andree, J. 1926. Neue Cavicornier aus dem Pliozän von Samos. — *Palaeontographica*, 67, 135-175.
- Barry, J., Morgan, M., Flynn, L., Pilbeam, D., Behrensmeyer, A., Mahmood Raza, S., Khan, I. A., Badgley, C., Hiks, J., Kelley, J. 2002. *Faunal and Environmental Change in the Late Miocene Siwaliks of Northern Pakistan*. — *Paleobiol. Mem.*, Memoir 3, supplement to 28, 2: 71 p.
- Bouvrain, G. 1988. Les *Tragoportax* (Bovidae, Mammalia) des gisements du Miocène Supérieur de Dittiko (Macédoine, Grèce). — *Annales de Paléontologie*, 74, 1, 43-63.
- Bouvrain, G. 1994. Un bovidé du Turolien Inférieur d'Europe Orientale: *Tragoportax rigosifrons*. — *Annales de Paléontologie*, 80, 1: 61-87.
- Bonis, L. de, Bouvrain, G., Geraads, D., Koufos, G. 1992. Diversity and paleoecology of Greek late Miocene mammalian faunas. — *Palaeogeography, Palaeoclimatology, Palaecology*, 91, 99-121.
- Gabashvili, E. 1956. The Miocene antelopes from the collections of the State Museum of Georgia. — *Journal of the State Museum of Georgia "Acad. Djanashia"*, 17a. (in Russian; not seen).
- Gaudry, A. 1861. Résultats des fouilles exécutées en Grèce sous les auspices de l'Académie. — *C. R. Acad. Sc. Paris*, 52, 297-300.
- Gaudry, A. 1865. *Animaux fossiles et géologie de l'Attique*. — F. Savi édit., Paris, 475 p.
- Geist, V. 1974. On the Relationship of Social Evolution and Ecology in Ungulates. — *American Zoologist*, 14, 205-280.
- Gentry, A. 1974. A new genus and species of Pliocene Boselaphinae (Bovidae, Mammalia) from South Africa. — *Annals of the South African Museum, Cape Town*, 65, 5, 145-188.
- Gentry, A. 1979. Fossil Bovidae (Mammalia) from Langewaanweg, South Africa. — *Annals of the South African Museum, Cape Town*, 79, 8, 213-337.
- Geraads, D., Spassov, N., Kovachev, D. 2001. New Chalicotheriidae (Perissodactyla, Mammalia) from the Late Miocene of Bulgaria. — *Journal of Vertebrate Paleontology*, 21, 3, 296-606.
- Geraads, D., Spassov, N., Kovachev, D. 2003 *Palaeoreas lindermayeri* (Wagner, 1848) from the upper Miocene of Bulgaria, and a revision of the species. — *Geodiversitas, Paris*, 25, 2, 405-415.
- Hadjiev, D. 1961. *The Late Sarmatian Hipparion-fauna from Eldar*. — Doctoral thesis. Publ. house of the Azerbaidjan Acad. Sci., Baku: 37 pp.
- Hristova, L., Kovachev, D., Spassov, N. 2003. *Hipparion brachypus* Hensel, 1862 from Hadjidimovo, South-western Bulgaria (Late Miocene). — *Comptes rendus de l'Académie bulgare des Sciences*, 56, 2, 77-84.
- Janis, C. 1986. Evolution of horns and related Structures in Hoofed Mammals. — *Discovery*, 19, 2, 9-17.
- Kojumdjieva, E., Nikolov, I., Nedialkov, P., Buzev, A. 1982. Stratigraphy of the Neogene in Sandanski Graben. — *Geologica Balkanica*, 12, 3, 69-81.
- Korotkevich, O. 1982. On the change of the name of the tragocere from Novaya Emetovka. — *Vestnik zoologii*, 4, 10. (in Russian).
- Korotkevich, O. 1988. *Genesis of the Hipparion-fauna of Eastern Europe*. Naukova Dumka, Kiev, 160 p. (in Russian).
- Kostopoulos, D., Koufos, G. 1996. Late Miocene Bovids (Mammalia, Artiodactyla) from the Locality "Nikiti" (NKT), Macedonia, Greece. — *Annales de Paléontologie*, 81, 4, 251-300.
- Kostopoulos D., Spassov N., Kovachev D. 2001. — Contribution to the study of *Microstonyx*: the Bulgarian case. *Geodiversitas, Paris*, 23, 3, 41-437.
- Kretzoi, M. 1941. Neue Antilopen-form aus dem Soproner Sarmat. — *Földtani Közlöny*, 71:7-12
- Kretzoi, M. 1968. New generic names for homonyms. — *Vertebrata Hungarica*, 10, 1-2, 163-166.
- Meladze, G. 1967. *The Hipparion-fauna from Arkneti and Bazaleti*. Mezniereba Publ. House, Tbilisi, 167 p. (in Russian).
- Morales, J., Nieto, M., Köhler, M., Moyá-Solá, S. 1999. Large Mammals from the Vallesian of Spain. — In: *Hominoid evolution and climatic change in Europe. Vol. 1. The evolution of neogene terrestrial ecosystems in Europe* (Eds. Agustí J., Rook, L., Andrews, P.). Cambridge Univ. Press, 113-126.
- Moyá-Solá, S. 1983. Los boselaphini (Bovidae, Mammalia) del Neogeno de la península Iberica. — *Publicaciones de geología, Universitat autonoma de Barcelona*, 18, 237 p.
- Nikolov, I. 1973. *The Genus Hipparion in Bulgaria*. Ph.D. Thesis. Inst. of Geology, Bulg. Acad. Sci. (in Bulgarian).
- Nikolov, I. 1985. Catalogue of the localities of Tertiary Mammals in Bulgaria. — *Paleontology, Stratigraphy and Lithology (Sofia)*, 21, 43-62.
- Pevzner, M., Vangengeim, E. 1993. Magnetostratigraphical age assignments of the Middle and Late Sarmatian Mammalian localities of the Eastern Paratethys — *Newsletters on stratigraphy, Berlin*, 29, 2, 63-75.
- Pilgrim, G. 1910. Notices of new Mammalian genera and species from the Tertiaries of India. — *Records of the Geological Survey of India*, 40, 1, 63-71.
- Pilgrim, G. 1937. Siwalik antelopes and oxen in the American Museum of Natural History. — *Bull. Amer. Mus. Nat. Hist.*, 72, 729-874.
- Pilgrim, G. 1939. The fossil Bovidae of India. — *Mem. geol. Surv. India. Palaeont. Indica* (n.s.), 26, 1, 1-356.
- Romaggi J.-P. 1987. — Les antilopes du Miocène supérieur du Coiron (Ardèche, France). Thèse Université Cl. Bernard — Lyon 1.
- Roth, J., Wagner, A. 1854. Die fossilen Knocheneuberreste von Pikermi, Griechenland. — *Abhandl. Bayer. Akad. Wiss.*, 7, 371-464.
- Schlosser, M. 1904. Die Fossilen Cavicornia von Samos. — *Beitrage Palaont. Geol.*, 17, 118 p.
- Solouias, N. 1981. The Turolian Fauna from the Island of Samos, Greece with special emphasis on the Hyainids and the Bovids. — *Contribution to Vertebrate Evolution*, 6, 1-232.
- Solounias, N., Plavkan, M., Quade, J., Witmer, L. 1999. The paleoecology of the Pikermian Biome and the savanna myth. — In: Agustí J., L. Rook, P. Andrews (Eds.), *"The Evolution of Neogene Terrestrial Ecosystems in Europe"*. Cambridge Univ. Press., 436-452.
- Spassov, N., Ginsburg, L. 1999. *Tapirus balkanicus* nov. sp., nouveau tapir (Perissodactyla, Mammalia) du Turolien de Bulgarie. — *Ann. Paleontol.*, 85, 40, 265-276.

- Spassov, N. 2002. The Turolian Megafauna of West Bulgaria and the character of the Late Miocene "Pikermian biome". — *Bollettino della Societa Paleontologica Italiana*, 41, 1, 69-81.
- Spassov, N., Tzankov, Tz., Geraads, D. 2004. Late Neogene Environments of South-West Bulgaria. 5th International Symposium on Eastern Mediterranean Geology. Thessaloniki, Greece, 14-20 April 2004. Proceedings. Ed. by A. Chatzipetros and A. Pavlides. Vol. 1: 504-506
- Spassov, N., Geraads, D. (in press). *Tragoportax* Pilgrim and *Miotragocerus* Stromer (Mammalia, Bovidae) from the Turolian of Hadjidimovo, Bulgaria, and a revision of the Late Miocene Mediterranean Boselaphini. — *Geodiversitas*, Paris.
- Stromer, E. 1928. Wirbeltiere im obermiozänen Fling Münchens. — *Abhandl. Bayer. Akad. Wiss. math.-naturwiss.*, 32, 1, 1-71.
- Thenius, E. 1948. Über die Entwicklung des Hornzapfens von *Miotragocerus*. — *Sitz-Ber. österr. Akad. Wiss., math-naturw. Vienne*, 157, 6-10, 203—221.
- Thomas, H. 1979. *Miotragocerus cyrenaicus* sp. nov. (Bovidae, Artiodactyla, Mammalia) du Miocène supérieur de Sahabi (Libye) et ses rapports avec les autres *Miotragocerus*. — *Geobios*, 12, 2, 267-280.
- Vatsev, M. 1980. Litostratigraphy of the Neogene sedimentary rocks of the Gotse Delchev basin. — *Annual of the Higher Inst. of Mine and Geol.*, 25, 103-115.
- Бакалов, П., Николов, И. 1962. — Фосилите на България, Том X. Терциерни бозайници. Изд. на БАН, София, 162 с. (French and Russian summaries).
- Спасов, Н., Жераадс, Д., Цанков, Ц. В търсене на изкопаеми хоминоиди: природната обстановка в късния миоцен на България. — *Списание на БАН*. (под печат)
- Цанков, Ц., Спасов, Н., Стоянов, К. Неогенско-кватернерна геодинамика и палеогеография по Средна Струма (Югозападна България). Изд. на Югозападния Университет. Благоевград (Engl. summary). (под печат)