Tragoportax Pilgrim, 1937 and *Miotragocerus* Stromer, 1928 (Mammalia, Bovidae) from the Turolian of Hadjidimovo, Bulgaria, and a revision of the late Miocene Mediterranean Boselaphini

Nikolai SPASSOV
National Museum of Natural History,
1 blvd Tsar Osvoboditel, 1000 Sofia (Bulgaria)
nspassov@nmnh.bas.bg

Denis GERAADS
UPR 2147 CNRS,
44 rue de l'Amiral Mouchez, F-75014 Paris (France)
dgeraads@ivry.cnrs.fr

ABSTRACT

A taxonomic revision of the late Miocene Boselaphini is proposed on the basis of the description of abundant Turolian material from the locality of Hadjidimovo, Bulgaria. The genus *Tragoportax* Pilgrim, 1937 as usually understood is divided into two genera – *Tragoportax* and *Miotragocerus* Stromer, 1928 – the latter itself divided into two subgenera – M. (*Miotragocerus*) Stromer, 1928 and M. (*Pikermicerus*) Kretzoi, 1941. The sexual dimorphism and the paleoecology of the taxa are discussed as well as the taphonomy of *Tragoportax* from Hadjidimovo.

KEY WORDS
Mammalia,
Bovidae,
Boselaphini,
Tragoportax,
Miotragocerus,
Pikermicerus,
late Miocene,
Bulgaria,
taphonomy,
ecology.

RÉSUMÉ

Tragoportax *Pilgrim, 1937 et* Miotragocerus *Stromer, 1928 (Mammalia, Bovidae) du Turolien de Hadjidimovo, Bulgarie, et révision des Boselaphini du Miocène supérieur de Méditerranée.*

À partir de la description de l'abondant matériel turolien de la localité de Hadjidimovo en Bulgarie, nous proposons une révision des Boselaphini du Miocène supérieur. Le genre *Tragoportax* Pilgrim, 1937 tel qu'il est habituellement compris est divisé en deux genres – *Tragoportax* et *Miotragocerus* Stromer, 1928 – ce dernier lui-même divisé en deux sous-genres M. (*Miotragocerus*) Stromer, 1928 and M. (*Pikermicerus*) Kretzoi, 1941. Le dimorphisme sexuel et la paléoécologie des taxons, ainsi que la taphonomie de *Tragoportax* de Hadjidimovo sont aussi discutés.

MOTS CLÉS
Mammalia,
Bovidae,
Boselaphini,
Tragoportax,
Miotragocerus,
Pikermicerus,
Miocène supérieur,
Bulgarie,
taphonomie,
écologie.

INTRODUCTION

The Bovids included in recent times in the genus *Tragoportax* Pilgrim, 1937 were among the most widespread in oriental and southeastern Europe, as well as in Western Asia (the "Balkano-Iranian" province: Spassov 2002; Geraads *et al.* 2003), in the upper 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 (southwestern Bulgaria). This also gives us the opportunity to review critically the taxonomic features mentioned in the literature, and to propose our own conceptions on the taxonomic frame of the "*Tragoportax-Miotragocerus* complex" as well as a new revision of the late Miocene Mediterranean Boselaphini.

THE LOCALITY 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 late Miocene fossil site with four 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 Dimitar Kovachev between 1985 and 1998.

More than 19,000 bone remains from Hadjidimovo (D. K. collection) are presently stored in the Assenovgrad Museum – a paleontological division of the National Museum of Natural History – 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; Kostopoulos *et al.* 2001; Hristova *et al.* 2002; Geraads *et al.* 2003). 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, or perhaps at the beginning of MN12 (Spassov 2002).

ABBREVIATIONS
HD   Hadjidimovo;
MNHN   Muséum national d'Histoire naturelle, Paris;
NHMW   Naturhistorisches Museum Wien;
NMNH   National Museum of Natural History, Sofia;
PIK   Pikermi;
PIM   Paläontologisches Institut Münster;
SAM   Samos.
Upper teeth are in upper case, lower teeth in lower case.

SYSTEMATICS

Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Subfamily BOVINAE Gray, 1821

Tribe BOSELAPHINI Knottnerus-Meyer, 1907

Sokolov (1953) created a new subtribe Tragocerina for the fossil antelopes *Tragocerus* Gaudry, 1861, *Miotragocerus* Stromer, 1928, *Paratragocerus* Sokolov, 1949 and *Sivaceros* Pilgrim, 1937, but the monophyly of this group is questionable. Moyá-Solá (1983) defines the

Boselaphini by several features as follows: subtriangular basal section on the horn-cores related to the presence of distinct anterior and postero-external keels; presence of rugosities and crests on the anterior part of the parietals. In fact, only the presence of the anterior keel is a constant feature for all taxa included in the Boselaphini. The other ones are only strong tendencies that may no be expressed in some species, or variably expressed within the same species.

Genus *Tragoportax* Pilgrim, 1937

Tragocerus Gaudry, 1861: 298 (type species: *Capra amalthea* Roth & Wagner, 1854) (non *Tragocerus* de Jean, 1821).

Tragoportax Pilgrim, 1937: 774.

Pontoportax Kretzoi, 1941: 341 (type species: *Tragocerus parvidens* Schlosser, 1904).

?*Gazelloportax* Kretzoi, 1941: 341 (type species: *G. gallicus* Kretzoi, 1941).

?*Mirabilocerus* Hadjiev, 1961: 3 (type species: *Tragocerus eldaricus* Gabashvili, 1956).

Tragoceridus Kretzoi, 1968: 165 (type species: *Capra amalthea* Roth & Wagner, 1854).

Mesembriportax Gentry, 1974: 146 (type species: *M. acrae* Gentry, 1974).

?*Mesotragocerus* Korotkevich, 1982: 10 (type species: *M. citus* Korotkevich, 1982).

TYPE SPECIES OF *TRAGOPORTAX*. — *Tragoportax salmontanus* Pilgrim, 1937 (Pilgrim 1937: 774) by original designation.

INCLUDED SPECIES. — *Tragoportax amalthea* (Roth & Wagner, 1854). Pikermi, most probably also Samos and Halmyropotamos (Greece) (= ?*T. frolovi* (M. Pavlow, 1913), Chobruchi [Moldova]); 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), Veles-Karaslari (Republic of Macedonia), Hadjidimovo (Bulgaria), Tudorovo (Moldova)?, Novoukrainka (Ukraine), Siwaliks (Pakistan) and possibly in Vathylakkos 2 (Greece), Maragha (Iran) and Kocherinovo-1 (Bulgaria), from the Vallesian/Turolian boundary to the middle/late Turolian.

?*Tragoportax curvicornis* Andree, 1926. Samos (= *T. browni* Pilgrim, 1937, Siwaliks, Pakistan, Turolian).
Tragoportax salmontanus Pilgrim, 1937. Siwaliks (Pakistan). (About 8.1 to 7.9 Ma, but this absolute date is doubtful: Barry *et al.* 2002).
Tragoportax maius Meladze, 1967. Bazaleti, Georgia (late Turolian). Perhaps a synonym of the poorly known *Tragoportax eldaricus* (Gabashvili, 1956), type species of the genus *Mirabilocerus* Hadjiev, 1961, from the late Vallesian/early Turolian of Eldar in Azerbaijan.
?*Tragoportax cyrenaicus* Thomas, 1979, Sahabi (Libya), probably late Miocene.
Tragoportax acrae (Gentry, 1974). Langebaanweg (South Africa), Mio-Pliocene.
Tragoportax macedoniensis Bouvrain, 1988. Dytiko (Greece; MN13).
A number of other specific names, several of them from Asia, often based upon fragmentary material, are of doubtful validity; we will mention them in the comparison and discussion but we will not try to revise them here.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION. — From the Vallesian/Turolian boundary (or late Vallesian?) to the end of the Turolian, perhaps earliest Pliocene in Africa. From southeastern 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).

NEW DIAGNOSIS. — Size generally large, approximately that of European *Cervus elaphus*. The post-cornual 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 (anti-clockwise on the right horn), so that the anterior keels first diverge in anterior view, but they re-approach towards the tips (Fig. 3). The intercornual 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.
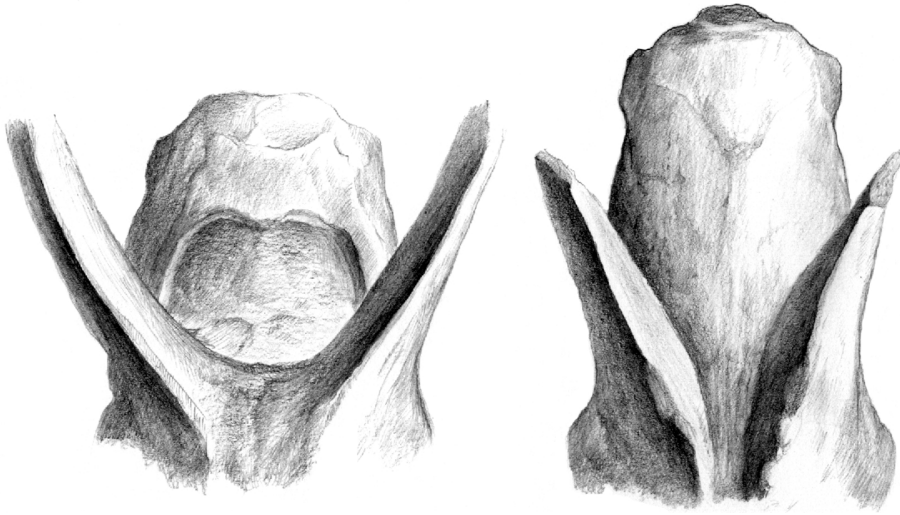
FIG. 1. — Postcornual fronto-parietal area in *Tragoportax* and *Miotragocerus*; **left**, *T. rugosifrons* (Schlosser, 1904) (HD-5125); **right**, *M.* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) (HD-5126). Hadjidimovo, coll. of the Museum of Palaeontology, Assenovgrad (Division of the NMNH) (drawings: V. Simeonovsky).
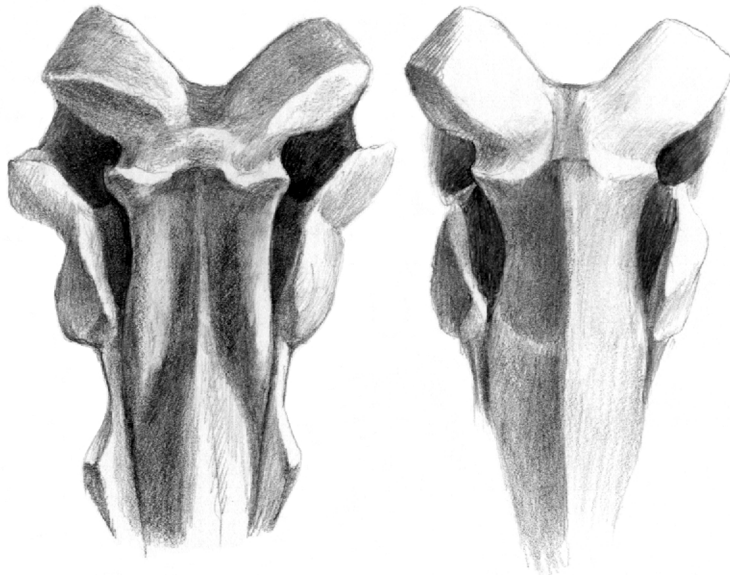

FIG. 2. — Basi-occipital area in *Tragoportax* and *Miotragocerus* (*Pikermicerus*); **left**, *T. rugosifrons* (Schlosser, 1904) (HD-5125); **right**, *M.* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) (HD-5126 and 2010). Hadjidimovo (drawings: V. Simeonovsky).

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 lingually inflated hypocone. Metaconid of p3-p4 larger than in *Miotragocerus*, splayed lingually and T-shaped on p4, with an open anterior valley.
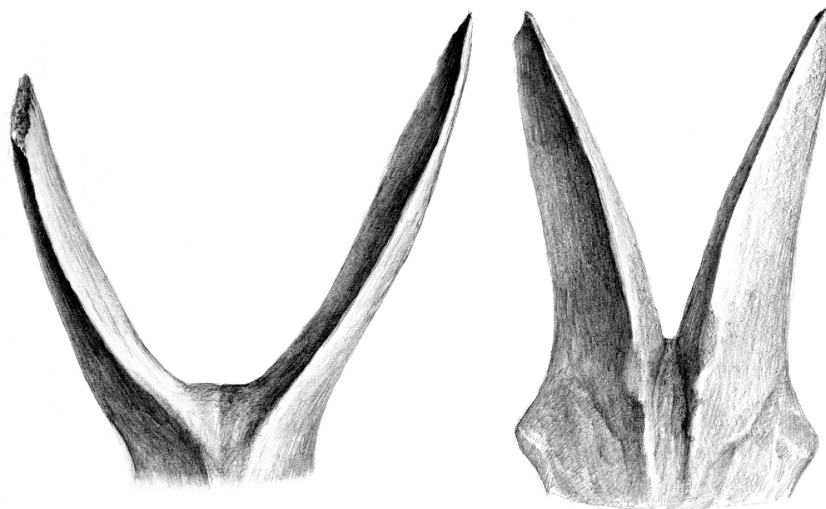
Fig. 3. — Course of the horn-cores anterior keels in *Tragoportax* and *Miotragocerus* (*Pikermicerus*); **left**, *T. rugosifrons* (Schlosser, 1904) (HD-5133); **right**, *M.* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) (HD-2010). Hadjidimovo (drawings: V. Simeonovsky).

Tragoportax rugosifrons (Schlosser, 1904)

HOLOTYPE. — Skull (Schlosser 1904: pl. 12, fig. 6).

TYPE LOCALITY. — Samos.

NEW 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 contrast to *T. amalthea*). The anterior keel is almost straight to slightly twisted in front view (Fig. 3).

DESCRIPTION OF THE HADJIDIMOVO MATERIAL (FIGS 4-6)

The *Tragoportax* sample from Hadjidimovo is more abundant than that of *Miotragocerus* and is the third most 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 tens of metapodials and metapodial fragments (see inventory numbers of the skull, mandibular and metapodial material in Annexe: Tables 1-4, Collection of the Assenovgrad paleontological division of the NMNH).

Skull

It is larger than that of *Miotragocerus* (Annexe: Tables 1; 2). There is probably a contact between the premaxilla and the nasal. There is a wide and deep ante-orbital fossa. The infraorbital 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 distinct 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 (Fig. 7), 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 intercornual 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 postcornual area is depressed 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 (Fig. 6A). Their teeth are well preserved, and they are both fully adults. Their size (skull and teeth, premolar/molar proportions) and morphology (shape of the fronto-parietal area, and basioccipital) are 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.

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 (Annexe: Table 2) and rather hypsodont with relatively less accentuated relief of the walls than in *Miotragocerus* (*Pikermicerus*) from the same locality. The premolar row is relatively shorter than in the smaller boselaphine from Hadjidimovo. 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 (Annexe: 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.

COMPARISONS

There are many differences between the two boselaphines from Hadjidimovo. *Tragoportax rugosifrons* from this site differs from *Miotragocerus* of the same locality 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, compared to the length; their triangular cross-section and normal torsion; the hypsodont teeth; the relative length and morphology of the premolars (Figs 1-11; Annexe: Tables 1-4).

The *Tragoportax* from Hadjidimovo has similarities with *T. amalthea* in its main features and general aspect, but also differs clearly by: the greater intercornual distance, the less robust horn-cores (Figs 12; 13), lesser development of
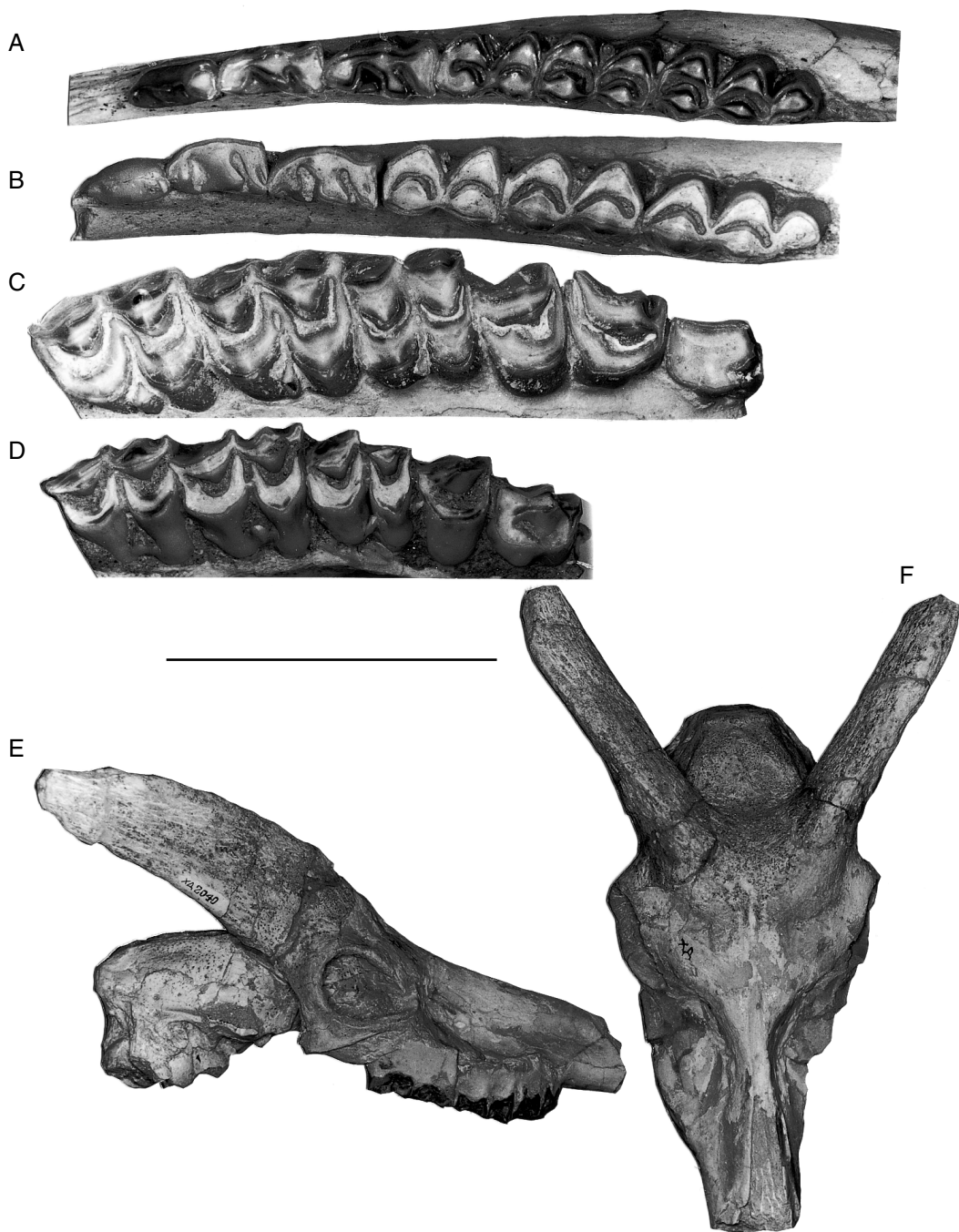
Fɪɢ. 4. — **A**, *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941), lower tooth-row (no No.); **B**, *Tragoportax rugosifrons* (Schlosser, 1904), lower tooth-row (HD-2443); **C**, *T. rugosifrons*, upper tooth-row (HD-3664); **D**, *M.* (*Pikermicerus*) *gaudryi*, upper tooth-row (P2 missing) (HD-3672); **E**, *T. rugosifrons*, skull (HD-2040), lateral view; **F**, same specimen, front view. Scale bar: A-D, 5 cm; E, F, 15 cm.
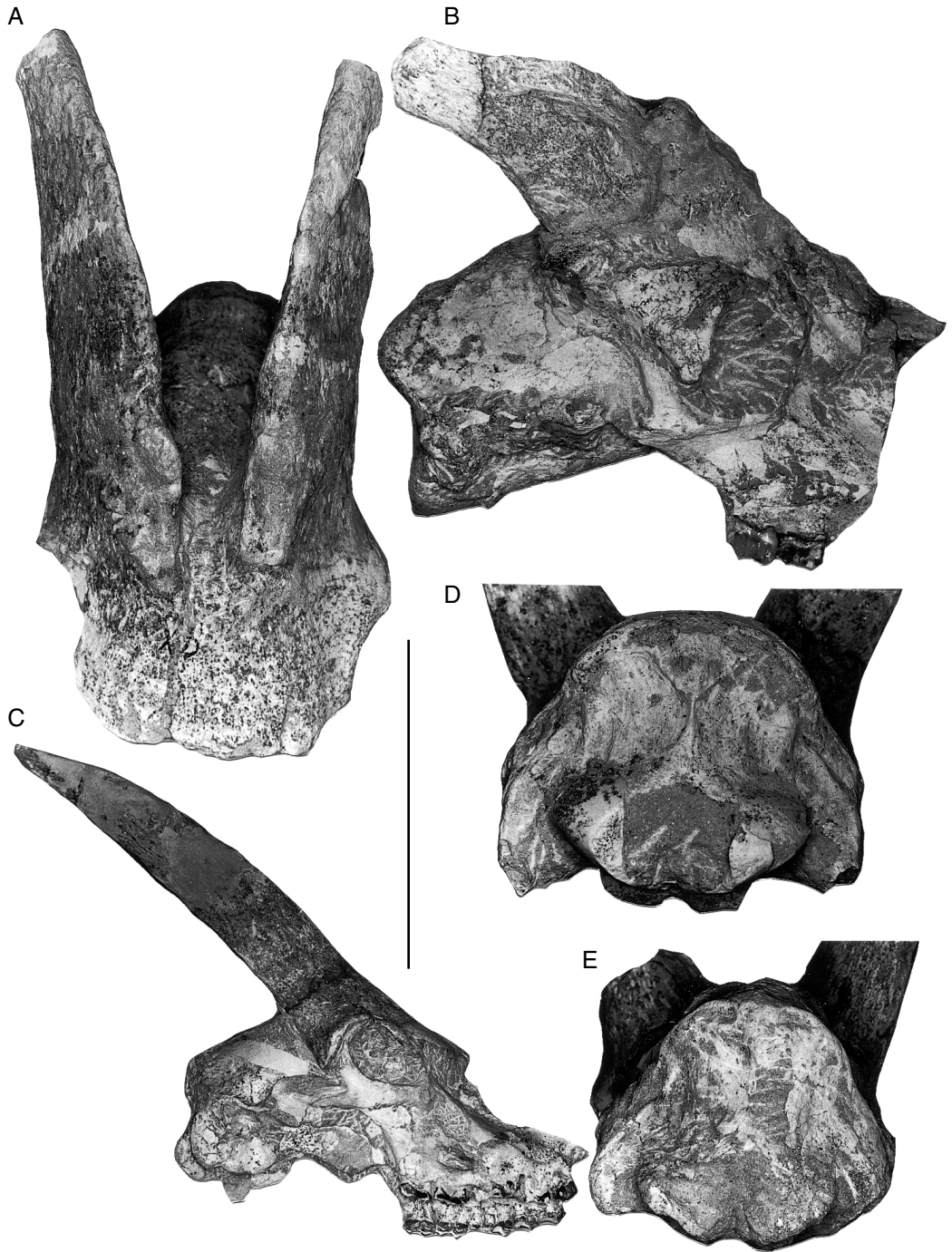
Fig. 5. — **A**, *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941), frontlet (HD-2010), front view; **B**, *M.* (*Pikermicerus*) *gaudryi*, braincase with horn-cores (HD-5519), lateral view; **C**, *Tragoportax rugosifrons* (Schlosser, 1904), skull (HD-5127), lateral view; **D**, *T. rugosifrons*, occipital (HD-5132); **E**, *M.* (*Pikermicerus*) *gaudryi*, occipital (HD-2039). Scale bar: A, B, D, E, 10 cm; C, 20 cm.
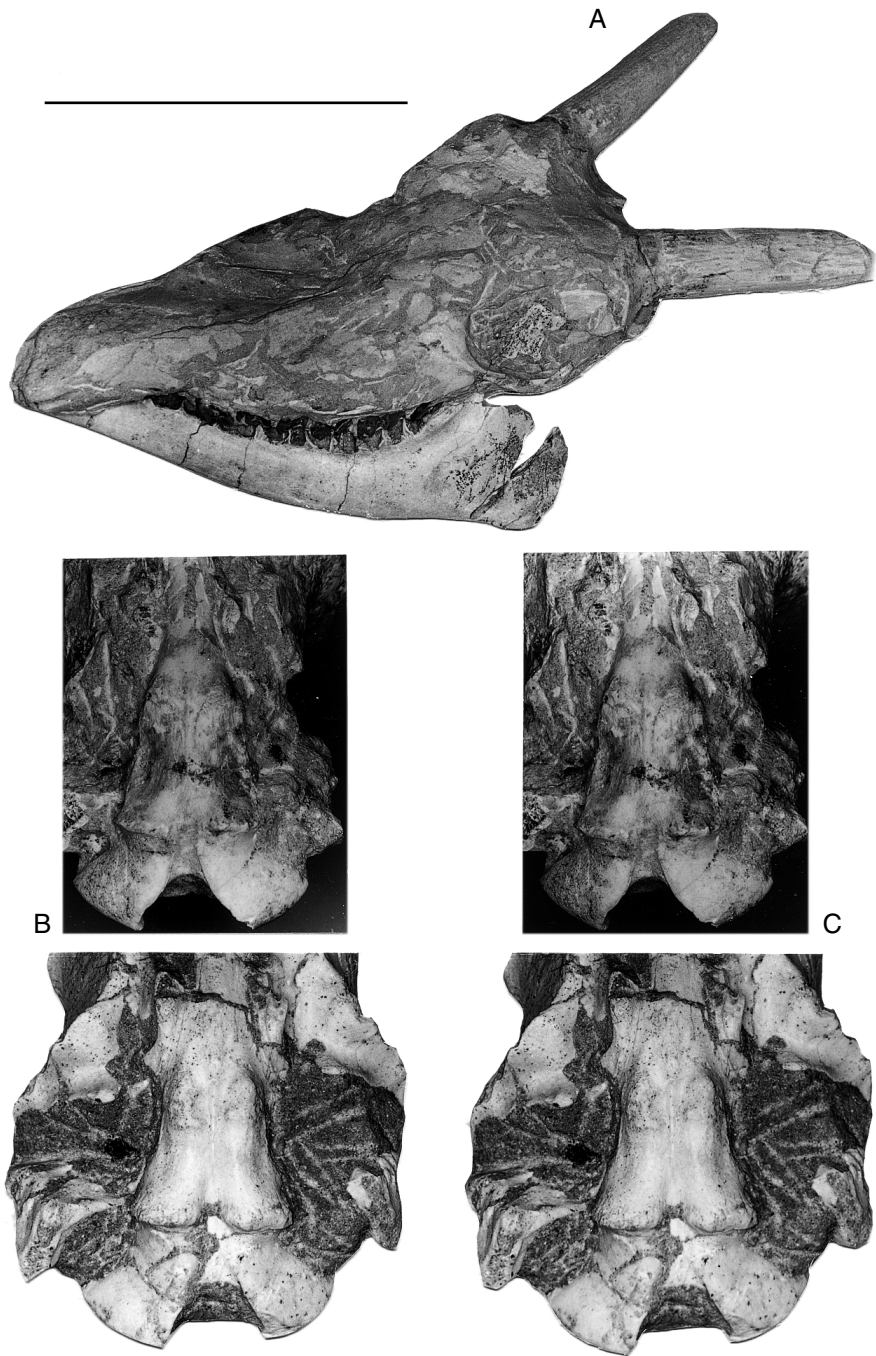
FIG. 6. — **A**, *Tragoportax rugosifrons* (Schlosser, 1904), female skull (HD-5138); **B**, *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941), basi-occipital (HD-2007) (stereo); **C**, *T. rugosifrons*, occipital (no No.) (stereo). Scale bar: A, 15 cm; B, C, 10 cm.

the rugosities on the anterior horn-core keel, lesser concavity of the 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 shows also some differences, having somewhat shorter premolar row in relation of the molars (Fig. 14).

From the specimens described as *T. curvicornis* (Andree 1926: pl. 12, figs 6, 7; 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, 1979 from Sahabi (Libya) differs by its curved and divergent horn-cores, but the species is illustrated by a single specimen. Should this difference be constant, it could be a valid species, otherwise, it could be closely related to *T. curvicornis*.

The single specimen from Novaya Emetovka (type of *Mesotragocerus citus* Korotkevich, 1982) 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. 27), the sample from Hadjidimovo differs by the larger and more quadrangular intercornual surface, the much stronger temporal lines and torus that surrounds the fronto-parietal postcornual depression. The horn-cores are less inclined and have a totally different profile, 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 intercornual 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 shows 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). Two undescribed *Tragoportax* adult male skulls in the National Museum of Natural History, Skopje (Republic of Macedonia) from Veles-Karaslari have large dimensions and horn-cores that are strongly divergent at the base, almost straight, with very weak torsion, and with continuous (not stepped) anterior keel, without marked rugosities. These skulls are 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. The skull PXM-17 (Bouvrain 1994) has smaller intercornual distance due to a lateral compression and deformation of the skull. The specimen PXM-93 has horn-cores curved backward, but this is probably due to individual variability.

DISCUSSION

The first described and best known species of *Tragoportax* is *T. amalthea* (Roth & Wagner, 1854). It is a large form which has relatively twisted and very robust horn-cores, with a tendency to clear demarcations on the anterior keel and with the tip of the horn-core well distinct from the general shape and direction of the horn-core. The type locality is Pikermi but some skulls very similar to the Pikermi sample have been found in Samos as well (see Andree 1926: pl. 10, figs 4-6, 8; Solounias 1981: fig. 28a-c) and probably represent a Samos subspecies of *T. amalthea*, seemingly characterized by longer and more slender horns. Specimens with similar horn-cores are also known from Halmyropotamos, Greece (Melentis 1967) and Chobruchi, Moldova (Korotkevich 1988).

Tragoportax rugosifrons (Schlosser, 1904) is probably the most widespread species (in number of localities and possibly in chronological longevity as well). It is also (together with *T.? eldaricus*) among the earliest species. The horn-cores of *T. rugosifrons* are nearly straight. The anterior keel is without or with a slight torsion (i.e. spiral) as well as almost without flat steps (demarcations), forming a continuous curve from base to tip. This horn structure is characteristic for most specimens of Schlosser's collection from Samos, for Hadjidimovo, for the adult and subadult male skulls from Veles-Karaslari and for several samples from Greece (see above) as well as for the specimens referred to *T. frolovi* by Korotkevich (1988) from Novoukrainka from the Black Sea region. The specimens from Samos described as *T. recticornis* (Andree, 1926) have the same horn-core morphology. The material, also from Samos, described and figured by Schlosser (1904) as "*Tragocerus amalthea* var. *parvidens*" is seemingly identical with *T. rugosifrons*. The skull described by Pilgrim (1910) from the Siwalik as "*Tragocerus punjabicus*" shares the same horn-core morphology as well, and could also be referred to *T. rugosifrons*. The skull from Prochoma (PXM-93) (Bouvrain 1994) with horn-cores relatively strongly curved backwards is rather atypical for the species (see above).

Pikermicerus

HD-2010   HD-5126

Tragoportax

HD-5133   HD-2040
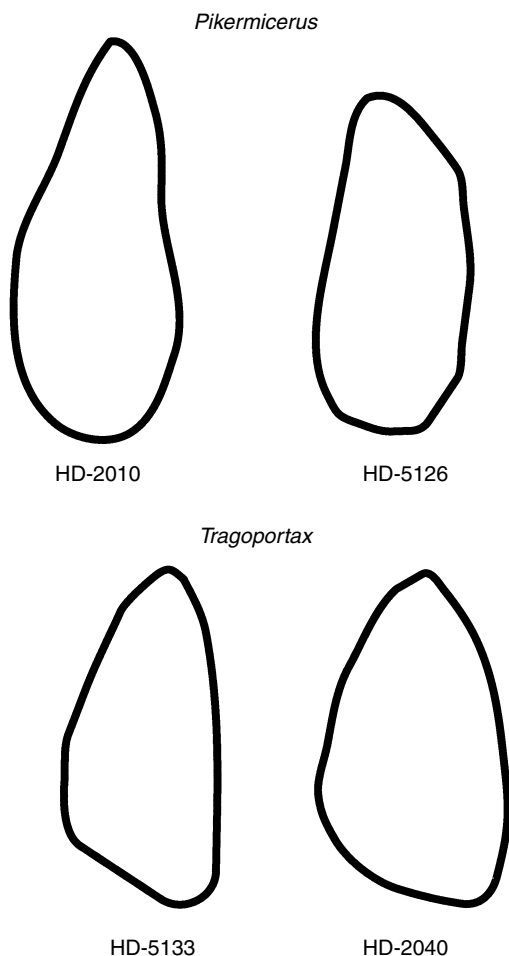
FIG. 7. — Horn-core cross-section in *Tragoportax* and *Miotragocerus* from Hadjidimovo, all shown as if from the right side (HD-5133 inverted). The front side is towards the top of the page, the lateral side to the right.

Tragoportax cf. *rugosifrons* is represented in Maragha, Iran, by some tooth-rows and a skull with horn-core (MNHNP MAR 1395; Mecquenem 1924: pl. 6, fig. 3). The skull shows the *Tragoportax* postcornual and basioccipital features and general horn-core shape close to *T. rugosifrons*. The preserved horn-core is also strongly curved backward, as in the Prochoma specimen.

Tragoportax curvicornis (Andree, 1926) from Samos is, according to several contemporary
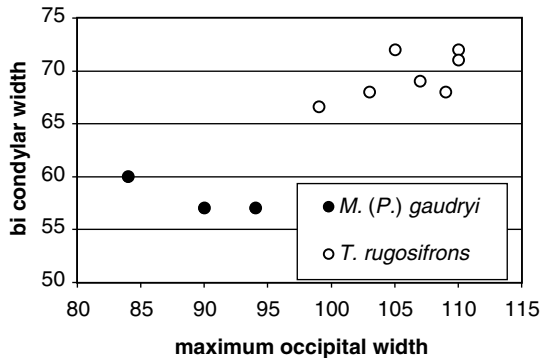
FIG. 8. — Neurocranial dimensions, in mm, in *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo.

FIG. 9. — Horn-core proportions and length, in mm, in *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo.

authors, a junior synonym of *T. rugosifrons* (or of "*T. punjabicus*") (Moyá-Solá 1983; Bouvrain & Bonis 1983; Bouvrain 1988). Given the scarcity of the material of *T. rugosifrons-T.* "*recticornis*"-*T.* "*curvicornis*" from Samos, this conclusion is quite logical, but not mandatory as, e.g., the various levels of Samos could yield different forms. Judging from the limited variability of the horn morphology in the other *T. rugosifrons* samples (Hadjidimovo, Tudorovo, Veles-Karaslari, etc.) we doubt that the strong curves of the horn-cores of the two specimens noted as *T. curvicornis* (Andree 1926: pl. 11, fig. 6; Solounias 1981: fig. 30C, H) could be included within the variation range of *T. rugosifrons*, and we prefer to keep *T. curvicornis* as a valid name. The horn-cores of *T. browni* Pilgrim, 1910 from the Siwaliks are similar in shape to *T. curvicornis* and both species could be identical. We are unable to take a decision on the taxonomic status of "*Mirabilocerus*" without direct observation of the Bazaleti, Eldar and Arkneti material included in this taxon by Meladze (1967). From the descriptions (Meladze 1967) and photos, one may suppose that the materials from Bazaleti – and perhaps from Eldar – represent *Tragoportax*. The profile of the horn-cores and the correlated triangular intercornual surface are similar to those of *Miotragocerus*, but the basioccipital and the postcornual morphology (preserved only in "*M.*" *maius* from Bazaleti) display the features of *Tragoportax*. The Arkneti

skull of "*M.*" *brevicornis* Meladze, 1967, of which we have seen unpublished photos, has a basioccipital without longitudinal groove, narrow intercornual surface and rather rounded anterior horn surface different from *Tragoportax* and seems to be a separate form.

The geographic remoteness and late geological age of *Mesembriportax acrae* Gentry, 1974 from the early Pliocene of South Africa would suggest generic distinction from *Tragoportax*, but it displays all the main cranial features of *Tragoportax* (Thomas 1979; and figures in Gentry 1974, 1980) and for the moment this generic distinction is not well supported.

"*Tragoceras leskewitschi*" Borissiak, 1914 from the late Vallesian of Sebastopol-1, regarded in several recent works as a *Tragoportax* species (Moyá-Solá 1983; Bouvrain 1988; Kostopoulos & Koufos 1996), must be excluded (as supposed by Bouvrain 1994) from this genus. The temporal crests are strong as in *Tragoportax*, bordering some kind of postcornual plateau (but not a depression?), but the basioccipital and the narrow, triangular occipital surface of the skull are mostly *Miotragocerus*-like. The horn-cores are not strongly flattened on the lateral and medial sides, in contrast to *Tragoportax* and *Miotragocerus*, and have more rounded anterior keels and small
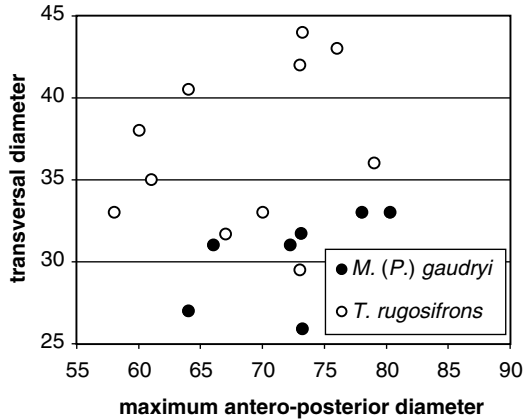
FIG. 10. — Basal horn-core diameters, in mm, in *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo.

FIG. 12. — Horn-core proportions, in mm, in *Tragoportax* taxa from various localities. Abbreviations: **HD**, Hadjidimovo; **PIK**, Pikermi; **DTK**, Dytiko; **RZO**, Ravin des Zouaves; **SAM**, Samos.
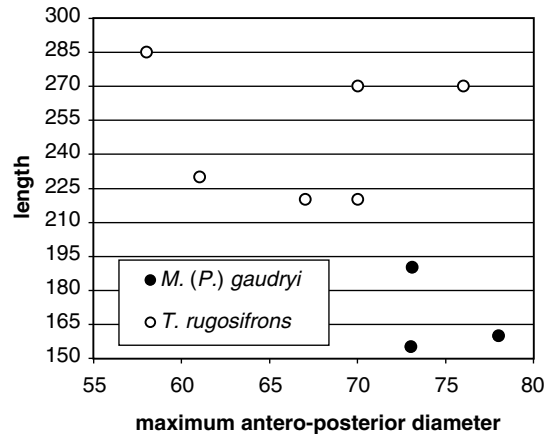

FIG. 11. — Mandibular teeth proportions, in mm, in *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo.
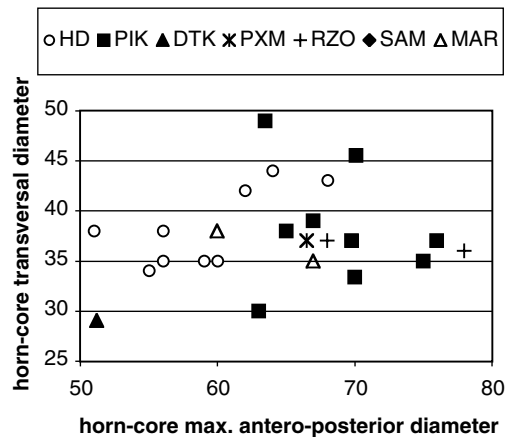
FIG. 13. — Basal horn-core diameters, in mm, in *Tragoportax* from various localities (the horn-cores from Maragha represent most probably *M.* (*Pikermicerus*), see text). Abbreviations: **HD**, Hadjidimovo; **PIK**, Pikermi; **DTK**, Dytiko; **PXM**, Prochoma; **RZO**, Ravin des Zouaves; **SAM**, Samos; **MAR**, Maragha.

antero-posterior diameter. Korotkevich (1988) refers this species to *Protragocerus*, and this is one of the possible identifications (but see also below the General discussion).

The form from Kazakhstan described as *Tragocerus irtyshense* (Musakulova-Abdrahmanova 1974) has a very broad intercornual surface, and oval section of the horn-cores. It does not display *Tragoportax* features either.

The genus *Tragoportax* has been reported from the Turolian of Kalimantsi (Bulgaria), by Bakalov &

Nikolov (1962). An unpublished skull fragment from this locality could belong to *T. rugosifrons* or to *T. amalthea*. It is represented in Nikiti-2, Greece (Kostopoulos & Koufos 1999). In both localities it co-exists with *Miotragocerus* (*Pikermicerus*) (see below), but the specific status of the *Tragoportax* specimens is unclear. Such a co-existence is likely in Maramena (end of MN13) as well (see Köhler *et al.* 1995).
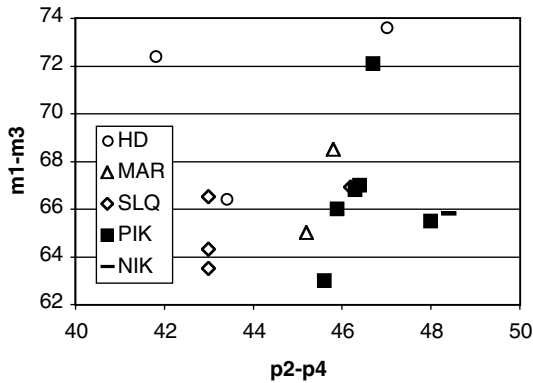
Fig. 14. — Mandibular tooth proportions and size, in mm, in *Tragoportax* from various localities. Abbreviations: **HD**, Hadjidimovo; **MAR**, Maragha; **SLQ**, "Thessaloniki", Arambourg's collection; **PIK**, Pikermi; **NIK**, *Tragoportax* sp., Nikiti-2.

Most of the *Tragoportax* species from the Dhok Pathan and Nagri formations of the Siwaliks (Thomas 1984; Bouvrain 1994) were described on fragmentary material (Lydekker 1878; Pilgrim 1939). Some of them (see above) could be synonymized with forms known from Europe. The taxonomic status of the *T. perimensis-T. salmontanus-T. aiyengari-T. islami* group is unclear (Thomas 1979; Moyá-Solá 1983; Bouvrain 1994). *T. salmontanus* could well be a distinct species. Photos of the type (kindly sent to us by E. Delson, American Museum of Natural History, New York) show a well expressed fronto-parietal postcornual depression with strong rugosities and a groove on the preserved part of the basioccipital. The skull is characterized by short and robust, twisted and inclined horns as well as by the skull dome relief: strong postcornual torus with V-shaped caudal part and a well marked connection of the temporal ridges behind it. The holotypes of *T. islami* Pilgrim, 1939 and *T. aiyengari* Pilgrim, 1939 must be referred to *Tragoportax*. *T. aiyengari* has some similarities with *T. rugosifrons* and could be a synonym. *T. islami* shows particularities in the postcornual surface morphology very similar to the skull dome relief of *T. salmontanus* and probably is a synonym of the latter. *Sivaceros* Pilgrim, 1937, from the Chinji stage of the Siwaliks, recalls *Tragoportax*, but is more

primitive by its straight slender horn-cores, that are inserted widely apart, with an incipient triangular cross-section, and by the longitudinal groove on the basi-occipital restricted to the posterior part.

The large *Mesotragocerus citus* Korotkevich, 1981 (Korotkevich 1988; Krakhmalnaya 1996) from the Turolian of Novaya Emetovka (Ukraine) should be referred to *Tragoportax* (even if it is not sure that *T. citus* is a *bona fide* species). The photos kindly sent us by Y. Semenov (National Museum of Natural History, Kiev) display the typical features of *Tragoportax* on the basioccipital and on the postcornual fronto-parietal surface.

Genus *Miotragocerus* Stromer, 1928

Miotragocerus Stromer, 1928: 36.

Pikermicerus Kretzoi, 1941: 342 (type species: *P. gaudryi* Kretzoi, 1941).

?*Indotragus* Kretzoi, 1941: 342 (type species: *I. pilgrimi* Kretzoi, 1941).

Dystychoceras Kretzoi, 1941: 336 (type species: *D. pannoniae* Kretzoi, 1941).

TYPE SPECIES OF *MIOTRAGOCERUS*. — *Miotragocerus monacensis* Stromer, 1928 (Stromer 1928: 36) by original designation.

INCLUDED SUB-GENERA. — *Miotragocerus (Miotragocerus)* Stromer, 1928; *Miotragocerus (Pikermicerus)* Kretzoi, 1941.

INCLUDED SPECIES. — *Miotragocerus (Miotragocerus) monacensis* Stromer, 1928. Oberföhring (Germany); Hostalets?, Ballestar? (Spain); *c.* 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 & Vangengeim 1993) and Grizev in Ukraine (Korotkevich 1988); late middle Miocene-Vallesian.
Miotragocerus (Pikermicerus) gaudryi (Kretzoi, 1941) with probably four subspecies (see below). Mostly at: Pikermi, Samos, Halmyropotamos (Greece, Turolian); Hadjidimovo (Bulgaria, early/middle Turolian), Veles-Karaslari (Republic of Macedonia, early or middle Turolian), Le Coiron, Ardèche (France, early Turolian); probably also at Belka (Ukraine, Turolian); Piera, early Turolian and Venta del Moro, late

Turolian (Spain); mont Lubéron (France, middle/late Turolian); Maragha (Iran, ?early Turolian); Nikiti-2 (Greece, early Turolian) and Maramena (Greece, Turolian/Ruscinian boundary). The presence of the species at Nikiti-1 (Greece, ?end of the 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 the end of MN13 of Europe and possibly the Middle East.

NEW DIAGNOSIS. — (The shape of horn-cores and those of associated structures are those of adult males). Size small (about that of fallow deer). The postcornual area of the skull is not depressed or raised as a low plateau (Fig. 1). Basioccipital, definitely known in the subgenus *Pikermicerus*, without median longitudinal groove between the anterior and the posterior tuberosities, but with a faint sagittal keel (Fig. 2). Strong temporal crests (at least in males) in early forms (*Miotragocerus*), weaker in more recent ones (*Pikermicerus*). Horn-cores moderately long to long in early forms and short in later ones, mediolaterally 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 (Fig. 7). 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 (Fig. 3). The intercornual 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.

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

TYPE SPECIES. — *Pikermicerus gaudryi* Kretzoi, 1941: 342. The subgenus is, in our conception, monospecific, with a possible second species from the late Vallesian of Western Europe.

DIAGNOSIS. — Cranial features as for genus. 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 and medial longitudinal groves (depressions); 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: 342.

Miotragocerus monacensis – Solounias 1981 (*pars*): 102.

Tragoportax gaudryi – Moyá-Solá 1983: 124.

HOLOTYPE. — Skull illustrated in Gaudry (1865: pl. 49, fig. 1).

TYPE LOCALITY. — Pikermi.

DIAGNOSIS. — That of the subgenus.

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

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 OF THE HADJIDIMOVO MATERIAL (FIGS 4-6)
(Coll. of the Assenovgrad paleontological division of the NMNH): complete and partial skulls (HD-2007, 2010, 2015-2016, 2019, 2039, 2325, 3704, 5519); several identified mandibles and metapodials (see inventory numbers in Annexe: Tables 2-4).

Skull

It is larger than those of *M. monacensis*, but smaller than those of *Tragoportax* from Hadjidimovo (Fig. 8). 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 (Figs 9; 15) 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 lateral 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 (Fig. 7), 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 intercornual plateau is usually long, narrow and triangular. The neurocranium is proportionally long and narrow compared to *Tragoportax* (Fig. 16). The fronto-parietal postcornual 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 labial walls of upper teeth. The premolar row is relatively longer than in *Tragoportax*. 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 (53.0 mm) falls within the size range of Pikermi (48.6-53.9 mm), it is slightly smaller than at Nikiti-1 (55.1 mm), but much larger than at Piera (45.0 mm).

Metapodials
The metapodials, of the size of the fallow deer, are relatively small compared with *Tragoportax* from the same locality (see Annexe: Table 4) and slender. The widening from diaphysis to epiphysis is clearly bovid-like with abrupt change of width of the distal epiphysis compared to *Tragoportax* of the same locality. The trochlear keels are prominent and sharp. The lateral longitudinal grove specific to the metapodials of ?*M. pannoniae* is absent here.

COMPARISONS
Comparison with ante-Turolian forms
The type of *Miotragocerus* (*M.*) *monacensis* from the Astaracian/Vallesian (Stromer 1928) has horn-cores smaller than those of Hadjidimovo (Fig. 15), and the temporal lines are stronger. 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. 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 (not 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 differences of the *M.* (*Pikermicerus*) *gaudryi* sample from Hadjidimovo with the graceful horn-cores of the type

of *M.* (*M.*) *monacensis* are clear. 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 horn-cores of the Hadjidimovo material are clearly larger.

Comparison with the Turolian samples: M. gaudryi
The differences between the accepted forms of *M. gaudryi* are mostly metrical. So, *M.* (*P.*) *gaudryi* (= *Tragoportax gaudryi* sensu Moyá-Solá 1983 and Bouvrain 1988) generally increases in size from early to late Turolian (Moyá-Solá 1983; Bouvrain 1988). The metrical data of the metapodials (Annexe: Table 4) as well as those of the mandibular/maxillar teeth and horn-cores (Annexe: Table 2; Figs 15; 17) 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 (Annexe: Table 2) are smaller than the latest as well as largest known form, *M. g. leberonensis* from mont Lubéron (MN12-13, 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 (Annexe: Table 1 and Figs 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*.

DISCUSSION
The type species of *Miotragocerus*, *M. monacensis* Stromer, 1928, was described from a partial skull from the Astaracian/Vallesian of Oberföhring on
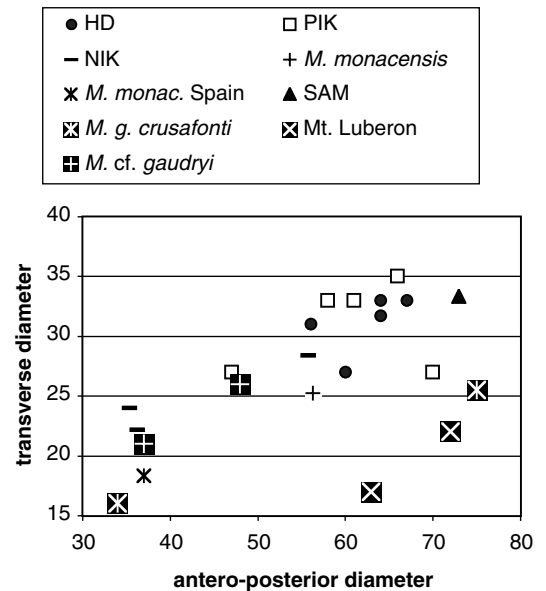
FIG. 15. — Horn-core proportions and dimensions, in mm, in various taxa of *Miotragocerus*. Abbreviations: **HD**, Hadjidimovo; **PIK**, Pikermi; **NIK**, *Tragoportax* sp., Nikiti-2; **SAM**, Samos.

which the main cranial features of *M.* (*P.*) *gaudryi* cannot be observed because of its fragmentary nature but the horn-core cannot be distinguished from those of this species. So, *Pikermicerus* Kretzoi, 1941 can be considered as a junior synonym of *Miotragocerus* Stromer, 1928 and we can include in *Miotragocerus* all forms with short and robust horn-cores, with sub-elliptic basal section and with all diagnostic feature noted above (see Diagnosis).

The variability of *Miotragocerus* is not so great as that of *Tragoportax*. The differences noted in the literature are mostly metrical. As we have noted above, not all features observed in the more recent subgenus *Pikermicerus* could be observed in the older subgenus *Miotragocerus*, represented by scarce and incomplete material. The cranial differences between the two subgenera are at present restricted to: the shape of the horn-cores, with a straighter caudal edge in *M.* (*Miotragocerus*); the more prominent temporal lines and most probably some ratio differences in horn-cores and teeth: more massive (short and robust)

horn-cores and possibly longer premolar row in *M.* (*Pikermicerus*). More material is needed to confirm this taxonomic (subgeneric) differentiation. If the characteristic lateral (as well as medial?) depression referred to "*Dystychoceras*" *pannoniae* metatarsals (Tobien 1953; see also Romaggi 1987) as well as to some Spanish pre-Turolian *Miotragocerus* (Moyá-Solá 1983) really represents a stable character, this feature would be also highly diagnostic. In this case, *Pikermicerus* might represent a genus distinct from the earlier *Miotragocerus*, or "*pannoniae*" might belong to a different genus (*Dystychoceras*) rather than to *Miotragocerus* (see below).

Dystychoceras Kretzoi, 1941 is often interpreted in the recent literature as a synonym of *Miotragocerus* and the type species *D. pannoniae* Kretzoi, 1941 from the late middle Miocene of Sopron (Hungary) as a species of the genus *Miotragocerus* (Thenius 1948; Moyá-Solá 1983). The horn-cores of *D. pannoniae* (see Kretzoi 1941) are inserted very wide apart; they are incompletely preserved, but seem to have a thickening near mid-length not found in other species. It is usually accepted, following Thenius (1948), that the type of *D. pannoniae* and the skull fragments from Mistelbach and Inzersdorf (also very straight but with several demarcations) represent successive ontogenic stages of one and the same form. For this reason most authors include *Dystychoceras* in *Miotragocerus* (Tobien 1953; Moyá-Solá 1983; Romaggi 1987). However, the horn-core A4264 (NHMW) from the Vallesian of Inzersdorf (even if from an adult individual) has a less flattened lateral surface and a more oval cross-section than the holotype of *Dystychoceras pannoniae*, from Sopron. A frontlet similar to the one from Sopron was also found at Grizev in Ukraine and identified and figured as "*Dystychoceras*" in Korotkevich (1988). More findings are necessary to solve the *Dystychoceras* taxonomy problem.

Tobien (1953) refers to "*M.*" *pannoniae* some metatarsals from Sopron and Eppelsheim with lateral longitudinal groove. The discovery of such metapodials in the Vallesian of Spain (Can Llobateres, Santiga) led Moyá-Solá (1983) to identify this material as *M.* aff. *monacensis* or *M. pannoniae*, by assuming that this metatarsal morphology is typical of this genus (versus *Tragoportax* sensu this author). As we have noted, lateral and medial depressions were described on the metatarsals from Höwenegg referred to *M. pannoniae* by Romaggi (1987). However, if "*M.*" *pannoniae* belongs to a genus distinct from *Miotragocerus* (see also the cladogram in Fig. 18), these metatarsals could belong to a distinct genus, *Dystychoceras*, not to *Miotragocerus*.

The referral of the pre-MN9 material from Spain (see Moyá-Solá 1983) to *Miotragocerus* is also doubtful. The horn-cores from Hostalets inferior as well as the horn-cores of *Miotragocerus* sp. from Puente de Vallecias, etc. (Moyá-Solá 1983) are very small and not very compressed laterally and do not display the typical features of *Miotragocerus*.

Bouvrain (1988) refers the *Tragoportax* material from Dytiko, Greece (MN13) to the "small form" – *Tragoportax gaudryi* (= *M.* (*P.*) *gaudryi* in our meaning) and creates a new subspecies, *T. g. macedoniensis* for it. Recently, Bouvrain (2001) includes this form in *Dystychoceras*. However, from our cranial criteria (the shape of the basioccipital and the presence of a fronto-parietal postcornual depression, a combination of features know only in *Tragoportax*) the Dytiko form belongs to *Tragoportax* s.s.

As mentioned above, the skull of *Mirabilocerus brevicornis* from Arkneti, Georgia (Meladze 1967) displays some features of the genus *Miotragocerus*, but more detailed observations are necessary for a correct taxonomic decision.

One strongly laterally compressed horn-core from Weierburg (NHMW), with a length of *c.* 220 mm, a change of the curve of the apical part forward and a sub-oval basal section could represent the genus *Miotragocerus*.

M. (*Pikermicerus*) *gaudryi* is mentioned by Kostopoulos & Koufos (1996) in Nikiti-1 (Greece, the very end of the Vallesian?), but the known horns are slender and could represent an earlier stage of the genus (see also Bouvrain

2001). *M.* (*P.*) *gaudryi* is also present at Nikiti-2 (MN11), together with *Tragoportax*, described by Kostopoulos & Koufos (1999). Indeed, some of the material described by these authors as *Tragoportax* aff. *rugosifrons* (for example the distal metacarpal NIK-428) belong instead to *M.* (*Pikermicerus*) *gaudryi*. This metapodial with a distal transverse diameter of 34.4 mm and a maximum antero-posterior diameter of 24.0 mm is too small for *T. rugosifrons*, but matches the size of *M.* (*P.*) *gaudryi gaudryi* (see Annexe: Tables 4; 5).

From our observations on the Mecquenem collection in the MNHN, *Miotragocerus* (*Pikermicerus*) is probably present also in the early Turolian of Maragha along with *Tragoportax*.

Thus, at least two and perhaps four species of *Miotragocerus* can be recognized: two pre-Turolian ones, *M.* (*M.*) *monacensis* and *M.* (*M.*) *pannoniae* (perhaps not of this genus), a larger mostly Turolian one, *M.* (*P.*) *gaudryi* (Kretzoi, 1941) and possibly a fourth one, the small "*Tragoportax* (*P.*) aff. *gaudryi*" sensu Moyá-Solá (1983) from the late Vallesian of Western Europe. There is a general trend of size increase in the successive subspecies of the Turolian form: from *M.* (*P.*) *g. crusafonti* from the early Turolian of Piera (Spain) through the most widespread *M.* (*P.*) *g. gaudryi* from the so called "Greco-Iranian" province, to the late Turolian form from Western Europe, *M.* (*P.*) *g. leberonensis*. The early Turolian form from Le Coiron, "*Graecoryx andancensis*" (Romaggi in Demarcq *et al.* 1989) probably represents also a separate subspecies with strongly curved horn-cores, especially in females. The finds from Maramena, Greece (end of MN13) (Köhler *et al.* 1995) belong most probably to a relatively small *M. gaudryi* but the scarce material is not sufficient for definite conclusions. It may be that some of the known subspecies of *M.* (*P.*) *gaudryi* are in fact different at species level from the nominal subspecies of *M.* (*P.*) *gaudryi* but available data are insufficient, neither for an interpretation of the populations of *M.* (*P.*) *gaudryi*, nor for a comprehensive comparison with the Vallesian forms.
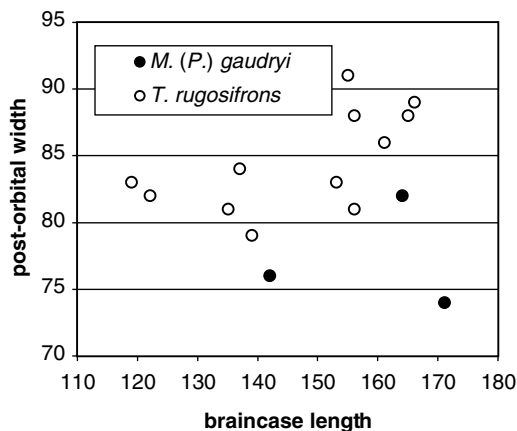
Fig. 16. — Neurocranial proportions, in mm, of *Tragoportax* and *M.* (*Pikermicerus*) from Hadjidimovo. Length of brain-case from front of horn-cores to top of occipital.

GENERAL DISCUSSION

THE HADJIDIMOVO MATERIAL AND THE TAXONOMY OF "*TRAGOPORTAX*" AND THE LATE MIOCENE BOSELAPHINI

Gaudry (1873) followed by Pilgrim & Hopwood (1928) was the first to note the presence in the site of mont Lubéron of a "race à cornes rapprochées" of a *Tragocerus amalthea* with short and massive, but not thick, horn-cores, inserted close to each other. Specimens from Pikermi with similar features were mentioned by Bohlin (1935) as "*Tragocerus* sp." as they differed from the "typical" *T. amalthea* based upon *Capra amalthea*. Today, most authors agree that there are 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 subtriangular in section (Moyá-Solá 1983). The smaller species, *T. gaudryi*, 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
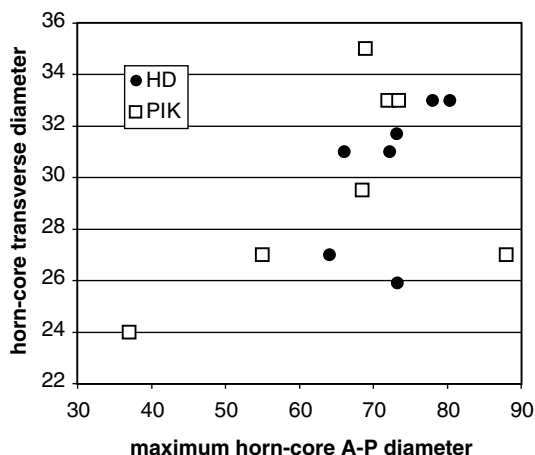
FIG. 17. — Comparison of the horn-cores proportions and dimensions, in mm, of *M.* (*Pikermicerus*) from Hadjidimovo and Pikermi. Abbreviations: **HD**, Hadjidimovo; **PIK**, Pikermi.

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).

Meanwhile, Solounias (1981) had divided, correctly in our opinion, the "*Tragoportax*" complex into two distinct genera: *Miotragocerus* (where he places the type specimen of "*Pikermicerus*" *gaudryi* Kretzoi) and *Tragoportax*. 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*. 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. 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. salmontanus.* In our conception, the genus *Tragoportax* includes the usually large Turolian forms with marked fronto-parietal postcornual depression and grooved basi-occipital as well as with horns long and clearly triangular in section (Figs 1; 2).

The parsimonious phylogenetic analysis of 16 cranial characters of 17 Boselaphini taxa (Annexe: Table 5) confirms largely the taxonomic conception proposed above (Fig. 18). It yields two trees that differ only slightly, in the position of "*Mirabilocerus*" *maius*. Both trees show that *Austroportax* diverged earlier than the other main Boselaphini clades: the *Protragocerus-Dystychoceras* clade, the *Miotragocerus* s.l. clade and the *Tragoportax* (*sensu* this paper) clade.

The position of *Dystychoceras* is not clear. As noted above, we include "*D.*" *pannoniae* into *Miotragocerus*, following Thenius' opinion (1948) that *Dystychoceras pannoniae* is a subadult individual belonging to the same taxon as the *Miotragocerus*-like horn-core from Inzersdorf. This hypothesis looks logical to some extent but is not proved. It is quite possible that *Dystychoceras* is a taxon distinct from *Miotragocerus* and closer to *Protragocerus*. On the other hand, the position of *Dystychoceras* in the cladogram could result from the large number of characters with dubious states. The position of "*Protragocerus*" *leskewitschi* close to *Miotragocerus* in the cladogram could also be an artefact of the large number of dubious character states, and the same is true of the position of *Protragocerus chantrei*. We can note that the horn-core surface structure and its degree of lateral flattening (not included in the cladogram characters) are similar for both latter taxa. "*Mirabilocerus*" appears, quite logically, as polyphyletic; this could be explained by the very different fronto-parietal and basioccipital characters in its two species. "*Mesembriportax*" and "*Mirabilocerus maius*" could be regarded as more distant members of the *Tragoportax* clade.

FIG. 18. — Cladogram of the main late Miocene Boselaphini taxa. Synapomorphies are shown for each node and for the terminal taxa. See Annexe: Table 5 for characters and states.

They do not seem to be closely related, as they share no exclusive synapomorphy. Finally, the grouping of *Miotragocerus monacensis*, "*Mirabilocerus brevicornis*" and *Pikermicerus gaudryi* in one clade (genus *Miotragocerus* sensu this paper) and on the other hand the clustering of "*Mesembriportax*", "*Mirabilocerus maius*" and the forms noted in the cladogram as *Tragoportax* s.s. in another clade is satisfactory: this distinction is mainly based upon the postcornual braincase surface and the basioccipital morphology – features that look more stable in evolution and less liable to quick adaptations than most horn characters.

THE *GRAECORYX* CASE

Graecoryx Pilgrim & Hopwood, 1928 was erected for *Tragocerus valenciennesi* Gaudry, 1865 based upon a skull fragment from Pikermi. The horn-cores and their disposition are very different from *Miotragocerus* (*Pikermicerus*) as well as from *Tragoportax*. The fronto-parietal postcornual morphology is not clear and the basioccipital structure is unknown because of the lack of the relevant parts of the skull. The taxonomic status of *Graecoryx* is controversial (Bohlin 1935; Gentry 1971; Thomas 1979; Moyá-Solá 1983; Bouvrain 1988), although further remains from

various localities were referred to this genus (Kretzoi 1941; Moyá-Solá 1983; Köhler 1987). Bohlin (1935) followed by Bouvrain (1988) expressed the opinion that the type of *Graecoryx valenciennesi* is a juvenile animal. The graceful horn-cores and the large intercornual surface of the type make this hypothesis quite likely.

The taxonomic alternative is the following:

– the type of *Graecoryx valenciennesi* and all *Graecoryx* specimens represent juvenile-subadult individuals of the *Miotragocerus-Tragoportax* complex. The fronto-parietal postcornual depression is not visible on the preserved part of the type but this could be a result of its young age. In this case the generic identity is unclear;

– *Graecoryx* represents a valid taxon of the *Miotragocerus-Tragoportax* complex. This second hypothesis is not supported by the available material, and is less parsimonious.

It would be wise, given this complicated and unclear situation, to restrict the use of the name *Graecoryx* to the type specimen of *G. valenciennesi*, without putting this name in synonymy with that of one of the members of the *Miotragocerus-Tragoportax* complex.

SEXUAL DIMORPHISM AND HORNS IN *TRAGOPORTAX* AND *MIOTRAGOCERUS*

The problem of the sexual dimorphism in *Tragoportax* s.l. was largely discussed in the literature (Meladze 1967; Solounias 1981; Moyá-Solá 1983; Thomas 1984; Bouvrain 1988; Korotkevich 1988). The opinions expressed differ widely according to the various controversial taxonomic views. The large Hadjidimovo sample and the new taxonomic conception suggest new interpretations on sexual dimorphism.

From the existing skull material, both sexes of *Miotragocerus* (*sensu* this paper) have horns. In *M.* (*Pikermicerus*), there are differences between sexes in horn-core shape and size, but they are not strong (much weaker than in *Tragoportax*). In size, general shape and limited number of demarcations, the females of *M.* (*Pikermicerus*) *gaudryi* are most probably similar to subadult males. In relation to this observation we generally agree

with Thenius (1948), Meladze (1967), Solounias (1981) and Moyá-Solá (1983).

The situation is more complex in *Tragoportax* (*sensu* this paper). In some species (probably in *T. curvicornis*; see Solounias 1981) females can be hornless. In the other forms, females possess horns, which are most probably much smaller than in males. Somewhat less pronounced is the horn sexual dimorphism in the late *T. macedoniensis* form, probably secondarily adapted to more forested conditions (see below). The two definite adult female skulls in the Hadjidimovo sample (HD-5130, HD-5138) demonstrate, against previous views, that females of *T. rugosifrons* have horns. These two skulls (as some other possible female skulls; Annexe: Table 1) have all typical cranial features of *Tragoportax*. In both specimens the skull size differences with male skulls are weak but the preserved horn-core bases have very small diameters and nearly round cross-section in spite of the marked postero-lateral keel (HD-5130). A *Tragoportax* frontlet (possibly *T. rugosifrons*) with the same shape and size of the horn-core (female features) is known from Kocherinovo 1 (SW Bulgaria, MN11?). At Prochoma, the young-adult skull PXM-17 displays male features in its horn-cores and probably belongs to young male (Bouvrain 1994: pl. I-1a, 1b, pl. II-2). On the other hand, from the description (Bouvrain 1994: 65), the frontlet PXM-89 could belong to a female. No definite hornless skull is known among the remains of *T. rugosifrons* and *T. amalthea*. In any case it seems that in the genus *Tragoportax*, living in more open landscapes (see below), the sexual dimorphism in horns is stronger than in *Miotragocerus*.

TAPHONOMY AND ECOLOGY OF *TRAGOPORTAX* AND *MIOTRAGOCERUS* AFTER THE HADJIDIMOVO DATA

AGE POPULATION STRUCTURE OF *T. RUGOSIFRONS* FROM HADJIDIMOVO-1 AND CAUSES OF BONE ACCUMULATION

The large number of *Tragoportax rugosifrons* mandibles and mandibular fragments from

Hadjidimovo-1 gives the opportunity to study the population structure of the taphocoenosis, using mortality curves (Klein 1982). Taking into account the influence of more complex factors (Valli 2001), they could be used to draw conclusions about the causes of the animals death. The 159 mandibles and mandibular fragments with teeth were sorted by us into six age classes. For this purpose the tooth eruption and replacement were examined on the more complete mandibles and tooth-rows. The more fragmentary mandibles were aged by means of comparison of their tooth wear with the stage of wear of the complete and classified tooth-rows. The age classes are determined as follows:

1) juveniles: tooth-rows with milk dentition and without permanent m2-m3;

2) subadults: m3 is visible, but not totally erupted;

3) young-adults: m3 is in place, but practically unworn;

4) adults: m3 slightly worn;

5) old-adults: tooth-row considerably worn, but more than half of the crown of m3 remains;

6) very old individuals (vetus stage): highly worn tooth-row (height of m1 hypoconid less than 7.1 mm).

To diminish the possible error these six age classes were reduced to four, following the example of Blumenshine (1991) (see Valli 2001) by fusion of groups 3 and 4 into a single group of adults, as well as groups 5 and 6 into a single group of old and very old specimens.

The histogram (Fig. 19) is characterized by a high number of adults in optimal individual age and smaller number of old individuals. The very low share of the juveniles (noted also for the other species of the taphocoenosis) is most probably related to the specific conditions in the Hadjidimovo taphocoenosis leading to the destruction of the more fragile bones. Such a curve shape differs from the attritional profile that is typical for age-dependent mortality in the accumulation. Instead, the curve is quite similar (Fig. 19) (see Valli 2001) to the catastrophic mortality curve, characteristic for accumulations related to natural disasters. This result is consis-
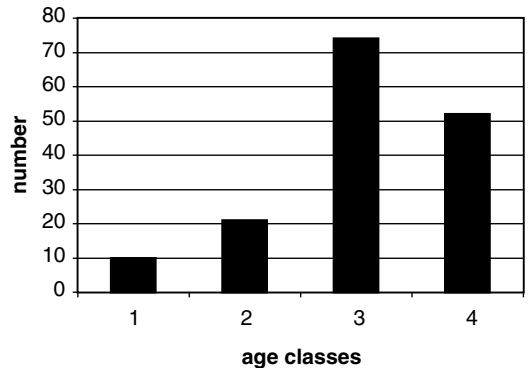
FIG. 19. — Mortality profile of *Tragoportax rugosifrons* (Schlosser, 1904) from the Hadjidimovo taphocoenosis.

tent with the hypothesis proposed recently for the formation of the whole taphocoenosis of the locality (Spassov 2002).

MORPHOFUNCTIONAL CHARACTERISTICS AND ECOLOGY OF *MIOTRAGOCERUS* (*PIKERMICERUS*) *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 walls. The horns are relatively short with little 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, the 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 than *M.* (*Pikermicerus*): Spassov 2002).

Sexual dimorphism in the horns of *M.* (*Pikermicerus*) is weaker than in *Tragoportax* but more expressed than in modern highly gregarious animal of the open spaces (see Janis 1986). This

particularity of *M.* (*Pikermicerus*), together 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 signals, 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 *M.* (*Pikermicerus*), in probable mosaic landscapes. In this respect, it is comparable to modern *Hippotragus*.

Our conclusions on the ecology and distribution of *Tragoportax rugosifrons* and *M.* (*Pikermicerus*) *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 in the same level at Hadjidimovo demonstrate, in contrast to previous opinions, that they can co-exist. It is likely, therefore, that they co-existed also in Pikermi, as they did in Halmyropotamos, Veles-Karaslari, Maragha and probably Nikiti-2 and Maramena (see above). The Turolian Pikermian biome (Solounias *et al.* 1999) of the "Greco-Iranian" province was dominated, according to these authors, by relatively homogenous woodlands. Alternatively, the Pikermian biome and especially the landscape from Hadjidimovo may have been represented by forest-savannah-like (in terms of physiognomy of the landscape) biotopes and not by hardly penetrable dense thickets and woods (Spassov 2002). The above mentioned ethological interpretations of the morphological characteristics of *M.* (*P.*) *gaudryi* and *T. rugosifrons* support mostly the second opinion. 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.

One of the latest representatives of *Tragoportax*, *T. macedoniensis*, could be a relic form of the wooded habitats, or probably documents a neotenic reversal (degradation of horn and body size) and additional new re-adaptation. Living in woody local conditions (Bonis *et al.* 1992), it reverted to some adaptations to forest environment, concerning size and proportions, as are well known in recent populations of various ungulates: relative brachyodonty and long premolar row, as well as relatively small body and horn size (see Bouvrain 1988).

CONCLUSIONS ON THE *MIOTRAGOCERUS/TRAGOPORTAX* COMPLEX. TAXONOMY, EVOLUTION, ADAPTATION AND DISTRIBUTION IN TIME AND SPACE

The skull characters show a clear distinction of two different genera within the group up to now referred to *Tragoportax*: *Miotragocerus* and *Tragoportax* s.s. The former could be divided into two subgenera – *M.* (*Miotragocerus*) and *M.* (*Pikermicerus*). The subgenus *M.* (*Pikermicerus*) appears later than *M.* (*Miotragocerus*) and is more evolved in horn characters. *Miotragocerus* is the earlier of the two genera (from the end of MN8? onwards) and has less evolved features (tooth morphology and cheek-teeth proportions, horn dimensions and dimorphism, body size) than *Tragoportax*. These morphological particularities could be interpreted as an indication of a life in more woody habitats as well as of probably less evolved sociality. Because of these habitat requirements, *Miotragocerus* ranges in the Turolian not only in the Balkano-Iranian province but also in the denser habitats of Western Europe. The more derived characters of the later genus *Tragoportax* s.s. indicate adaptation towards relatively more open space and more grazing foraging strategy. That is why it could not penetrate in the more forested landscapes of Western Europe, but is more common in the Turolian Balkano-Iranian province than *Miotragocerus*. *M.* (*Pikermicerus*)

and *Tragoportax* coexisted in the eastern parts of the *M.* (*Pikermicerus*) range, in the Turolian mosaic landscapes close in physiognomy to the forest-savannah, where they occupied different ecological niches.

Acknowledgements

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ANNEXE

TABLE 1. — Skull dimensions, in mm, and morphological features of *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo (coll. of the Assenovgrad Paleontology Museum), *T. amalthea* and *M.* (*Pikermicerus*) *gaudryi* from Pikermi (MNHN, University of Athens) and *Tragoportax* from Samos (NHM-Wien; PIM).

	HORN-CORES									
	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	Mini. post-orbital width	Max. occipital width	Bi-condylar width
HD-2007, ♂	64	60	27	-	107	38	-	76	84+	60
HD-2039, ♂	30.3	64	33	-	106	38	46	82	94	57
HD-5519, ♂	78	67	33	145+	-	-	-	-	-	-
HD-2010, ♂	73.1	64	31.7	175+	99	34	41.6	74	90	57
HD, mean, ♂	72	62	31	168	104	38	44	79	91	58
MNHN-PIK-2439	-	-	-	-	-	-	-	-	93	58
MNHN-PIK-2366, ♂	88	70	27+	-	-	-	-	-	-	-
MNHN-PIK-2285	80	70	33.4	240+	-	-	-	-	-	-
MNHN-PIK-2286	90	76	33+	-	-	38	-	78.4	98.5	57
MNHN-PIK-2287	79.2	70.1	45.5	-	123	37	-	82.7	110	-
MNHN-PIK-2288, ♂	88.8	63	30	-	-	-	-	-	95+	59+
MNHN-PIK-2376	-	-	-	-	-	-	-	-	105	64
MNHN-PIK-2379	-	-	-	-	-	-	-	-	100	58
PIK-Athens	83	63.5	49	285	127	-	47	-	97.5	-
PIK, mean	80	67	39	274	118	38	45	82	102	60
NHMW-SAM-V,12, ♂	73.5	68.5	33	325	105	-	37	82	102	-
PIM-SAM-66	-	-	-	-	110	-	42	82	-	58
PIM-SAM-70, ♂	74	65.5	40.3	360	119	-	55	83	109	68
HD-5140, ♂ sub-adult	-	34.4	32.4	-	-	48	-	77	85+	-
HD-3034, ♂ sub-adult	-	35.5	33.8	-	-	-	-	79	96	-
HD-2011, ♂	76	68	43	235+	-	-	-	81	-	-
HD-2327, ♂ sub-adult	-	37	30	-	107	42.5	42	81	99	66.6
HD-2322	37?	34.4	29.5	-	109	42	-	82	-	-
HD-2006, ♂	60	51	38	-	116	50	-	83	103	68
HD-2027, ♂	61	56	35	210+	127	61	-	83	105	72
HD-2326	-	31	30	-	108	50	-	83	-	-
HD-5130, ♂	-	37	32	-	-	-	-	84	-	-
HD-2023, ♂	79	-	36	-	-	61	-	86	115	-
HD-2001, ♂	71	64	44	-	123	-	-	88	-	-
HD-5129, ♂	67	56	38	200+	117	-	36	88	-	-
HD-5132, ♂	73	62	42	-	128	-	54	89	110	71
HD-5125 (= 2040), ♂	70	60	35	-	123	-	56	91	109	68
HD-5127, ♂	58	55	34	285	-	-	-	-	110	72
HD-2306, ♂	-	-	-	-	-	-	-	-	107	69
HD, mean, ♂	68	59	38	243	122	59	49	87	108	70

BRAIN-CASE												
Occipital height	Width over post. tuberosities of basioccipital	Width over ant. tuberosities of basiocipital	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
M. (P.) gaudryi												
43	36	25	22	162	142	163	-	-	-	-	-	-
44	-	-	-	192	164	178	-	-	-	-	-	-
43	-	-	-	152	169	110	-	-	-	-	-	-
42	33	24.5	29	191	171	182	-	-	-	-	-	-
43	35	25	21	182	159	173	110	-	-	-	-	-
45	-	-	-	-	-	-	-	-	-	52	-	-
-	37.5	-	-	-	155	-	-	159	-	52	-	99
T. amalthea												
57	-	-	-	157	-	-	-	-	-	-	-	-
50	-	28.5	42	174	-	-	-	-	-	-	-	-
50	-	-	-	-	164	-	-	-	-	-	-	-
53	-	-	-	179	-	-	-	-	-	-	-	-
46	38	36	-	-	-	-	-	-	-	-	-	-
45	34	26	40	-	-	-	-	-	-	-	60	-
-	-	-	-	-	-	-	-	-	-	-	47	-
50	35	29	41	170	164	-	-	-	-	-	-	-
T. amalthea?												
41+	-	-	-	165	147	170	-	-	-	-	-	-
T. amalthea												
-	32.3	23.7	-	148	-	-	-	-	-	-	-	-
T. curvicornis												
49.5	32.7	26.4	42.3	172		183						
T. rugosifrons												
47	-	-	-	-	-	-	-	-	-	-	-	-
-	-	36.3	37	155	139	-	-	-	-	-	-	-
-	-	-	35	-	156	-	-	-	-	-	-	-
41.6	41	29	37	159	135	154	-	-	-	-	-	-
40	36	28	37	-	122	-	-	-	-	-	-	-
46	42	25	37	-	-	-	-	-	-	-	-	-
50	44	25	38	165	153	183	-	-	-	-	-	-
-	-	-	26	-	119	-	-	-	-	-	-	-
-	-	-	37	145	137	-	-	-	-	61	42.7	103
48	42	26	42	-	161	-	-	-	-	-	-	-
-	-	-	44	171	156	-	-	-	-	62.5	42	103
47	46	27	-	173	165	-	139	-	-	-	-	-
45	43	30	42	173	166	187	135	243	260	65.5	46	109
45	41	24	35	169	155	177	132	236	256	66.3	-	111
41	39	23	43	-	145	183	134	232	-	-	44.3	103
42	43	28	-	-	-	-	-	-	-	-	-	-
46	43	26	40	170	157	183	135	237	258	-	-	-

TABLE 2. — Mandibular teeth dimensions, in mm, of *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo.

Measurements	p2-m3	m1-m3	p2-p4
Tragoportax rugosifrons			
HD-2506	-	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	-	68.0	-
HD-2489	-	68.2	-
HD-2519	-	67.9	-
HD-2524	-	70.3	-
HD-3896	-	69.1	-
HD-2527	110.1	72.4	41.8
HD-2480	-	71.7	-
HD-2484	-	70.5	-
HD-2489	-	68.2	-
HD-2440	121.0	73.6	47.0
HD-2518	-	68.6	-
HD-2524	-	70.5	-
HD-2497	-	-	-
HD-2445	-	65.4	-
HD-2501	-	67.1	-
HD-2468	-	-	-
HD-2565	-	66.9	-
HD-2493	-	68.7	-
HD-2520	-	68.7	-
Miotragocerus (*Pikermicerus*) *gaudryi*			
HD-3839	102.0	59.2	46.2
HD-3825	101.0	57.7	45.0
HD-3894	-	57.4	-
HD-3895	96.0	59.4	40.1
HD-2499	93.5	52.8	39.8
HD-2469	-	-	-
HD-3590	-	55.4	-
HD-3828	-	53.8	-
HD-3588	-	-	-

TABLE 3. — Metacarpal dimensions, in mm, of *Tragoportax rugosifrons* (Schlosser, 1904) from Hadjidimovo.

	Proximal transverse diameter	Proximal antero-post. diameter	Distal transverse diameter	Distal antero-post. diameter	Minimum width of shaft	Length
38001	40.5	29.1	41.5	30.8	25.1	254.0
38059	-	-	39.8	30.0	24.4	-
38061	-	-	42.3	30.3	23.9	-
38010	-	-	42.7	30.7	23.4	-
38039	-	-	44.7	30.9	25.0	-
38374	41.6	28.7	-	-	24.0	-
38035	-	-	38.4	30.0	23.1	-
38022	-	-	41.0	29.6	24.0	-
38030	-	-	41.2	30.6	-	-
38034	-	-	41.5	29.5	-	-
38026	-	-	42.0	28.5	-	-
38071	-	-	42.0	28.3	-	-
38023	-	-	41.8	30.0	-	-
38047	-	-	41.2	29.0	-	-
38041	-	-	40.3	29.8	-	-

TABLE 4. — Metatarsal dimensions, in mm, of *Tragoportax rugosifrons* (Schlosser, 1904) and *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941) from Hadjidimovo.

	Proximal transverse diameter	Proximal antero-post. diameter	Distal transverse diameter	Distal antero-post. diameter	Minimum width of shaft	Length
Tragoportax rugosifrons						
38002	36.0	38.7	42.7	30.4	24.5	258.0
32004	35.7	36.0	40.8	29.8	24.3	265.0
38003	39.0	39.6	43.6	30.0	24.9	257.0
38043	-	-	-	28.5	23.5	-
38042	-	-	41.2	29.5	-	-
-	-	-	42.9	28.9	24.0	-
38060	-	-	-	27.8	24.3	-
38036	-	-	41.2	30.0	-	-
38076	-	-	43.5	30.1	-	-
38057	-	-	43.2	30.2	-	-
38006	-	-	38.6	28.5	-	-
38055	-	-	39.6	27.8	-	-
38029	-	-	41.2	30.0	-	-
Miotragocerus (*Pikermicerus*) *gaudryi*						
38370	32.0	29.7	-	-	19.0	220?
38007	-	-	31.5	23.0	17.7?	-
-	-	-	31.7	25.8	-	-
38015	-	-	33.8	24.6	-	-
38053	-	-	33.5	25.3	-	-

TABLE 5. — Matrix of cranial features used in the cladistic analysis illustrated in Figure 18.

	Character	State 0	State 1	State 2	State 3
1	basioccipital	keel	groove		
2	occipital	triangular	rectangular		
3	fronto-parietal depression	absent	present		
4	temporal lines	strong	moderate	weak	
5	intercornual plateau	very broad	broad, rectangular	narrow, triangular	
6	females with horns	no	yes		
7	horn-cores proportions	long and slender	short and slender	short and thick	
8	caudal border	very concave	concave	straight	convex
9	change of curvature	no	yes		
10	divergence	weak	strong		
11	basal section	triangular	triangular, rounded	oval, with anterior keel	
12	course of keels in anterior view	double convex	straight	double concave	
13	steps	no	1 or 2	very marked	
14	grooves on horn-cores	absent or weak	strong		
15	rugosities on bases	absent or weak	moderate	strong	
16	premolars	short	long		
17	size	small	large		

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Primitive	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	0
Protragocerus chantrei	?	?	?	?	?	?	?	2	0	?	1	?	?	?	?	?	0
Protragocerus ?leskewitschi	0	0	0	1	1	?	1	0	0	0	1	0	?	0	0	1	1
Austroportax latifrons	1	1	0	1	0	?	1	1	0	0	0	0	0	1	0	?	0
"Dystychoceras" pannoniae	?	?	?	?	?	?	1	2	1	0	1	0	2	0	0	?	0
"Mirabilocerus" brevicornis	0	?	?	2	2	?	2	1	1	0	2	?	1	0	0	?	1
M. (Pikermicerus) gaudryi	0	0	0	2	2	1	2	1	1	0	2	2	2	0	2	1	1
M. (Miotragocerus) monacensis	?	?	0	0	0	?	2	2	1	0	2	1	1	0	0	?	1
Tragoportax rugosifrons	1	1	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1
Tragoportax amalthea	1	1	1	1	1	1	0	1	1	0	0	0	1	0	1	0	1
"Mesembriportax" acrae	1	1	1	1	1	?	0	3	1	1	1	0	1	0	0	1	1
Tragoportax cyrenaicus	?	?	?	?	?	?	0	1	0	1	0	0	0	0	0	?	1
Tragoportax curvicornis	1	1	1	0	1	?	0	0	0	0	0	1	1	0	0	?	1
Tragoportax macedoniensis	1	?	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1
"Mirabilocerus" maius	1	1	1	1	1	?	2	1	1	0	?	?	2	0	0	?	1
Protragocerus labidotus	1	0	0	1	0	0	1	3	1	0	2	0	1	0	0	0	0