The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey

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ABSTRACT

KEY WORDS
Mammalia,
Artiodactyla,
Bovidae,
late Miocene,
middle Turolian,
Akkaşdağı,
Central Anatolia,
Turkey.

The study of the bovid material from Akkaşdağı allows the identification of seven species: *Gazella* cf. *capricornis*, *Gazella* aff. *pilgrimi*, *Prostrepsiceros rotundicornis*, *Miotragocerus valenciennesi*, *Tragoportax* aff. *amalthea*, *Pachytragus crassicornis*, and *Palaeoryx majori*. The balanced bovid assemblage of the locality indicates an upper middle Turolian age (MN 12). Several aspects of the late Miocene bovid taxonomy and systematics are also discussed. Hence, the re-instatement of *Miotragocerus valenciennesi* over *Tragoportax gaudryi* and the priority of *Miotragocerus* over other generic names are suggested (*Tragocerus*, *Graecoryx*, *Sivaceros*, *Pikermicerus*, *Dystychoceras*). Moreover, *Palaeoryx majori* is recognized as a valid species and the chrono-spatial relations of *Prostrepsiceros* and *Protoryx/Pachytragus* lead to some alternative working hypotheses.

RÉSUMÉ

MOTS CLÉS
Mammalia,
Artiodactyla,
Bovidae,
Miocène supérieur,
Turolien moyen,
Akkaşdağı,
Anatolie Centrale,
Turquie.

Les Bovidae (Mammalia, Artiodactyla) du Miocène supérieur d'Akkaşdağı, Turquie.
Sept espèces de Bovidae sont déterminées dans l'assemblage faunique d'Akkaşdağı : *Gazella* cf. *capricornis*, *Gazella* aff. *pilgrimi*, *Prostrepsiceros rotundicornis*, *Miotragocerus valenciennesi*, *Tragoportax* aff. *amalthea*, *Pachytragus crassicornis* et *Palaeoryx majori*. D'après les bovidés, l'âge du gisement peut être placé dans la partie supérieure du Turolien moyen. La systématique de divers taxons de Bovidae du Miocène supérieur a été discutée. Cette étude suggère l'usage de *Miotragocerus valenciennesi* plutôt que celui de *Tragoportax gaudryi* et la priorité de *Miotragocerus* sur d'autres noms de genres (*Tragocerus*, *Graecoryx*, *Sivaceros*, *Pikermicerus*, *Dystychoceras*). De plus, *Palaeoryx majori* est reconnu comme une espèce valide, alors que les rapports spatio-temporels de *Prostrepsiceros* et *Protoryx/Pachytragus* conduisent à proposer des hypothèses de travail alternatives.

INTRODUCTION

An important quantity of bovid material including about 480 specimens determinable at bone-level was unearthed from old and new fieldwork at the late Miocene mammal locality of Akkaşdağı (Central Anatolia, Turkey). Preliminary reports from Akkaşdağı (Kazancı *et al.* 1999) already indicate a significant bovid association. New data provided from the 2000-2001 campaigns notably enrich the faunal record of the locality, allowing the recognition of six bovid genera and seven species.

The material comes from the excavations at Akkaşdağı between 1997 and 2001. The bone pockets, all at the same stratigraphic horizon, are numbered as AK2, AK3... (2000-2001 excavations) or AKA and AKB (1997 excavations). Material is preserved at the Natural History Museum in Ankara (MTA).

Late Miocene bovids from Turkey are already quite well known through the works of Ozansoy (1965), Tekkaya (1973a, b), Bosscha-Erdbrink (1978), Köhler (1987), Bouvrain (1994a), Geraads & Güleç (1999) and Gentry (2003). The bovid association from Akkaşdağı provides, however, new data on the systematics of late Miocene Bovidae and improves the Turkish record.

The bovid material from Akkaşdağı includes cranial, dental and postcranial elements. The limb bones are, however, not statistically significant in order to provide reliable information although they can sometimes be attributed to the determined forms. Thus, the study is mainly focused on skulls and dentitions. The description of dental material follows the terminology used by Heintz (1970). All measurements are in millimetres.

ABBREVIATIONS
Museums and localities

AeMNH	Aegean Museum of Natural History-Zimalis Foundation, Samos island, Greece;
AK (A, B, K, 1-14)	Akkaşdağı new collection;
AMNH	American Museum of Natural History, New York;
BMNH	Natural History Museum, London;
DTK	Dytiko 1, Axios valley, Greece;

GOK	Akkaşdağı Heintz' collection;
KTA,B,D	Kemiklitepe A,B,D, Turkey;
LGPUT	Museum of the Geological Department, Aristotle University of Thessaloniki;
MGL	Musée cantonal de Géologie, Lausanne;
MNHN	Muséum national d'Histoire naturelle, Paris;
MTA-MA	Maden Tetkik ve Arama Museum [Geological Survey], Ankara;
NHMW	Naturhistorisches Museum Wien;
NKT & NIK	Nikiti-1 & 2, Greece;
PIK	Pikermi, Greece;
PIM	Geological and Paleontological Institute of Münster;
PXM	Prochoma, Axios valley, Greece;
RZO	Ravin des Zouaves 5, Axios valley, Greece;
VTK	Vathylakkos 2, Axios valley, Greece.

Measurements

7	at 7 cm from the base;
b	base;
DAP	anteroposterior diameter;
dex	right;
DT	transverse diameter;
H	height;
L	length;
sin	left;
W	width.

SYSTEMATICS

Genus *Gazella* Blainville, 1816

Gazella cf. *capricornis* (Wagner, 1848)

MATERIAL EXAMINED. — Part of skull: AK5-598, AKB-29, AK2-443; frontlets: AK2-72B, AK2-68, AK2-444, AK4-78, AK5-600, AK5-602, AK5-599, AK6-293, AK12-72; isolated horn-cores: AK2-72Asin, AK2-153dex, AK2-154dex, AK2-44Bsin, AK2-447dex, AK2-446, AK2-449, AK2-450dex, AK2-455sin, AK2-66dex, AK2-67sin, AK2-71sin, AK2-76dex, AK3-120sin, AK3-71sin, AK3-193dex, AK4-74, AK4-79, AK5-190dex, AK5-603sin, AK5-640dex, AK6-65sin, AK6-66sin, AK6-67dex, AK7-163dex, AK7-30dex, AK11-60, AK11-76, AK13-24dex, AK14-15, AKK-193sin, AKK-76, AKK-98, GOK-188, GOK-189; upper toothrows: AK6-82sin, AK6-224dex, AK6-157sin, AK7-32dex, AK3-169dex, AK12-73sin, AK12-74dex, AK12-76dex, AK13-25dex; lower toothrows: AK2-65sin, AK3-77sin, AK3-189sin and dex, AK3-
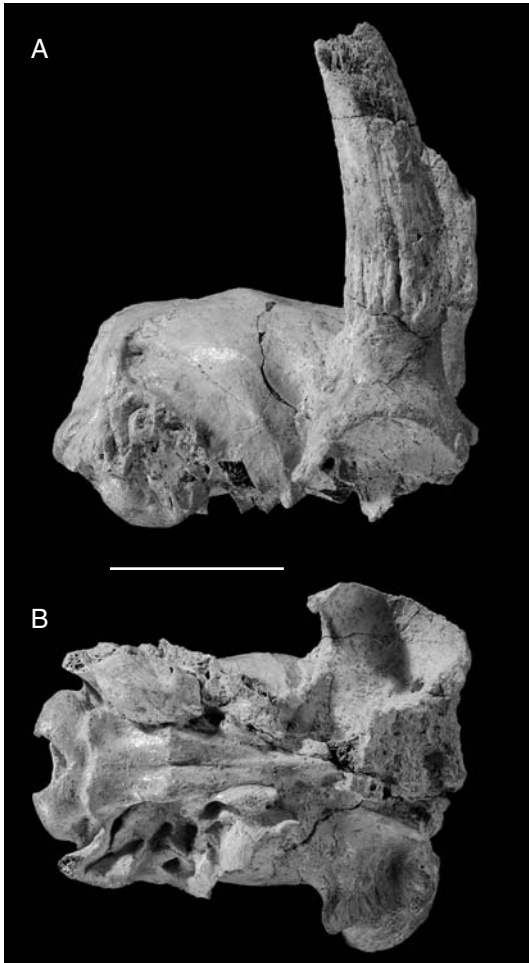
FIG. 1. — *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı, skull AKB-29; **A**, lateral view; **B**, ventral view. Scale bar: 5 cm.
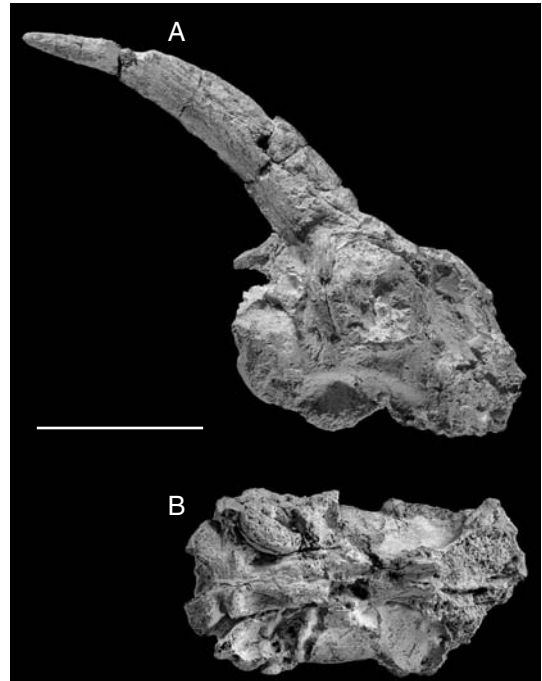

FIG. 2. — *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı; **A**, skull AK2-443, lateral view; **B**, skull AK5-598, ventral view. Scale bar: 5 cm.

301dex, AK4-89dex, AK12-83sin, AK5-205sin, AK5-206sin, AK5-262dex, AK5-257sin, AK6-73sin, AKB-72, AKB-93, GOK-211.
Tentatively attributed: distal part of humerus: AK3-191, AK4-82, AK5-46; proximal part of radius: AK3-192, AK7-174; metacarpals III+IV: AK6-309, AK4-205 (young); astragals: AK4-84, AK4-83, AKK-198, AK7-177; calcaneum: AK3-74; proximal part of metatarsals III+IV: AK4-122, AK7-106; phalanx I: AK6-84, AK11-4, AK3-195, AK4-87.

DESCRIPTION
Skull
The description of the skull morphology is based on the specimens AKB-29, AK5-598 and AK2-443

(Appendix: Table 1). In lateral profile the braincase is slightly convex (Fig. 1A). The interparietal is large. The face bends on the cranial roof at an angle of about 140° (AK5-598). The frontals form two shallow depressions at the postero-medial side of the pedicles. The frontoparietal and interfrontal sutures are open and the latter one appears slightly constricted between the horn-cores. The pedicles are relatively high. The supraorbital foramens are placed into triangular pits. The postcornual groove is elongated and usually deep. The orbit is large and rounded (Fig. 2A). Its anterior end is placed above the anterior lobe of M3. The lacrymal fossa is shallow and wide. The infraorbital foramen opens above the limit P2-P3. The palate is deep. The choane opens behind M3 and the median indent behind the lateral one. The angle basioccipital-occiput is 82° (AKB-29). The occiput is low and pentagonal shaped with strong nuchal crest. The occipital foramen is large comparatively to the condyles. The elongated and narrow paroccipital
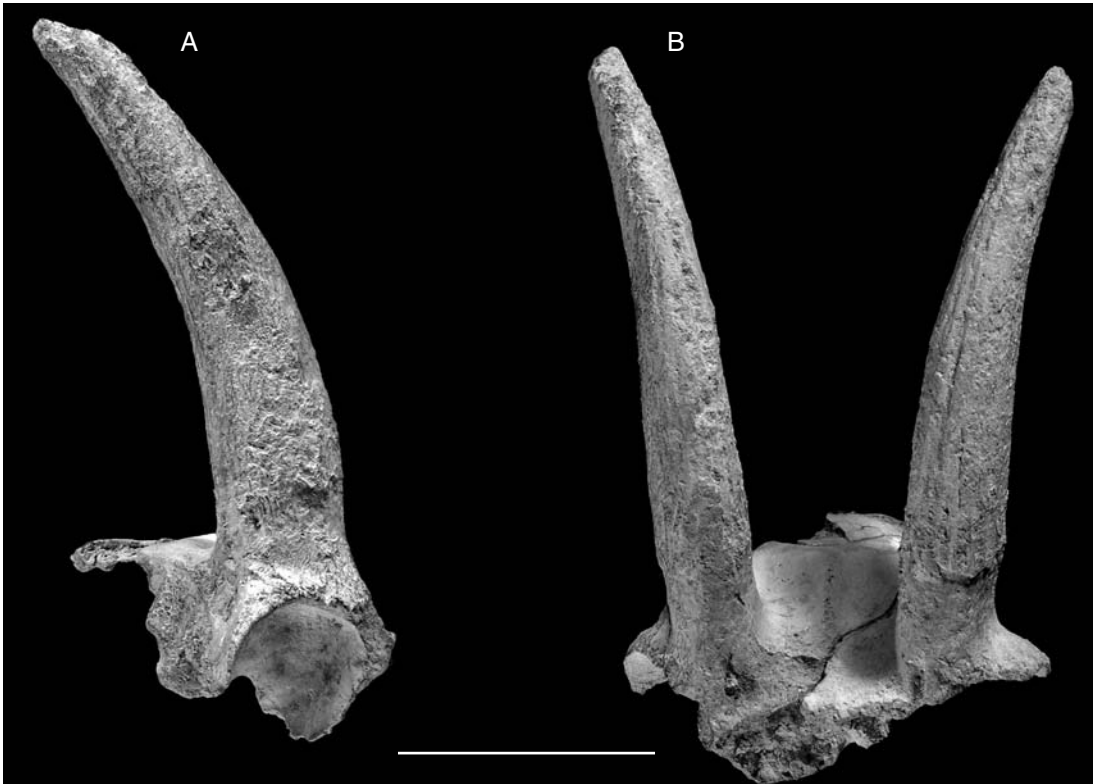
FIG. 3. — *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı, frontlet AK12-72; **A**, lateral view; **B**, frontal view. Scale bar: 5 cm.

processes are curved medially. The auditory bulla is large (length 27 mm in AKB-29 and 20 mm in AK5-598) and its posterior end is placed slightly behind the posterior tuberosities. The general shape of the basioccipital is trapezoid (Figs 1B; 2B). The posterior tuberosities are large, crest-like and vertical to the sagittal plane. The anterior tuberosities are smaller, sub-rounded and bulbous with their greater axis parallel to the sagital plane. A wide furrow is formed between them. The oval foramen is large, opening just in front of the anterior tuberosities.

Horn-cores
The horn-cores are relatively short and robust, inserted just above the orbits, moderately tilted ($\approx 75°$ with the cranial roof) and smoothly curved backwards (Figs 1A; 3A); the curvature index ("Length along the anterior face of the horn-core against height of its posterior face $\times 100$") varies between 116 and 136 (n = 7). The lateral face of the horn-cores is flat and the internal one slightly convex. They are widely separated on the frontals (internal distance at the base between 22.3 and 28.0 mm; Fig. 3B). Their average divergence angle is about 25° (22-27°) but the degree of divergence increases from the base (almost parallel) to the top (strongly directed laterally). The cross section passes from elliptical at the base to round towards the tips (Appendix: Table 2). The anterior and posterior surfaces of the horn-cores bear one to three deep longitudinal grooves. One of them, placed in a posterocentral position, seems to be the most stable.

Although the horn-core general morphology follows the above-mentioned characters, their development varies considerably, affected mainly by ontogenetic growth. The mean length of young

adults and adults is 117.4 mm (n = 18), varying between 105 and 125 mm. Young individuals present shorter horn-cores (90-100 mm). The mean index DT × 100/DAP is 80.76 at the base and 85.94 at 7 cm from the base, indicating a reduction of the mediolateral compression from the base to the top. Excluding young individuals these values slightly decrease (80.41 and 85.68 respectively). DAP_b presents a negative allometry in relation to DT_b (a = 0.85), which means that the transverse diameter increases more rapidly that the anteroposterior one. This is mainly true for adult individuals (a = 0.6) while the relation is rather isometric in the young ones (a = 1.05). On the contrary, at 7 cm from the base, the regression presents a plasmatic isometry (a = 1.03) for the total sample, being always negative for the adults (a = 0.78) but strongly positive for the youngs (a = 1.27). In other words it seems that the anteroposterior diameter increases more rapidly in the immature individuals than in the adults.

Dentition

The skull specimens AK5-598 and AK2-443 preserve their upper dentition, helping the determination of isolated toothrows (Appendix: Tables 3; 4). The premolar row is short comparatively to the molars; the premolar/molar ratio varies between 67.7 and 74.6 for the upper toothrow and 55.2 and 56.4 for the lower one. P2, 3 are slightly bilobed and asymmetrical. There is no basal pillar on the upper molars; their paracone is strong and the metastyle weak.

The paraconid and the parastylid are independent in the upper half of the lower third premolar crown. The metaconid directs backward and fuses with the entoconid. p4 is similar with p3 but the metaconid, entoconid and entostylid fuse together more rapidly. m1 and m2 bear a small basal pillar (Fig. 5B). m3 has a strong parastylid. The talonid of m3 has flat lingual face and bears a strong postero-lingual stylid.

Postcranials

Although the available postcranials attributed to *Gazella* are quite numerous, there is no way to be distinguished at species level.

FIG. 4. — *Gazella* aff. *pilgrimi* Bohlin, 1935 from Akkaşdağı, frontlet AK5-601, lateral view. Scale bar: 5 cm.

Gazella aff. *pilgrimi* Bohlin, 1935

DESCRIPTION

Despite the great variability observed in the predominant *Gazella* cf. *capricornis* from Akkaşdağı, several specimens with clear gazelline morphology are placed out of the suggested limits (either morphologically or dimensionally), indicating the presence of a second, badly documented *Gazella* species. Three specimens can be certainly placed in this form: the frontlet AK5-601 (Fig. 4) and the horn-cores AK5-642 and GOK-184.

In contrast to the previous gazelle, the horn-cores of this form are more closely situated at the base, longer (> 130 mm), less diverged and more tilted and curved backwards (52° in AK5-601) with a
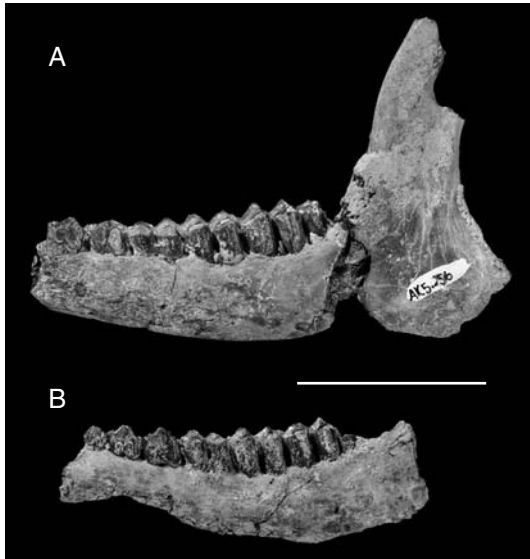
FIG. 5. — *Gazella* from Akkaşdağı, mandibles, labial view; **A**, *G.* aff. *pilgrimi* Bohlin, 1935, AK5-256; **B**, *G.* cf. *capricornis* (Wagner, 1848), AK3-189. Scale bar: 4 cm.

shorter pedicle, smaller and shallower postcornual groove and slightly larger mean size (Appendix: Table 5). They lack the deep longitudinal grooves on their surface and they appear more compressed mediolaterally, especially in their upper half (Appendix: Table 5). The index DT × 100/DAP varies between 75.1 and 84.5 at the base becoming smaller towards the top (Appendix: Table 5), indicating an opposite pattern comparatively to the described *G.* cf. *capricornis*.

Several other horn-core specimens (GOK-183, AKA-42, AKA-49, AKB-45) showing longer horn-cores, shorter pedicles and/or stronger mediolateral compression than in *G.* cf. *capricornis*, seem also to belong to this form.

A part of skull (AK2-442) and a mandibular ramus (AK5-256) can also provisionally be ascribed to them. The skull specimen AK2-442 preserves only the braincase and part of the frontals. The maximum width of the braincase is 64.6 mm versus 51.9-58.0 mm in *G.* cf. *capricornis*, indicating a slightly larger size (at about 25%). The teeth of the mandible AK5-256 (Fig. 5A) are slightly larger than that of *Gazella* cf. *capricornis*

(length m1-m3: 40.6 mm in AK5-256) but of the same hypsodonty. The molars bear basal pillars and the second valley of p3 is rather open.

COMPARISON

Gazella is recorded in the Akkaşdağı fauna by two unequally represented species of slightly different size. The predominant species is characterized by medium size, short premolar row, robust and relatively short horn-cores uprightly inserted on the cranial roof, moderately to strongly curved and divergent, well grooved with at least one deep posterocentral furrow and smoothly compressed mediolaterally. The second, less documented species presents a slightly larger size, a shorter pedicle and more tilted, longer and more compressed mediolaterally horn-cores.

More than one dozen of different *Gazella* species have been described from the late Miocene of Eurasia, leading to an extremely complex systematic and synonymy status, which resolution is, however, beyond the subjects of the present work. Both Akkaşdağı gazelles differ by their larger size and horn-core setting and morphology from the small Vallesian species *G. ancyrensis* Tekkaya, 1973 from middle Sinap (Turkey), *G. gracile* Korotkevitch, 1976 from Berislav (Ukraine) and *G. praegaudryi* Arambourg, 1959 from Bou Hanifia (Algeria) (Tekkaya 1973a; Korotkevitsch 1976; Bouvrain 1996). *Gazella lydekkeri* Pilgrim, 1937 from Pakistan is also smaller with longer premolars, shorter, slenderer and remarkably less compressed horn-cores than the Akkaşdağı gazelles. *G. schlosseri* Pavlow, 1913 from Grebeniki and adjacent territories (Pavlow 1913; Korotkevitsch 1976) differs by its shorter, more rounded, deeply grooved and almost uncurved horn-cores with swelling anteroproximal face and flattened posterior one.

The systematic status of *G. pilgrimi* Bohlin, 1935 from Samos is quite complicated (Bohlin 1939; Bouvrain 1996). The species is characterized by short pedicles, long horn-cores, strongly inclined backwards and moderately diverged with strong mediolateral compression and well grooved surface. These features resemble those of the second and less documented gazelle from Akkaşdağı,
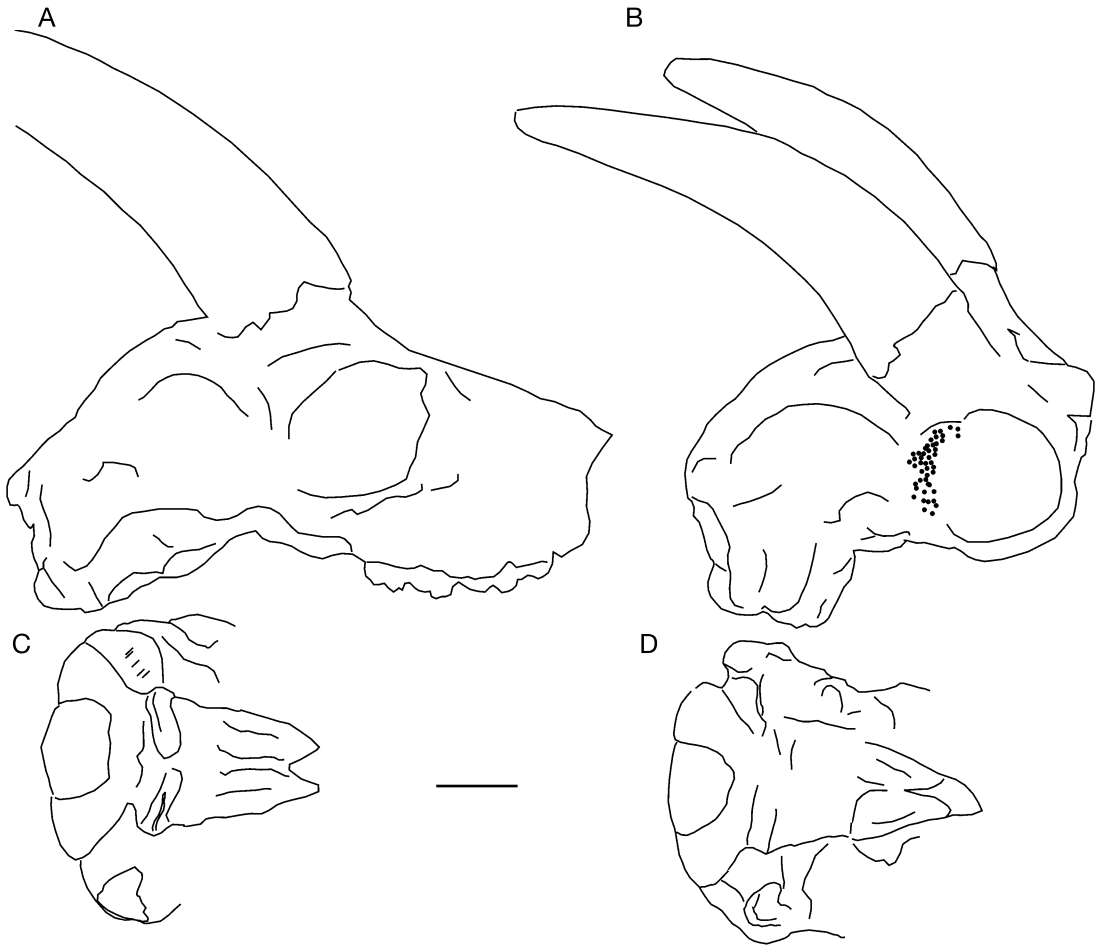
Fig. 6. — Drawings of Pikermian *Gazella*; **A**, **C**, BMNH M11440; **B**, **D**, BMNH M13005; **A**, **B**, cranium in lateral view; **C**, **D**, basioccipital in ventral view. Scale bar: 2 cm.

which is, therefore, referred to *Gazella* aff. *pilgrimi*. Two types of posterior curvature can be seen in *G. pilgrimi*: weakly curved posterior face (the type specimen from Samos figured by Schlosser [1904: pl. XIII, fig. 1]; *G. gaudryi* of Arambourg & Piveteau [1929]; *G. pilgrimi* from PXM and RZO [Bouvrain 1996]) and strongly curved posterior face, especially in the distal part of the horn-core (*G. longicornis* Andree, 1926 [pl. XVI, figs 3, 6]; *G. longicornis* from Ukraine [Korotkevitsch 1976]; *G. capricornis* of Solounias [1981: fig. 46]; *G. pilgrimi* from Vathylakkos [Bouvrain 1996]). Although the significance of

this character is not clear (e.g., in the Ukrainian sample of *G. longicornis* intermediate types of the horn-core's curvature are present; Korotkevitsch 1976: pls XIV-XVIII), the second gazelle from Akkaşdağı approaches the "curved type".

The general morphological and proportional characters of the predominant gazelle from Akkaşdağı recall those of *G. mytilinii* Pilgrim, 1926, *G. capricornis* (Wagner, 1848) and *G. deperdita* (Gervais, 1847). The characters used by Solounias (1981) to differentiate *G. mytilinii* from *G. capricornis* seem unreliable as they are mostly referred to *G. pilgrimi* (synonym of *G. capricornis* according
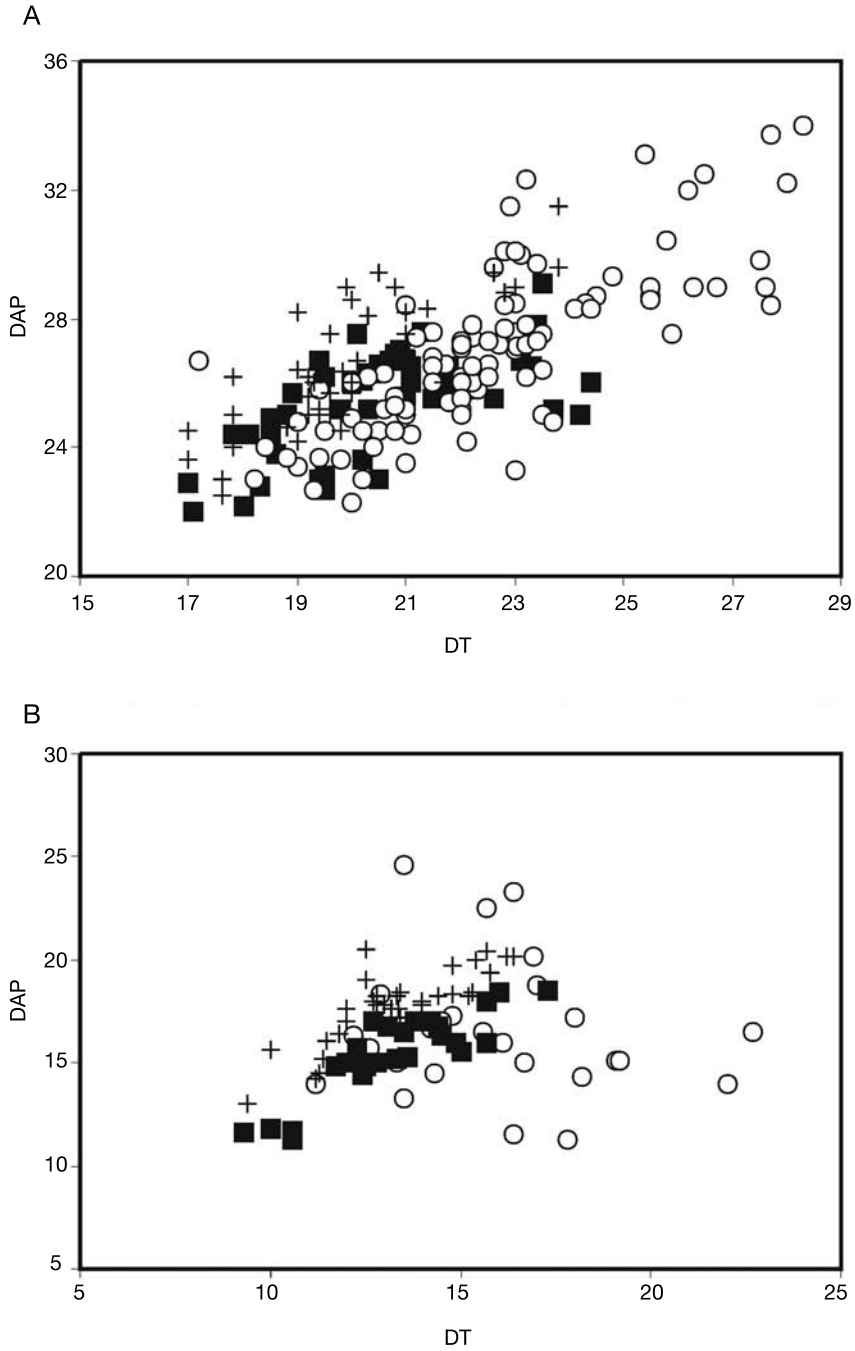
A

B

Fɪɢ. 7. — Size distribution of *Gazella* horn-core, measurements at the base (**A**) and at 7 cm above the base (**B**). ■, *G.* cf. *capricornis* (Wagner, 1848), Akkaşdağı; ○, *G. capricornis*, Pikermi; +, *G. deperdita* (Gervais, 1847), Lubéron/Cucuron (France). Abbreviations: **DAP**, anteroposterior diameter; **DT**, transverse diameter.

to Solounias 1981). *G. mytilinii* is a little known species, recorded from Samos island (Greece; Solounias 1981). It shares with some specimens referred to *G. capricornis* (such as the specimen figured by Gaudry [1862-1867: pl. LVI, fig. 1] as *G. brevicornis* Roth & Wagner, 1854 and the Pikermi skull BMNH M13005 mentioned by Pilgrim & Hopwood [1928]), the relatively more uprightly inserted horn-cores with medium curvature and compression, the similar basioccipital structure, and the similar premolar/molar ratio. It is quite interesting that the skull specimen M13005 stored in BMNH differs from the second available Pikermi *Gazella* skull M11440 in having higher occiput, shorter and more inflated opisthocranium, shorter basioccipital, stronger basioccipital-palate angle and more uprightly inserted and less laterally diverged horn-cores with more circular cross-section especially toward the apexes (Fig. 6). This set of characters has been seen on the type specimen of *G. mytilinii* NHMW A4777 and the probably conspecific AMNH 20706 from Q1 of Samos. We should therefore admit that the variation limits of the Pikermian *G. capricornis* are wide enough to include the "morphotypes" of *G. mytilinii* and M13005 or that a second nameless species occurs at Pikermi but such a revision is also beyond the purposes of the present work.

G. capricornis shares several morphological characters and presents a great dimensional overlap with *G. deperdita* from Cucuron and Mont Lubéron (France), allowing some authors to regard them as conspecific or local races of the same species. *G. capricornis* differs, however, from *G. deperdita* in the slightly larger size, relatively longer and more uprightly inserted horn-cores with lesser degree of posterior curvature and weaker mediolateral compression (Fig. 7; Appendix: Table 6). Moreover, the toothrow of *G. capricornis* is smaller than that of *G. deperdita* but with more elongated premolar row (Appendix: Table 6). The p4 of *G. capricornis* is elongated (Appendix: Table 6) with usually free metaconid instead of short with usually closed talonid in *G. deperdita* (Heintz 1971; Roussiakis 1996).

Concerning the horn-core structure (Fig. 7), the p4 proportions and the toothrow length, the main gazelle from Akkaşdağı approaches better the Pikermian species, and especially the "M11440 morphotype". Nevertheless, the posterolingual wall of p4 appears closed in the Akkaşdağı gazelle and the premolar/molar ratio are significantly smaller than in the typical sample of *G. capricornis*. Such a short premolar row occurs however, in some populations of *Gazella capricornis* from Ukraine (Korotkevitsch 1976). Skull comparison between the specimens M13005 and M11440 (BMNH) and PIK 2001 (MNHN) of *G. capricornis* from Pikermi and AKB-29, AK5-598 shows that the Akkaşdağı form has slightly wider and more elongated opisthocranium (W of bimastoid = 52-56 in *G. capricornis* versus 57.6-59.5 in the Akkaşdağı form; L of the posterior face of the horn-core to nuchal crest = 62-75 in *G. capricornis* versus 78.4 in AKB-29). Finally, according to the poor available data the hypsodonty seems more advanced in the Akkaşdağı form than in the typical sample of *G. capricornis* (92 versus 72 for m2 [one specimen respectively] and 78 versus 71 for m3 [two and one specimens respectively]).

Judging from the comparison, the Akkaşdağı gazelle seems to approach *G. capricornis* from Pikermi. A direct attribution to this species seems however difficult because of the shorter premolar row and the apparently more advanced hypsodonty observed in Akkaşdağı and the possible presence of another gazelle species in the Pikermian sample, increasing taxonomic vulnerability. Therefore, I suggest referring the main gazelle at Akkaşdağı to *Gazella* cf. *capricornis*.

Turkish gazelles are well known from several late Miocene localities but species determination is usually obscure. The gazelle from KTD is significantly smaller than the Akkaşdağı forms and close to *G. gracile* from Berislav (see also Bouvrain 1994a). A similar horn-core pattern also occurs in Garkın and Mahmutgazi (Type III and part of Type II and IVa of Köhler 1987) that could be equally related to *G. ancyrensis*
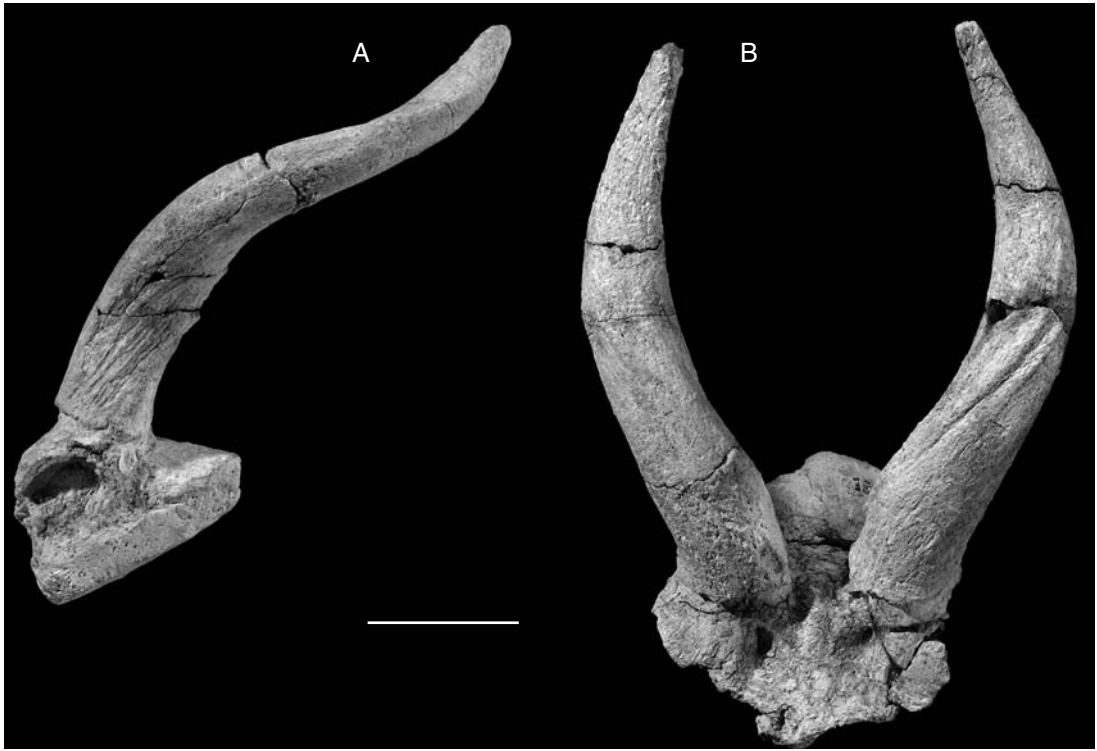
Fig. 8. — *Prostrepsiceros rotundicornis* (Weithofer, 1888) from Akkaşdağı, frontlet AK5-641; **A**, lateral view; **B**, frontal view. Scale bar: 5 cm.

from Middle Sinap. The gazelle from Kayadibi (Type I of Köhler 1987) forms a well distinct sample from the rest of Turkish gazelles, including the Akkaşdağı ones. This form is characterized by straight and rounded horn-cores of larger size than in the previous group and in accordance with Köhler (1987) I consider it as probably belonging to *G. schlosseri*. The horn-core morphology and proportions and the short premolar row of the Kemiklitepe A-B gazelle (Bouvrain 1994a) indicate close relations with the predominant gazelle from Akkaşdağı. Anyway, the Kemiklitepe A-B material includes some horn-core specimens with slightly different proportions (KTA-149, KTB-79), which could suggest the presence of a second species. Specimens similar to the main Akkaşdağı form can also be found at Mahmutgazi, Kınık (part of Type IVa and b of Köhler 1987) and Çoban

Pınar (sp. 1917 MTA-MA). The skull specimen SaG 7-5/45 from Garkın, attributed by Köhler (1987: fig.74) to her Type II, as well as some other specimens ascribed to the same form (Köhler 1987: pl. VIII, fig. 3), seem quite distinct from the rest of the Garkın material and Akkaşdağı either. Their morphology and horn-core proportions rather approach those of *G. "mytilinii"* from Samos. The gazelle from Küçükyozgat (Şenyürek 1953) resembles *G.* aff. *pilgrimi* from Akkaşdağı and *G. pilgrimi* from Axios valley (Bouvrain 1996). A single available specimen from Kavakdere (sp. 2276-AAK/26, MTA-MA) is significantly larger than that of the Akkaşdağı gazelles, indicating similarities with the specimen BMNH M5420 from Samos and RZO-159, 160, for which Bouvrain (1996) suggests the creation of a new taxon outside of *Gazella*.

Genus *Prostrepsiceros* Major, 1891

Prostrepsiceros rotundicornis (Weithofer, 1888)

MATERIAL EXAMINED. — Frontlet: AK6-64, AK5-641; horn-cores: AK2-75dex, AK3-70sin, AK2-73dex, AK2-74sin, AK3-68sin, AK3-69sin, AK4-189sin; part of frontlet: AK5-152; part of horn-core: AK6-135, AKB-28; P4-M3: AK3-220sin; P3-M3: AK5-51sin; M1-M3: AK6-72dex, AK2-45dex, AK4-195sin; p2-m3: AK7-102sin, AK2-459sin, AK5-618sin, AK5-615sin, AK2-323dex, AK2-318dex; p3-m3: AK3-76sin, AK5-639sin, AK2-457sin, AK3-190dex; p4-m3: AK5-617sin, AK6-191sin; m1-m3: AK4-200dex, AK5a-259dex, AK5a-207dex, AK2-458dex; p3-p4: AKA-6; m3: AK5-50sin, AKK-79; distal part of humerus: AK2-79; radius: AK2-326; metacarpal: AK2-474; distal part of tibia: AK14-20; astragal: AK7-176; calcaneus: AK3-75; metatarsal: AK3-222, AK9-309; phalanx I: AK2-79, AK5-252; phalanx II: AK5-373.

DESCRIPTION
Skull
Prostrepsiceros rotundicornis represents a medium sized antelope with moderately long horn-cores, relatively robust at their base (Fig. 8; Appendix: Table 7). The width of the skull behind the horn-cores ranges between 65 and 68 mm (Appendix: Table 7). The interfrontal suture rises as a ridge and is visible ahead of the horn-cores. The frontals are not elevated between the horn-cores and appear slightly convex in lateral view (Fig. 8A). There are no internal sinuses in the frontals or reaching into the pedicles. In the postero-distal part of the medial side (around the pedicles) the frontals are significantly depressed. The supra-orbital foramens are relatively large, situated in large and deep pits which extend forwards like depressions; their lateral border is higher than the medial one. The rather rounded orbits (antero-posterior axis 32-36 mm) are moderately project-ed with widely extended dorsal rim. The postcornual grooves are rounded and shallow. The pedicles are sub-rounded and short. Their contact with the horn-cores is sharp anteriorly but less developed posteriorly. The horn-cores are situated over the orbits, strongly tilted backwards (≈ 40° with the cranial roof) and slightly divergent (≈ 50-60°); their anteroproximal margin is placed above the anterior third of the orbital rim. They are closely situated at their bases and lyri-form in frontal view. At about 5 cm above the base, the horn-cores curve moderately backwards, whereas they are re-curved upwards at their top. The horn-core's cross-section is elliptical at the base (Appendix: Table 7) with strongly convex medial side and slightly convex lateral one. Their greater anteroposterior axis at this level forms an angle of about 50° with the sagittal plane. 7 cm above the base the cross-section becomes subsquarish with the greater axis parallel to the sagittal plane. In the uppermost part of the horn-cores the cross-section becomes sub-triangular. The horn-cores are about 230 (AK5-641) to 240 mm (AK6-64) long, normally (anticlockwise) and relatively tightly spiraled and slightly torsioned. Thin dis-continuous furrows run along their surfaces. Two keels are present. The "anterior" one descends to the postero-medial side of the base, forming a complete gyre towards the apex. It is smooth in the lower part of the horn-core but becomes sharper in its upper half (Figs 8; 9). A deep longi-tudinal furrow, starting 2-3 cm above the base, runs in parallel with this keel or even replaces it (Figs 8; 9). Nevertheless, the presence and deve-lopment of this furrow is variable: it is very deep in AK4-189, well expressed but less deep in AK6-64, AK2-75, AKB-28, weak in AK2-73 and double in AK5-641 and AK3-70. The second keel descends over the anterior margin of the postcornual groove and also forms a complete gyre towards the top. In the lower 3/4 of the horn-core it is weak but becomes thin and spiky towards the uppermost part. Deep furrows asso-ciate with this keel in the proximo-lateral face of the horn-cores, while in some specimens a deep and narrow furrow follows the keel towards the middle of the horn-core's height (AK3-70, AK5-641). In two specimens (AKB-28 and AK4-189) the furrow is projected to the pedicle.

Hornless skull (AKB-97)
A badly preserved skull of a medium-sized ante-lope (AKB-97) is included into this species. The skull maintains just the braincase, the frontal region and part of the basioccipital. The total

FIG. 9. — *Prostrepsiceros rotundicornis* (Weithofer, 1888) from Akkaşdağı, horn-core AK4-189, antero-internal view. Scale bar: 5 cm.

orbital rim and directed posteriorly and upwards, where it gradually disappears. The occiput is short and wide, forming an angle of about 78° with the basal axis. The mastoid is large. The basioccipital is short and trapezoidal shaped. The posterior tuberosities are small and globular, forming a smooth crest, placed vertical to the sagittal plane. The anterior tuberosities, situated behind the small oval foramen, are smaller than the posterior ones and elongated-hilly shaped. A weak crest runs along the basioccipital groove. The auditory bulla is short and oblique comparatively to the sagittal plane (32°). The condyles are strong and distant. The foramen magnum is wide. The paroccipital process is situated more anteriorly than in *Gazella* (AKB-29) and projects laterally.

The morphological characters of the skull point to a representative of *Prostrepsiceros* (Bouvrain 1982; Bouvrain & Thomas 1992), while the dimensions indicate a similar size category with the previously described frontlets.

Dentition

A few upper toothrows are known (Appendix: Table 8). The length M1-M3 varies between 39.1 and 42.5 mm whereas the upper premolar length is unknown. P3, 4 have strong paracone and parastyle. P4 is slightly asymmetrical and bears traces of a possible hypoconal islet. The upper molars have strong styles, angular protocone and wide hypocone. A small central islet is present. The metastyle of M3 is strong directed backwards.

The length p2-m3 ranges between 68.8 and 75.1 mm with short premolars comparatively to the molars (premolar/molar ratio: 62-71) (Appendix: Table 9). In p3 (Fig. 10) the paraconid is independent from the larger parastylid until the middle of the crown's height. The metaconid is extended posteriorly, fused quickly with the entoconid. The p4 is morphologically similar to p3 but with more rounded metaconid and stronger hypoconid. The lower molars bear a thin basal pillar and a smoothly developed goat fold (Fig. 10). The third lobe of m3 is formed by a single tubercle and has a slightly concave lingual face.

absence of horn-cores indicates a female individual. The cranial roof is strongly convex and the braincase more bulky than that of *Gazella* (AKB-29). The frontals form an angle of about 115° with the cranial roof. The interfrontal suture is simple. The orbit is strongly projected laterally with wide dorsal orbital rim. The supraorbital foramen is small and there are no pits. The parietal crest is strong, starting just behind the dorsal
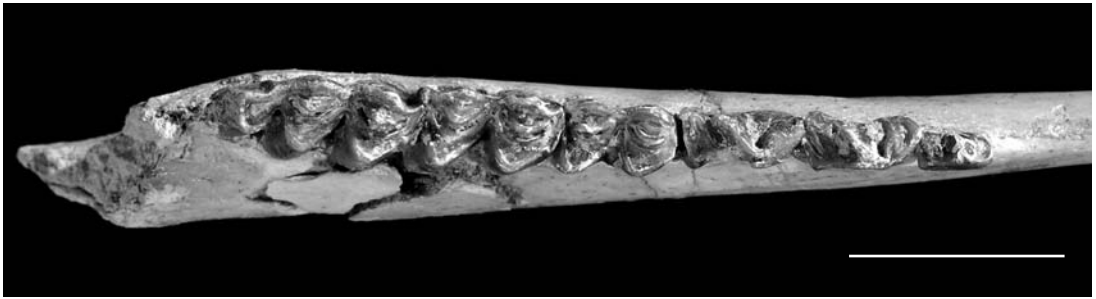
Fig. 10. — *Prostrepsiceros rotundicornis* (Weithofer, 1888) from Akkaşdağı, mandible AK2-323, occlusal view. Scale bar: 2 cm.

Postcranials

The metapodials are elongated and slender (length of MtIII+IV = 203 mm, DTdia = 16 mm, robusticity index: 7.9; length of MtIII+IV = 212.2 mm, DTdia = 16 mm, DTdistal = 26.2 mm, robusticity index: 7.5). The index "Length of metacarpal/Length of radius × 100" is 0.76 and the index "Length of metacarpal/Length of metatarsal × 100" about 0.95, indicating a fast runner.

COMPARISON

The general morphological characters of the available frontlets and horn-cores allot the medium sized antelope of Akkaşdağı to *Prostrepsiceros* (Gentry 1971; Bouvrain 1982; Bouvrain & Thomas 1992). Although late Miocene *Prostrepsiceros* is well known from several localities of the Greco-Iranian province, it is scarcely recognized in Turkey (Şenyürek 1952; Ozansoy 1965; Tekkaya 1973b; Köhler 1987; Bouvrain & Thomas 1992; Gentry 2003). In my knowledge the Akkaşdağı sample constitutes at present time the best known evidence of this genus in the country.

Prostrepsiceros vallesiensis Bouvrain, 1982, known from the late Vallesian (MN 10) localities of Greece and Turkey (Gentry 2003), differs from the Akkaşdağı *Prostrepsiceros* in its significantly smaller size, lack of supraorbital pits, shorter, more slender and more tightly spiraled horn-cores with strong mediolateral compression and sharp keels, as well as, in the comparatively longer basioccipital.

The Akkaşdağı *Prostrepsiceros* also differs from *P. syridisi* Kostopoulos & Koufos, 1996 (*fide* Bouvrain & Heintz pers. comm.) from the latest Vallesian locality Nikiti-1, Greece (Bonis & Koufos 1999) in the longer premolar row (premolar/molar ratio = 62-71 in Akkaşdağı versus 56-60 in NKT), the constricted interfrontal suture, the large supraorbital foramens into deep pits, the more robust horn-cores inserted more uprightly and situated more closely on the frontals with less developed keels, more rounded cross section and more medially descended anterior keel.

The type species of the genus, *P. houtumschindleri* (Rodler & Weithofer, 1890), originally described from Maragha, Iran, differs from the Akkaşdağı *Prostrepsiceros* in the feebler facio-cranial angle, the smaller supraorbital foramens and postcornual grooves, the wider separation of the horn-cores on the frontals, their stronger mediolateral compression (Fig. 11) and tighter twist and in the presence of a vigorous posterior keel. *Prostrepsiceros vinayaki* (Pilgrim, 1939) is a poorly known species. According to the available data from several localities (Pilgrim 1939; Gentry 1999; Bouvrain & Heintz pers. comm.) it differs from the Akkaşdağı *Prostrepsiceros* in the longer and slenderer horn-cores, which are more torsioned than spiraled and extremely compressed mediolaterally. The deep anterior furrow, the short pedicles, the close setting of the horn-cores at their base, the large supraorbital foramens into pits and the weak postcornual fossa observed in Akkaşdağı *Prostrepsiceros* are also present in the large *P. lybicus* Lehmann & Thomas, 1987 from
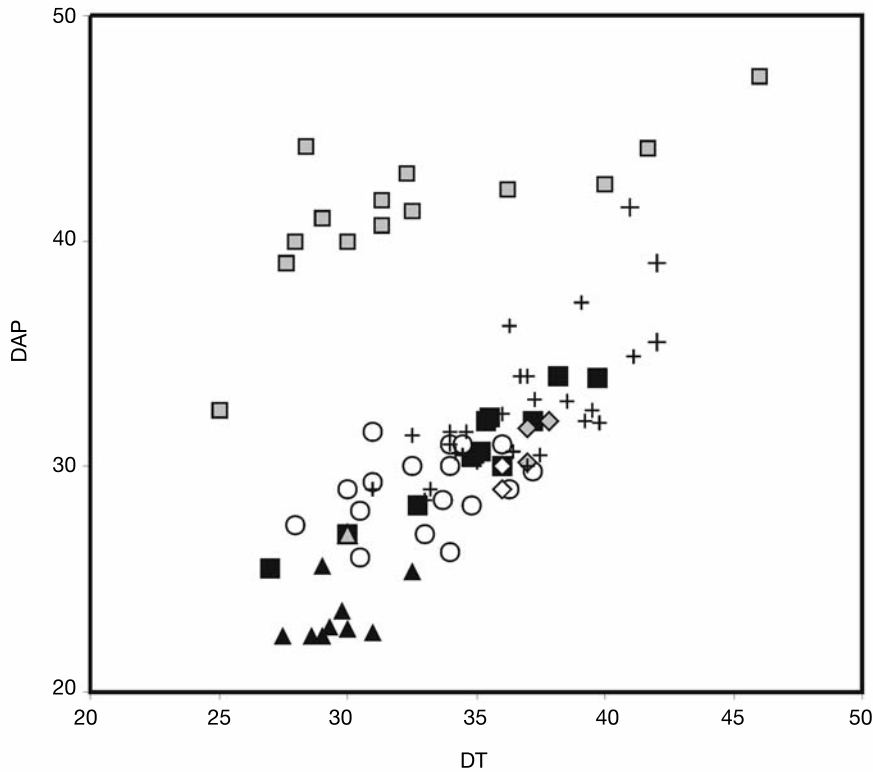
Fɪɢ. 11. — *Prostrepsiceros* horn-core distribution of basal measurements. ■, *P. rotundicornis* (Weithofer, 1888), Akkaşdağı; ○, *P. rotundicornis*, Pikermi; ◆, *P. rotundicornis*, RZO; ◇, *P. rotundicornis*, Gökdere; ▨, *P. houtumschindleri* (Rodler & Weithofer, 1890), Maragha; **+**, *P. fraasi* (Andree, 1926), Maragha, Samos; ▲, *P. zitteli* Schlosser, 1904 type, Samos; ▲, *P. axiosi* Kostopoulos, 2004, RZO, PXM. Abbreviations: **DAP**, anteroposterior diameter; **DT**, transverse diameter. Data from Gentry 1971; Watabe 1990; Bouvrain & Thomas 1992; and pers. data.

Sahabi, Libya, which, however, has significantly longer horn-cores, more compressed mediolaterally and less torsioned.

Prostrepsiceros zitteli Schlosser, 1904 is originally known from Samos and also described from Kavakdere, Turkey (Geraads & Güleç 1999; Kostopoulos 2004). It is slightly smaller than the Akkaşdağı form with feebler facio-cranial angle, absent interfrontal suture ahead of the horns, more laterally projected orbits, absent postcornual grooves, more widely separated horn-cores on the frontals, stronger anterior keel, tighter torsion and stronger distal curvature. *Prostrepsiceros axiosi* Kostopoulos, 2004 from Axios valley, Greece, is significantly larger than the Akkaşdağı *Prostrepsiceros*; its horn-cores are more widely spa-

ced on the frontals, stronger curved backwards and torsioned, stronger keeled and more compressed anteroposteriorly (Kostopoulos 2004).

Prostrepsiceros fraasi (Andree, 1926) is originally described from Samos by a single frontlet. A similar form from Maragha was described under various names (Mecquenem 1924; Andree 1926; Watabe 1990). Gentry (1971) and Solounias (1981) regarded the species as a synonym of *P. rotundicornis* from Pikermi, but Bouvrain (1982), Bouvrain & Thomas (1992), Gentry & Heizmann (1996) and Gentry *et al.* (1999) consider *P. fraasi* as a valid species. Recently, Bouvrain & Heintz (pers. comm.) suggest referring to the Maragha form under the name *P. gaudryi* Mecquenem, 1908. *P. fraasi*

(including the Maragha form) is somewhat larger than the Akkaşdağı *Prostrepsiceros* (Fig. 11) with similarly inclined face but without postcornual grooves, ridge-like frontoparietal suture, wider separated, more strongly diverged and less torsioned horn-cores with a vestigial anterior keel and no posterior one (Bouvrain & Thomas 1992; Gentry 1999; pers. obs.).

The Pikermi *P. rotundicornis* (Weithofer, 1888) is the more allied species to the Akkaşdağı form, both morphologically and metrically. The medium size, the moderately inclined face, the projected orbital margins, the constricted interfrontal suture in front of the pedicles, the large supraorbital foramens into pits, the robust horn-cores comparatively to the skull, inserted in the posterior part of the orbits, their close setting on the frontals, their weak anteroposterior compression, their moderate torsion and closed spiraling and the presence of a weak anterior keel descending anteromedially, which is sometimes accompanied by a longitudinal furrow (two of four specimens in BMNH) are common characters in both Pikermi and Akkaşdağı forms. However, the Turkish *Prostrepsiceros* differs in the larger supraorbital foramens situated in deeper and wider depressions, the shallower postcornual grooves, the higher pedicles (especially on the lateral face), the weaker divergence and the persistence of keels instead of furrows.

Bouvrain (1982) also refers to *P. rotundicornis*, the large *Prostrepsiceros* from Ravin de Zouaves 5 (Axios valley). This form is known by two frontlets (RZO-223 and RZO-120, LGPUT) that look identical to those from Akkaşdağı: both have a weak but visible posterior keel, descending to a postero-lateral insertion and strengthening upwards, large supraorbital foramens (however smaller in Akkaşdağı) in wide depressions of the frontals, shallow postcornual grooves, lyriform pattern of the horn-core's divergence, short pedicles, tending to disappear posteriorly, and strongly grooved baso-lateral surface. Similarly to the Akkaşdağı form a weak longitudinal furrow associates the posterior keel of RZO-223 in its proximal part, while an anterior furrow is also present but less developed. Finally, both forms

have similar horn-core length and basal dimensions that appear to be slightly larger than those of the Pikermi population. Based on the cone impression of a horn-core, its robusticity could be expressed as the relation of the horn-core length [L] measured along the anterior face, to the basal area [BA = $\pi(D/2)^2$], considered as a circle with diameter D equivalent to the mean diameter of the base. Thus, the Horn-core robusticity index, HcRI = BA/L ranges from 3.7 to 4.6 (n = 2) in Akkaşdağı *Prostrepsiceros*, being very close to the estimated values for the two RZO frontlets (3.5-3.8) and slightly larger than those of Pikermi (3.3-3.4; n = 2).

Şenyürek (1952: figs 45-47) also mentioned two horn-cores from Gökdere ascribed to *P. rotundicornis*. They are slightly smaller than the studied form and closer to the Pikermi one, but similarly to Akkaşdağı, they seem to bear a well developed posterior keel and an anterior furrow. Although Bouvrain (1994a) mentioned the absence of *Prostrepsiceros* in Kemiklitepe (Turkey), the original comparison of the material showed that the specimen KTA-189 (distal part of a left horn-core) included in ?*Oioceros wegneri* by Bouvrain (1994a) rather corresponds to *Prostrepsiceros*, being similar to that from Akkaşdağı. The specimen bears a deep anterior furrow like the Akkaşdağı form and an even more marked posterior keel.

I certainly regard the Akkaşdağı and RZO *Prostrepsiceros* as conspecific. The Gökdere form seems to be very close to this group, which also occured in Kemiklitepe A-B. The relations with the Pikermi *P. rotundicornis* are obviously strong, and the small differences cannot be considered as overpassing intraspecific variation.

Genus *Miotragocerus* Stromer, 1928

Tragocerus Gaudry, 1861: 393 (*pars*).

Miotragocerus Stromer, 1928: 36.

Graecoryx Pilgrim & Hopwood, 1928: 54 (type species: *G. vallenciennesi* (Gaudry, 1861)).

Sivaceros Pilgrim, 1937: 792 (type species: *S. gradiens* Pilgrim, 1937).

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

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

NOMENCLATURAL REMARKS. — Most of the late Miocene boselaphines from the eastern Mediterranean region originally referred to the genus *Tragocerus* Gaudry, 1861 (Gaudry 1862-1867, 1873; Schlosser 1904; Pavlow 1913; Borissiak 1914; Mecquenem 1924; Andree 1926; Pilgrim & Hopwood 1928) have been lately transposed either to *Miotragocerus* Stromer, 1928 or to *Tragoportax* Pilgrim, 1937. The main differences between these two genera concern the horncore pattern, some cranial and dental features and the presence of horns in females. Nevertheless, opinions among authors vary significantly and thus several species appear to interchange between the two genera (see discussions in Kretzoi 1968; Gentry 1971; Thomas 1979; Solounias 1981; Moyà-Solà 1983; Bouvrain & Bonis 1984; Bouvrain 1988, 1994b; Spassov & Geraads 2004; Bouvrain & Heintz pers. comm.). A long debate also took place about the validity of *Graecoryx* Pilgrim & Hopwood, 1928, based on *Tragocerus valenciennesi* Gaudry, 1861 from Pikermi. Several authors consider this taxon artificial, founded upon material of young and female individual of other related genera (Bohlin 1935; Bouvrain 1988; Spassov & Geraads 2004), while others allot a true value to the genus (Moyà-Solà 1983; Köhler 1987; Romaggi 1987). Avoiding long repetitions of the systematic history of all these taxa, I shall focus on the most recent options found in the literature, trying to eliminate distortion on nomenclature.

Moyà-Solà (1983) placed *Dystychoceras pannoniae* Kretzoi, 1941 from Sopron, Hungary, in *Miotragocerus* and restored *Graecoryx* for *G. valenciennesi*. Romaggi (1987) followed Moyà-Solà (1983) about *Miotragocerus* but rejected *Tragoportax* and placed all the classical European tragoceres under *Graecoryx*. Furthermore, he disagreed with the synonymy of *Graecoryx* with *Miotragocerus* putting the argument of the different premolar/molar pattern (more advanced in *Miotragocerus* according to this author). My observations do not support his conclusion; the observed variability in the dental structure of these taxa cannot be considered as exceeding that of forms belonging to the same genus, and indeed, it is significantly smaller than the differences observed between species included by the author in *Graecoryx*.

In a more recent review, Bouvrain (2001) and Bouvrain & Heintz (pers. comm.) propose to restrict the name *Miotragocerus* only to the type species *M. monacensis* Stromer, 1928 and – on the basis of horned females – to place the rest of the related species (*D. pannoniae*, *P. gaudryi*, *T. leskewitschi* (Borissiak, 1914) and probably *S. gradiens*) in *Dystychoceras* Kretzoi, 1941 because *Miotragocerus* seems to them insufficiently established. In my opinion, the basic

skull and horn-core characters that can be extracted from Stromer's specimen are present in *D. pannoniae* and they seem sufficient to both define these two forms at generic level and distinguish them from other genera (see also Moyà-Solà 1983; Romaggi 1987). As Kretzoi (1941: 338) sets out, the Sopron frontlet presents great similarity with *Sivaceros* Pilgrim, 1937 and extending his thought, it is evident that the differences between the type species of *Dystychoceras* and *Mioragocerus* do not exceed those observed between *S. gradiens* and *S. vedicus* Pilgrim, 1939. Actually, *Sivaceros* appears close to *Miotragocerus* and *Graecoryx* and a synonymy is possible, as it is already suggested by other authors. *Phronetragus* Gabuniya, 1955 (type species *P. arknetensis*; Meladze 1967) also shows a great number of common characters with both *Miotragocerus* and *Graecoryx* and its distinction at genus level does not seem to me justifiable but final conclusion presupposes the study of the original material.

Spassov & Geraads (2004) revise both *Tragoportax* and *Miotragocerus*. Although I do not agree with all the interpretations, especially at subgeneric and species level, and the consequent phylogenetic relationships, I have no substantial objections to the *Miotragocerus* concept provided by the authors but I certainly regard *Pikermicerus* as a junior synonym of *Graecoryx* since the type species of both genera are based on material representing the same taxon in the Pikermi fauna (see below). Hitherto, the synonymy status between *Miotragocerus* and *Graecoryx* has been unclear since both genera were founded the same year. Gentry (1971: 234, footnote) wrote that the copy of Pilgrim & Hopwood's book was accessioned in the Palaeontology Library of the British Museum (Natural History) at a date close to 28 June 1928. Ms Polly Smith, Assistant Archivist, and Ms Susan Snell, Archives Manager of the Natural History Museum, London, informed me (pers. comm. 2002, 2003) that the book is first mentioned in the Publications Presentations Books (ref. DF 508/5) on Saturday 23 June 1928. On that day the book was read and discussed in the Standing Committee of the British Museum (Natural History), confirming its price and a copy was set before the Museum Trustees. Hence, it seems that the book would not have been made available to members of the public outside the Museum before Monday 25 June 1928 at the earliest. Anthea Gentry (pers. comm. 2002) suggests that since the date of publication of a book is when copies are first distributed, the 23 June 1928 could look like a first distribution and therefore the date of publication. But it is more likely that the committee meeting constituted the formal last stage of pre-publication vetting and, indeed, seems to have been the occasion on which the selling price of the book was decided. According to the Publication Sales register of that period (Ms S. Snell, pers. comm. 2003) the first sales of Pilgrim & Hopwood's book to two firms of retail booksellers, Oxford Press and Bernard Quaritch were only registered on 3 July 1928 (ref. DF 500/5). In this

case it seems logical to accept as first publication date, a date in-between 25 and 29 June. This date clearly postdates that of Stromer's monograph, given as 5 May 1928 on the front cover of the journal and therefore, *Miotragocerus* does have priority over *Graecoryx*.

Miotragocerus valenciennesi (Gaudry, 1861)

Tragocerus valenciennesi Gaudry, 1861: 393, pl. VIII, figs 4, 5; 1862-1867: 288, pl. XLVIII, figs 2, 3.

Graecoryx valenciennesi – Pilgrim & Hopwood 1928: 55, pl. VIII, fig. 2, pl. IX, figs 4, 5. — Moyà-Solà 1983: 103. — Romaggi 1987: 277.

Pikermicerus gaudryi Kretzoi, 1941: 342, fig. 2.

Miotragocerus monacensis – Solounias 1981: 102, fig. 26.

Miotragocerus valenciennesi – Solounias 1981: 105.

Tragoportax gaudryi – Moyà-Solà 1983: 124.

Dystychoceras gaudryi – Bouvrain 2001: 238.

Miotragocerus (*Pikermicerus*) *gaudryi* – Spassov & Geraads 2004: 353.

NOMENCLATURAL REMARKS. — The present situation does not resolve the issue of how many boselaphine species exist in the Pikermi fauna. In addition to *Tragoportax amalthea* (Roth & Wagner, 1854), two more species have been described: *Graecoryx valenciennesi* and *Tragoportax gaudryi*. The last species is admitted into the Pikermian sample by Moyà-Solà (1983) on the basis of *Pikermicerus gaudryi* Kretzoi, 1941 (also referred to as *Dystychoceras gaudryi* or *Miotragocerus gaudryi*). The dental material of Pikermi does not support, however, a third species in the locality. The frontlet BMNH M12992 ascribed to *Graecoryx valenciennesi* by Pilgrim & Hopwood (1928) most probably belongs to a young male individual (age classes ?I-II, see below) of a form with horn-core pattern that should allow (through the morphotypes BMNH M11423a and M32170) to a mature morphology similar to that of *T. gaudryi* (BMNH M11423b; MNHN PIK 2366, PIK 2448). The data from Sebastopol (Borissiak 1914), Halmyropotamos (Melentis 1967), Hoewenegg (Romaggi 1987) and Akkaşdağı fully support such a conclusion. The type specimen of *Graecoryx valenciennesi* (MNHN PIK 2367) and the skull specimen BMNH M11430 are attributed to the same species by Pilgrim & Hopwood (1928); the last specimen is erroneously referred to as hornless by Solounias (1981: 107) and figured later as *T. gaudryi* by Moyà-Solà (1983: pl. 17, fig. 1). Actually, both specimens belong to horned females, whose morphology strongly resembles the boselaphine females from Nikiti-1 (Kostopoulos & Koufos 1996), Piera (Moyà-Solà 1983), Dytiko (Bouvrain 1988), Hoewenegg

(Romaggi 1987), Pikermi (Roussiakis 1996) and Akkaşdağı (see below), and making due allowances, they should be regarded as conspecific with PIK 2366 (type specimen of *Pikermicerus gaudryi*). Moreover, the dentition of BMNH M11430 is indistinguishable from those referred to *T. gaudryi*. Thus, *Graecoryx valenciennesi* of Pilgrim & Hopwood (1928) and *Tragoportax gaudryi* of Moyà-Solà (1983) from Pikermi are the same species (see also Romaggi 1987). From this point of view, the name *valenciennesi* is preferable to *gaudryi* because the principle of priority should be applied even if "two or more generations, forms, stages, or sexes of a species are named as different nominal taxa" (ICZN 1999: Art. 23.3.2.2). Hence, we should recognize *Miotragocerus valenciennesi* (Gaudry, 1861) as the second boselaphine of Pikermi, in contrast to previous suggestions (e.g., Spassov & Geraads 2004: 360 and literature listed herein).

MATERIAL EXAMINED. — Skull: AK5-597; part of skull: AK11-64 (a, b, c); left horn-core: AK14-14; P2-M3: AK5-605dex (LPM = 92.3, LP = 42.0, LM = 49.8), AK12-75sin (LPM = 95.5, LP = 44.4, LM = 53.9); p2-m3: AK2-322dex (Lpm = 98.6, Lp = 42.5, Lm = 56.3), GOK-196sin (Lpm = 102.0, Lp = 47.9, Lm = 55.0).

DESCRIPTION
Skull

The skull specimen AK5-597 is beautifully preserved, except for the anterior part of the muzzle (nasals, premaxillae) that is missing (Fig. 12; Appendix: Table 10). Judging from the horn-cores and dentition it belongs to an adult male. Retaining the palate horizontal, the cranial roof forms an angle of about 120° with the face. The frontals are strong and clearly elevated between the horn-cores. The fronto-nasal suture forms a reverse "U". Ahead of the horn-cores the frontals form a wide furrow towards the nasals; its lateral margins consist of the frontal prolongation of the horn-core's keels. The sub-triangular supraorbital foramens are not sunken into pits. The inter- and opisthofrontal area of the cranial roof is rough, forming a wide rugose area. Just behind the horn-cores the frontals are slightly depressed. There are no postcornual grooves. The narial notch seems to be large; its posterior end is placed above P3. The infraorbital foramen is large, situated above P2-P3. The lachrymal bone is wide and probably touches the premaxillar. A relatively long and
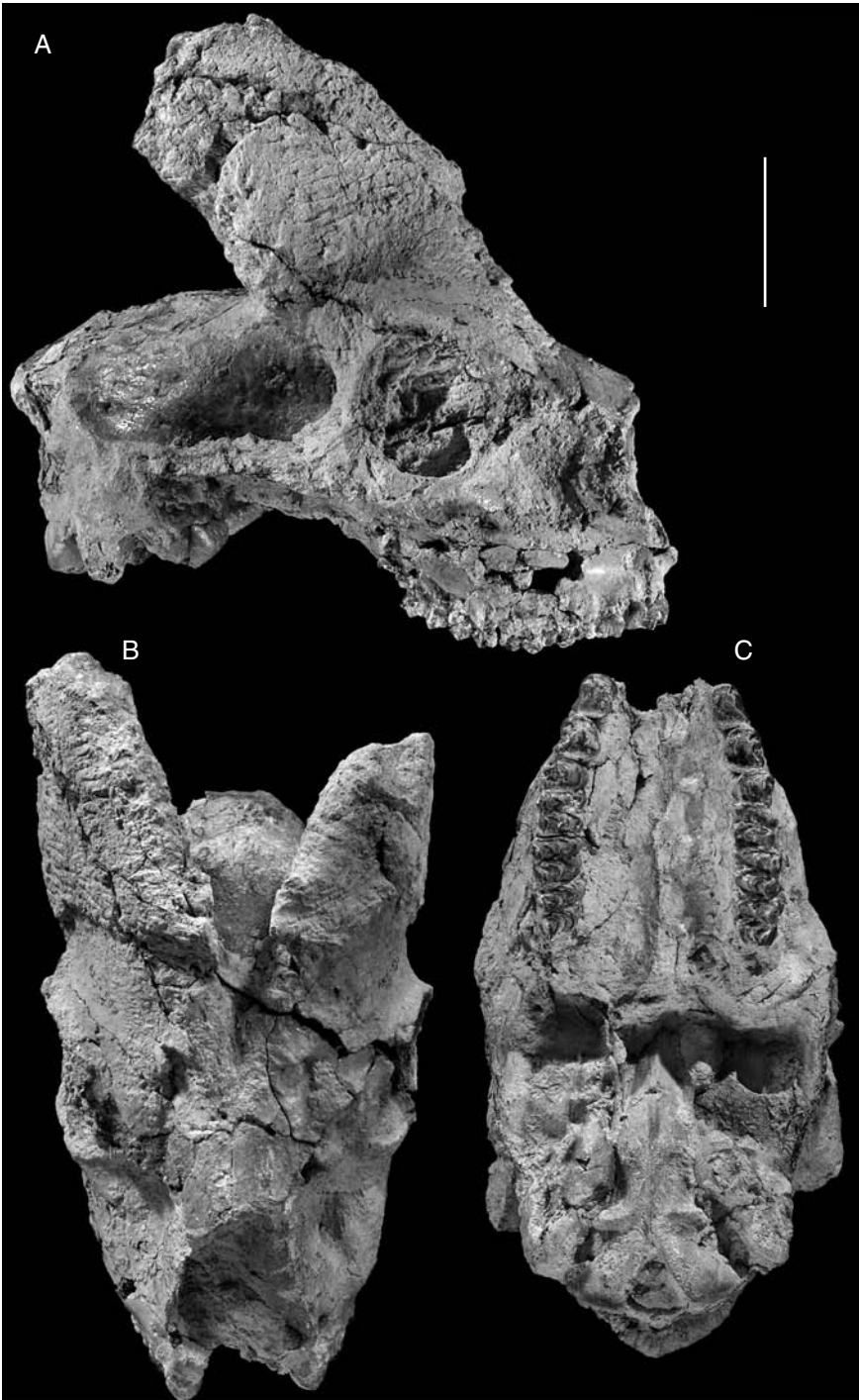
Fig. 12. — *Miotragoceros valenciennesi* (Gaudry, 1861) from Akkaşdağı, skull AK5-597; **A**, lateral view; **B**, frontal view; **C**, ventral view. Scale bar: 5 cm.
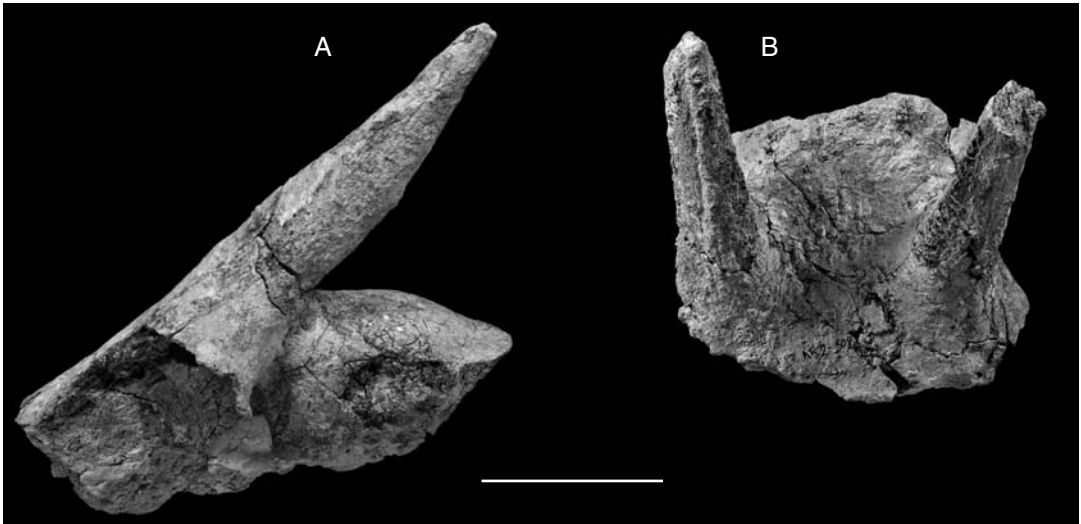
Fig. 13. — *Miotragoceros valenciennesi* (Gaudry, 1861) from Akkaşdağı; **A**, skull of young male AK11-64, lateral view; **B**, frontlet of female AK2-502, frontal view. Scale bar: 5 cm.

narrow ethmoidal fissure opens between the frontal, nasal and lacrymal bones. The lacrymal fossa ("larmier" according to Gaudry) is placed just in front of the upper half of the orbit (Fig. 12A). It is elliptical-rounded in shape, deep and well delimited (20×15 mm with vertical greater axis). The orbit is slightly projected laterally, small and well rounded. Its anterior end is placed above the middle of M2. The facial crest is well developed, blunt and bulge, limited above P3-M3. Above P4 and in front of the orbit appears a deep oval fossa with well developed posterior border (preorbital fossa). The zygo-temporal arch runs parallel to the braincase and the temporal ridges are strongly developed. The interparietal is well developed and rhomboid shaped ending posteriorly in a well developed supraoccipital. The braincase is narrow and relatively long. The occiput is pentagonal shaped concave in lateral view and with strong and sharp nuchal crest. The strong paroccipital processes project below the lower level of the condyles, and in lateral view they are placed slightly in front of them. The condyles are small. The basioccipital axis is parallel to the cranial roof and the basioccipital-palatal angle very obtuse. The posterior tuberosities of the basioccipital are strong, elongated crest-like and vertical to the

sagittal plane (Fig. 12C). The anterior tuberosities are smaller, oval shaped and slightly swelling. A single ridge runs along the basioccipital axis between the anterior and posterior tuberosities but it is replaced by a narrow groove in front of the anterior tuberosities. The small oval foramen is placed well in front of the anterior tuberosities. The auditory bulla is small, elliptical and with major axis parallel to the sagittal plane. The palate is wide and flat. The median indent at back of the palate opens anteriorly to the lateral ones and well behind M3 (Fig. 12C). The pedicle is short, especially in the posterior part and its contact with the horn-core is well marked. The horn-cores set close together anteriorly at the base and tilt moderately backwards (Fig. 12A, B). Their anterior end is situated above the middle of the orbit and their posterior face above the middle of the temporal fossa. In frontal view the divergence angle of the horn-cores is about 50°. Their cross-section is weakly sub-triangular at the base becoming rapidly elliptical and strongly compressed laterally. The postero-internal dihedre is not strongly developed but the level of maximum transverse width lies posteriorly. A smooth anterior keel is present. The anteroposterior axis of the horn-core base forms an angle of 40° with the sagittal plane. The

Fig. 14. — *Miotragoceros valenciennesi* (Gaudry, 1861) from Akkaşdağı, horn-core of immature individual AK14-14, lateral view. Scale bar: 2.5 cm.

anterolateral surface of the horn-core bases bears strong exostoses. The lateral face is slightly convex and the median one almost flat.

Young individuals (AK11-64, AK14-14)
The skull AK11-64 (Fig. 13A) preserves the frontal and part of the parietal region as well as both horn-cores. The face slopes smoothly on the cranial roof. The distance between the supraorbital pits, situated far below the horn-core bases, is

33.5 mm. The interfrontal and frontoparietal sutures are open. The frontals are not elevated between the horns. The length from the fronto-nasal suture to the nuchal crest is 140 mm and the length of the mid-frontals is about 88 mm. The orbits are strongly projected laterally. The pedicles are long and bear sinuses. There are no postcornual grooves. The horn-cores are distant at the base and almost parallel between them. They are inserted above the posterior part of the orbits obliquely to the sagittal plane and strongly inclined backwards in side view. From the base to the top they present a slight reverse torsion (clockwise). The horn-core cross-section is elliptical with traces of a blunt anterior keel. Their dimensions are: DT_b = 21 mm; DAP_b = 30.3 mm and their length at about 90 mm. In lateral view the posterior face of the horn-core appears convex, whereas the anterior one from convex at the base becomes concave in the upper half, following a relatively abrupt reduction of the horn-core dimensions towards the apex. A similar morphology is observed on a left horn-core AK14-14 (Fig. 14), which, however, is larger (DT_b = 31 mm, DAP_b = 45.4 mm; L > 80 mm), significantly heavier (more compact internal texture) and with swelling basal part.

Females (frontlet AK2-502)
The horn-cores are almost straight, without keels, inserted above the posterior part of the orbits, strongly sloping backwards (40° with the cranial roof) and slightly diverged (Fig. 13B). They are far apart at their bases and strongly compressed medio-laterally, especially in their upper parts (DT_b = 22.6dex and 22.1sin; DAP_b = 32.4dex and 32.0sin). Their internal surface is almost flat, while the lateral one is smoothly convex. The contact with the pedicles is not well marked. The frontals are not elevated and there is not postcornual groove. The width of the skull just behind the horn-cores is about 76 mm. The general morphology of this frontlet clearly reminds that of female individuals of late Miocene miotragoceres described from Spain, Germany, France and Greece (Moyà-Solà 1983; Romaggi 1987; Bouvrain 1988; Kostopoulos &
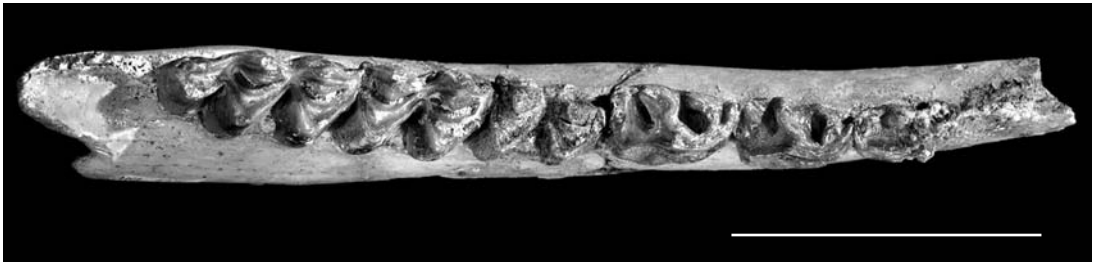
Fig. 15. — *Miotragoceros valenciennesi* (Gaudry, 1861) from Akkaşdağı, lower toothrow AK2-322, occlusal view. Scale bar: 4 cm.

Koufos 1996; pers. obs.). Therefore, I provisionally assign the specimen AK2-502 to a female individual of the previously described form.

Dentition
The mandibular ramus (GOK-196) is shallow (height between p4-m1 = 27 mm; in front of p2 = 19.3 mm). The mental foramen opens 32.5 mm in front of p2.
The teeth are brachyodont with rough enamel and strong upper and long-narrow lower premolars (Fig. 15). The premolar/molar ratio varies between 81 and 85 for the upper toothrow and from 75 to 87 for the lower one. P2 is as long as P3 while P4 is clearly shorter. The P2 is bilobed with strongly developed paracone-parastyle-protocone complex. The P3 is quadrangular and less molarized than P2. Among the molars, the M2 predominates because of its larger size. The labial styles and ribs are well developed but not strongly projected. A small central islet is occasionally present in M1,2 but is usually missing on M3, where a basal cingulum is present. A vestigial basal pillar is also occasionally present. Lingually, the lower premolars are slightly molarized. The paraconid of p2 is very weak. The p3 has stronger paraconid than parastylid, situated vertically to the anteroposterior axis of the tooth but projected posteriorly towards the base. The metaconid of p3 is free, elongated and backwardly directed. The entoconid is sub-triangular and stronger than the entoconid. The p4 is similar to p3 but with stronger paraconid, forming sometimes a posterior vane that tends to touch the metaconid

(Fig. 15). The latter one is extended anteroposteriorly. The entoconid of p4 is strong, fused rapidly with the endostylid. The lower molars bear a weak anterior fold and a small basal pillar that increases from m1 to m3. On the lingual face there is also a thin basal pillar. The talonid of m3 is single-tubercled.

BOSELAPHINE HORN DEVELOPMENT
Several palaeobiologists discussed the changes of boselaphine horn-cores due to ontogenetic growth and their effects on the taxonomy of the tribe (Bohlin 1935; Thenius 1948; Thomas 1979, 1984; Solounias 1981, 1990; Janis & Scott 1987; Bouvrain 1988). Trying to evaluate this morphological plasticity in relation to the Akkaşdağı specimens, I examined the skull collection of extant *Boselaphus tragocamelus* (Pallas, 1766) stored in the Natural History Museum of London. Since females of this species are hornless, I have chosen a set of 15 male skulls bearing toothrows, as the basis for my observations. My results, divided in four age classes, are as follows:
– Class I: ≈ 1-2 years old (M3 still within the alveoli, M2 just erupted, D2-D4 weakly-moderately worn): the pedicle directs posterolaterally and it is well developed, cylindrical, and longer anteriorly than posteriorly. The horn-core inserts behind the orbit, placed normally above the pedicle, and directs backwards and slightly upwards. It is short and slender and in side view shows a slightly concave upper (anterior) and slightly convex lower (posterior) surface; the cross-section is regularly rounded to oval. In its proximal part the horn-core surface bears shallow

discontinuous longitudinal grooves, while distally it is more porous. The temporal ridges are well developed but they do not raise like a ridge and they do not touch each other distally. The frontals are smooth, non elevated, and there is no rugose area.

– Class II: ≈ 3 years old (P2-P4 unworn, D4 worn, M3 just erupted): the horn-cores are identical with Class I but slightly larger, certainly longer and directed more upwards. The frontals form two elongated bulges between the pedicles and the supraorbital pits. There is no rugose area on the frontoparietal region, but the temporal ridges are stronger, ridge-like and touch each other posteriorly.

– Class III: ≈ 4-5 years old (full permanent dentition in first stage of wear): the frontals are slightly raised between the horn-cores forming a distinct broad intercornual plateau. The horn-core stops lengthening. Significant amount of new bone has been added above the frontal bulges and around the pedicle, enlarging and prolonging anteriorly the horn-core base. The appositional process in the anterobasal part also allows to the formation of a strong anterior keel restricted in the lower third. A postero-internal dihedre develops and the cross-section becomes triangular at the basal half. The temporal ridges are very strong and a rugose area appears on the frontoparietal region (behind and between the horn-cores).

– Class IV: > 6 years old [full permanent dentition in advanced stage of wear]: the rugose area extends above the orbits and both the intercornual plateau and the fronto-parietal depression become stronger. The horn-core is similar with that of age class III but slightly thicker anterobasally and showing several deep longitudinal furrows. The contact between the terminal end of the anterior keel and the upper unkeeled part of the horn-core forms a step, while another step is formed close to the base. The sheath presents two clear demarcations in its anterobasal part reflecting the internal steps. The length difference between sheathed and unsheathed horn at this stage is small (≈ 15%)

Evidently, the horn-core and frontal morphology of the specimen AK11-64 fits pretty well with that of a *Boselaphus* Blainville, 1816 in age Class I. The horn-core AK14-14 cannot be placed exactly in this scheme but, relatively speaking, it could correspond to a stage between age Classes II and III. Both Janis & Scott (1987) and Solounias (1990) discuss the issue of the horn development in Bovidae and especially in Boselaphini, concluding, however, in somewhat conflicting results. My observations show that the early development of horns in *Boselaphus* does not differ structurally from that of other Bovidae. Horned females of late Miocene boselaphines seem also to follow the normal process described by Janis & Scott (1987: 10-14). Moreover, the horn-cores (and consequently the sheath) of juvenile *Boselaphus* clearly resemble those of adult living *Tetracerus* Leach, 1825, early-middle Miocene *Eotragus* Pilgrim, 1939 and middle Miocene *Strepsiportax* Pilgrim, 1937 and they appear to be similar to the morphology observed in female and young male individuals of late Miocene boselaphines (e.g., AK11-64, AK2-502). Hence, I will agree with Janis & Scotts' statement (1987: 14) that there is no reason to believe that the horn growth-mechanism of extant and extinct boselaphines is any different from other bovids, and, as a result, I should refuse the hypothesis of Solounias (1990: 435) for a boselaphine taxonomic distinction based on a bovid biphyly.

In contrast to the horn growth-mechanism of boselaphines proposed by Bohlin (1935) and Solounias (1981, 1990), my data show that until age Class II the main developmental process of *Boselaphus* horns is the lengthening. Somewhere between age Classes II and III lengthening is slowing significantly down, the sheath extends downwards covering the pedicle and the back-end of the pre-formed frontal bulges and thus preosteous substance (see Janis & Scott 1987) expands anterobasally, adding appositionally new bone around the base. From age Class III and then after horn growth occurs mainly around the base with a progressive extension of the described mechanism anterobasally as the horn increases slowly in length. Depending on the rates of horn-core lengthening (which in turns may reflect
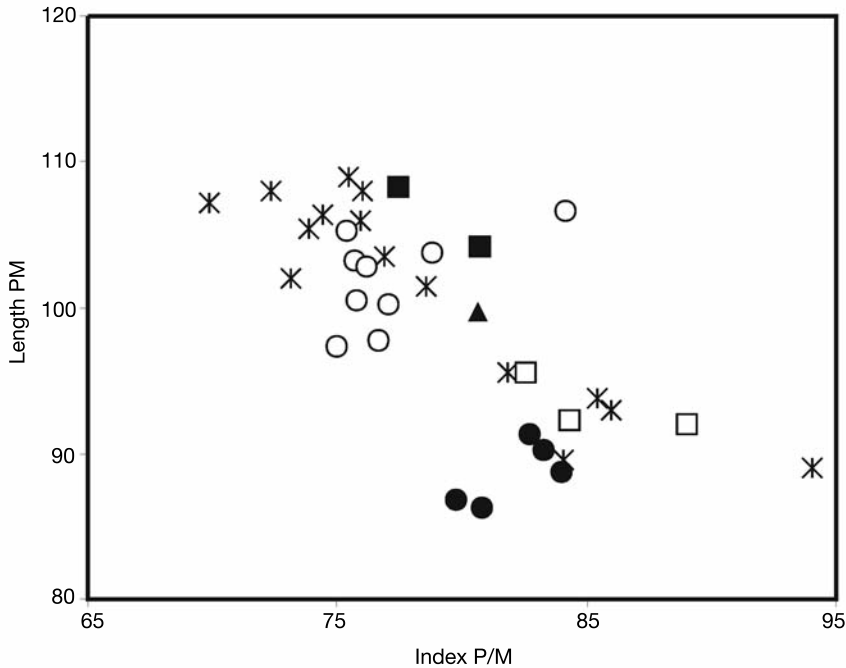
Fig. 16. — Premolar/molar index against toothrow length (upper dentition) in *Miotragocerus* and *Tragoportax*. □, *Miotragocerus valenciennesi* (Gaudry, 1861), Akkaşdağı; ■, *Tragoportax* aff. *amalthea* (Roth & Wagner, 1854), Akkaşdağı; ●, *M. macedoniensis* Bouvrain, 1988, Dytiko; ○, *T. rugosifrons* (Schlosser, 1904), Axios valley; ✳, *Miotragocerus* and *Tragoportax* from Pikermi; ▲, *M.* cf. *pannoniae* (Kretzoi, 1941), Nikiti-1.

ecological factors), the process produces successive steps along the keeled anterior face, which is a result of the dihedral apposition of bone on the frontal bulges. The anterior horn-core steps are expressed as demarcations on the anterior sheath surface.

Although particular, the described mechanism is not unique among Bovidae and analogies can be detected in the horn development of ovibovines (Allen 1913). The described procedure seems also to explain pretty well the horn-core morphology of late Miocene boselaphines, given that different rates (or stability) in length development between the early and late ontogenetic stages in combination with a continuous forward growth could provide different horn-core shapes in distinct taxa. Solounias (1990) is right, however, to suggest relations between the horn base of the late Miocene boselaphines and the protrusion fields above the frontal bulges of *Boselaphus*. But to my

viewpoint, these fields are the rudiments of an appositional process that occur(ed) later in the ontogenetic development of horns and which seems to have been degenerate in *Boselaphus*. The main difference between *Boselaphus* and late Miocene boselaphines is that the frontal bulges of the earlier forms are entirely covered by horn bone, whereas in the living form the process is incomplete, leaving a long rough area between the horn base and the supraorbital pits.

As Janis & Scott (1987) point out, the hypothesis of multi-tined *Miotragocerus* sheath is unlikely to be correct. Based on *Boselaphus*, I think, however, quite possible that the external horn morphology of Miocene boselaphines could follow the internal one.

COMPARISON

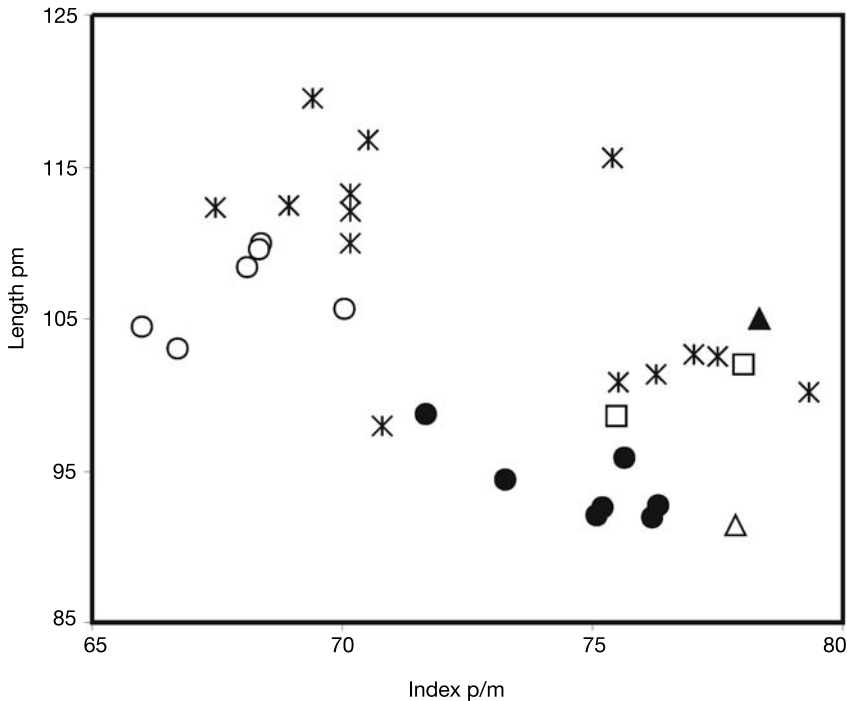Hitherto boselaphines have been scarcely recognized in the late Miocene of Turkey (see Köhler

FIG. 17. — Premolar/molar index against toothrow length (lower dentition) in *Miotragocerus* and *Tragoportax*. Symbols as in Figure 16 and △, VTK-38, *M. valenciennesi* (Gaudry, 1861) from Vathylakkos (Bouvrain 2001).

1987; Gentry 2003). The Akkaşdağı form shows clear affinities with *Miotragocerus* (horned females, backwardly inclined and untwisted male horn-cores smoothly keeled with an anterior demarcation, high premolar/molar ratio) and especially with the species *M. valenciennesi* from Pikermi. The skull AK5-597 is almost identical to the specimens MNHN PIK 2366 and PIK 2448 sharing in common a similar sloping of the face on the cranial roof, a relatively short opisthocranium, a small and well defined lacrymal fossa placed in the anterosuperior part of the orbit, a relatively deep preorbital fossa limited posteriorly above M1-P4, an infraorbital foramen placed above P2, and a small auditory bulla, placed just in front of the strong posterior tuberosities of the basioccipital. The dental proportions of the Akkaşdağı form fall within the range of the Pikermian sample (Figs 16; 17), being clearly distinct from those of *Tragoportax amalthea* (Roth & Wagner, 1854) and *T. rugosifrons* (Schlosser, 1904). It is therefore no

doubt for the inclusion of the Akkaşdağı boselaphin in *Miotragocerus valenciennesi*. The species is also present in the whole fauna of Samos (AMNH 22766 from Q6, AMNH 86556 and 86557 from Q2, AMNH 20572 from Q5, PIM 65 and AeMNH MTLA11). Melentis (1967) described from the middle Turolian locality of Halmyropotamos, Greece, several races of *Tragoportax amalthea*. Roussiakis (1996) recognizes in this material several specimens that could be attributed to "*Tragoportax gaudryi*" (Melentis 1967: pls XV, XVI, figs 2, 3, pl. XVII, fig. 2) and in agreement with him I refer this material to *Miotragocerus valenciennesi*. The adult skull from Achladi (Euboea, Greece) figured by Mitsopoulos (1947: fig. 3) as "*Tragocerus*" *amalthea* is also ascribed with some confidence to *Miotragocerus valenciennesi*.

Moyà-Solà (1983) and Bouvrain (1988) followed by Spassov & Geraads (2004) recognize several subspecies of *M. valenciennesi* to which Bouvrain

& Heintz (pers. comm.) impute lately specific value. This makes that *Miotragocerus* is a highly diversified genus. Except for *M. monacensis* and *M. pannoniae* from the Vallesian of Central Europe and *M. valenciennesi* from the middle Turolian of E Europe, *M. crusafonti* is known from the early Turolian of the Iberian Peninsula and *M. macedoniensis* from the late Turolian of Greece. The unpublished *Miotragocerus* (= *Graecoryx*) "*andancensis*" (Romaggi 1987) from France appears to be very similar to *M. crusafonti* from Piera both on the male and female morphology, and I suggest that they could be regarded as synonyms. These two forms from the early Turolian of Western Europe present some interestingly distinctive characters from the eastern ones (such as the reduced size and details of female skull morphology) that merit a more careful approach. The form from Piera (Spain) shows a stronger cranio-facial angle, a more inflated braincase and a certainly smaller size than the Pikermi and Akkaşdağı *Miotragocerus*. The attribution of the Mont Lubéron form to *M. valenciennesi* (Moyà-Solà 1983) seems quite doubtful and Romaggi (1987) considers this form as belonging to *Tragoportax amalthea*.

Miotragocerus macedoniensis Bouvrain, 1988 from Dytiko is different from the Akkaşdağı form in having a generally smaller size, smaller and probably longer horn-cores, un-concave occiput vertical to the cranial roof, larger auditory bulla, shorter basioccipital and slightly smaller premolar/molar ratio associated with a clearly smaller toothrow (Figs 16; 17). Spassov & Geraads (2004: 341, 356) throw doubt upon the generic affinities of the Dytiko form and prefer to transfer it to *Tragoportax* because of "the shape of the basioccipital and the presence of a fronto-parietal post-cornual depression". I believe, however, that most of the characters ascribed by them to the Dytiko form (Spassov & Geraads 2004: table 5) are rather misinterpreted: the basioccipital of the Dytiko form shows a strong median crest which is not placed into a groove formed by paired broadly blunt ridges between the anterior and posterior tuberosities on each side; the occiput narrows relatively abruptly towards its top; the temporal lines are moderately developed; the intercornual region is definitely narrow and not raised; the horn-core divergence is certainly weaker than in *Tragoportax* and the horns run rather parallel to each other; the postero-internal dihedral is not developed; the premolar row is certainly longer comparatively to *Tragoportax* (compare values in Bouvrain 1988, 1994b; Spassov & Geraads 2004) and the p3, p4 are positively *Miotragocerus*-like. In my opinion, this set of characters lets little doubt about the attribution of the species to *Miotragocerus*. The interpretation of the post-cornual depression is more delicate: the intenseness of this character is a relation of how much the intercornual plateau is raised and how strongly the temporal ridges appear. Both features are not exaggerated in the Dytiko boselaphin and they do not significantly differ from those observed in other specimens ascribed to *Miotragocerus* (such as AK5-597 from Akkaşdağı, I-122 from Sebastopol, NKT-220 from Nikiti-1, U-57 from Höwenegg, PIK 2366 from Pikermi, AMNH 86556 from Samos and HD-2010 from Hadjidimovo). Nevertheless, the development of rugosities is quite stronger in Dytiko than in *M. valenciennesi*.

Among the material of *Tragocerus leskewitschi* Borissiak, 1914 from Sebastopol, there is a part of skull (Borissiak 1914: pl. IV, fig. 5) with clear affinities to that of *Miotragocerus*. Borissiak (1914) regards the horn-core pattern of this specimen as a different morphotype than that of the type I-122, but a cast of the latter specimen stored in BMNH (M15761) shows that the horn-cores are badly attached to the skull: a relatively thick zone of plaster interposes between the pedicles and the preserved part of the horn-cores. Bouvrain (1994b), Spassov & Geraads (2004) and Bouvrain & Heintz (pers. comm.) suggest a provisional generic similarity of this Vallesian species with *Miotragocerus*/*Dystychoceras* and I fall in with them, maintaining however *Miotragocerus*. *Miotragocerus leskewitschi* also presents interesting similarities with *Sivaceros vedicus* (which is however based on a relatively immature skull), as well as to *Graecoryx bonus* Korotkevich, 1981 from Belka. In comparison with the Akkaşdağı form, *M. leskewitschi* differs in the less inclined face,

simpler and smaller P2, more posteriorly placed orbit and more inclined horn-cores.

The Nikiti-1 boselaphin is originally ascribed to *Tragoportax gaudryi* by Kostopoulos & Koufos (1996) and referred to as *Dystychoceras* sp. in Bouvrain (2001) but seems to be closer to the Hungarian species *M. pannoniae*. The male skull NKT-220 is almost identical to the male morphology of the latter species (according to the figures and descriptions of Romaggi 1987), while the female skull NKT-120 slightly differs in the longer opisthocranium and the curved horn-cores. I suggest therefore referring the NKT form to *Miotragocerus* cf. *pannoniae*. Nikiti-1 boselaphin differs from the Akkaşdağı form in its smaller size, the shorter opisthocranium, the less developed rugose region and temporal ridges and the un-concave occiput.

Genus *Tragoportax* Pilgrim, 1937

Tragoportax aff. *amalthea* (Roth & Wagner, 1854)

MATERIAL EXAMINED. — P2-M3: AK2-314 (LPM = 104.2, LP = 46.5, LM = 57.6), AKB-52 (LPM = 108.2, LP = 48, LM = 62); p2-p4: AK12-82 (Lp = 49.2); p3-p4: AK3-119; p4: AK2-461.

DESCRIPTION AND DISCUSSION

The presence of a second tragocere at Akkaşdağı is documented by a few toothrows with clear boselaphin morphology. In contrast to the previous form, it has a slightly larger size, shorter premolars comparatively to the molars, strong and posteriorly extended metastyle on M3 (goat-like), P2 equally long as P3, both with weaker paracone-parastyle complex, p4 longer than p3, metaconid of p4 directed posteriorly, paraconid of p3,4 less developed and not projected posteriorly. The morphological features and the proportions of the dentition (Figs 16; 17) are very close to the Pikermian *Tragoportax amalthea*, a species to which it could be attributed. *T. rugosifrons* (Schlosser, 1904) from Samos and Axios valley is also close dimensionally but with slightly different tooth structure (strong and projected parastylid and wider metaconid on lower premolars, more developed paracone-parastyle

complex on the upper premolars) (Solounias 1981; Bouvrain 1994b; Roussiakis 1996).

Genus *Pachytragus* Schlosser, 1904

Pachytragus crassicornis Schlosser, 1904

MATERIAL EXAMINED. — Part of skull: GOK-181+182; frontlet: AK2-503, AK12-70, AK3-200; isolated part of horn-cores: AK7-126, AK7-161, AK6-316, AK4-80, AK4-190; D2-M3: AKB-67; D2-M2: AK11-73; P2-M3: AK2-312, GOK-210, AKB-95; P3-M2: AK2-157, AK5-204, AKB-69; P4-M3: AK2-156; P2-M1: AK5-445; P2-M2: AK2-312; P3-P4: AK3-194; M1-M3: AK5-426, AK5-293, AKB-70; d2-m2: AK12-80; d4-m3: AK11-59; mandible without vertical rami: AK2-63; i1-m3: AK4-123; p3-m3: AK2-64; p2-m2: AK5-616, AK2-155, AK7-66, AK12-79; m1/2: AK2-159, AK7-104, AK12-35; m3: AK2-325, AK6-68, AK12-81, AK5b-254, AK12-84.

DESCRIPTION
Skull
The opisthocranium is elongated and narrow (Fig. 18; Appendix: Table 10). The occiput is relatively high with strong mastoidal crests. It forms an angle of about 115° with the cranial roof. The foramen magnum is large comparatively to the condyles. The mastoid faces both laterally and posteriorly. The paroccipital processes are probably short and sub-rounded in cross-section. The external auditory meatus is placed just above the upper level of the condyles. The elongate basioccipital is parallel to the flat cranial roof (Fig. 19A). Its anterior tuberosities are elongated and parallel to the sagittal plane. The posterior tuberosities are larger and bulge with main axis vertical to the sagittal plane. Between the anterior and posterior tuberosities a weak, wide and shallow central groove runs along the basioccipital. The oval foramen is large, squarish and opens just in front of the anterior tuberosities. The frontoparietal and interfrontal sutures are complicated (Fig. 19B). The first one forms a forward indentation. The latter one is constricted between the horn-core bases. The frontals form two shallow depressions in the postero-medial side of the pedicles. The supraorbital pits are

Fig. 18. — *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı, skull GOK-181+182, lateral view. Scale bar: 5 cm.

Fig. 19. — *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı, skull GOK-181+182; **A**, ventral view; **B**, dorsal view. Scale bar: 5 cm.

small, opening at about 40 mm below the horn-core base. There is no postcornual groove. The pedicle is rather short with well marked contact with the horn-core. It contains sinuses that however do not continue into the horn-cores. The horn-cores are moderately long (maximal length along the anterior surface at about 280 mm), sabre-like, slightly curved backward and moderately diverged from the sagittal plane (Figs 18; 20A, B). They are placed above the posterior part of the orbits, slightly tilted backwards (77° with the cranial roof). Their lateral face is flat while the internal one is slightly convex. Their section is elliptically shaped with narrower posterior part at the base but wider towards the apex. The medio-lateral compression increases from the base to the top (Appendix: Table 11). The anteroposterior axis of the horn-core base is oblique comparatively to the sagittal plane (≈ 25°). Discontinuous longitudinal grooves run along the horn-core surface. There is no real keel but a blunt anterodistal constriction is present.

Dentition
Several maxillas and mandibles are assigned to this form (Appendix: Tables 12; 13). The teeth are hypsodont with strong styles and reduced premolar row. P3 is bilobed lingually and longer than P2. Upper molars do not bear basal pillars (Fig. 21A).
The mandible is elongate and narrow with shallow rami and moderately long snout. In the best

FIG. 20. — *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı, frontlet AK2-503; **A**, lateral view; **B**, frontal view. Scale bar: 5 cm.

preserved specimen AK2-63 (Fig. 21B) the length i1-m3 is about 185 mm, the diastema p2-c is 69.6 mm and the length p2-m3 97.3 mm. The mental foramen opens 46.5 mm in front of p2. The height of the mandibular ramus at p4-m1 level varies between 27 and 32.2 mm (n = 2) with mandibular width at the same point 12.6-12.9 mm (n = 2).

The lower canine is symmetrical and in contact with the incisors but not very incisiform (rather oval shaped), while its width is slightly larger than that of i3. i2 is as much long as i3 and both are slightly asymmetrical with a weak lingual ridge. i1 is rather symmetrical, more

shovel and about 20% larger than i2 (Fig. 21B). p2 is simple without paraconid but with strong metaconid and entoconid. p3 has well developed parastylid and paraconid, fused each other at the crown base. The metaconid is independent, but the second valley usually closes at the base due to an elevation of the enamel. The entoconid and the endostylid are elongated and they are fused rapidly together. Lingually, there is a weak furrow separating protoconid from hypoconid. p4 is similar to p3 (Fig. 21B) but the paraconid fuses with the parastylid from the first stages of wear, the metaconid is stronger and wider towards the base and the lingual fur-
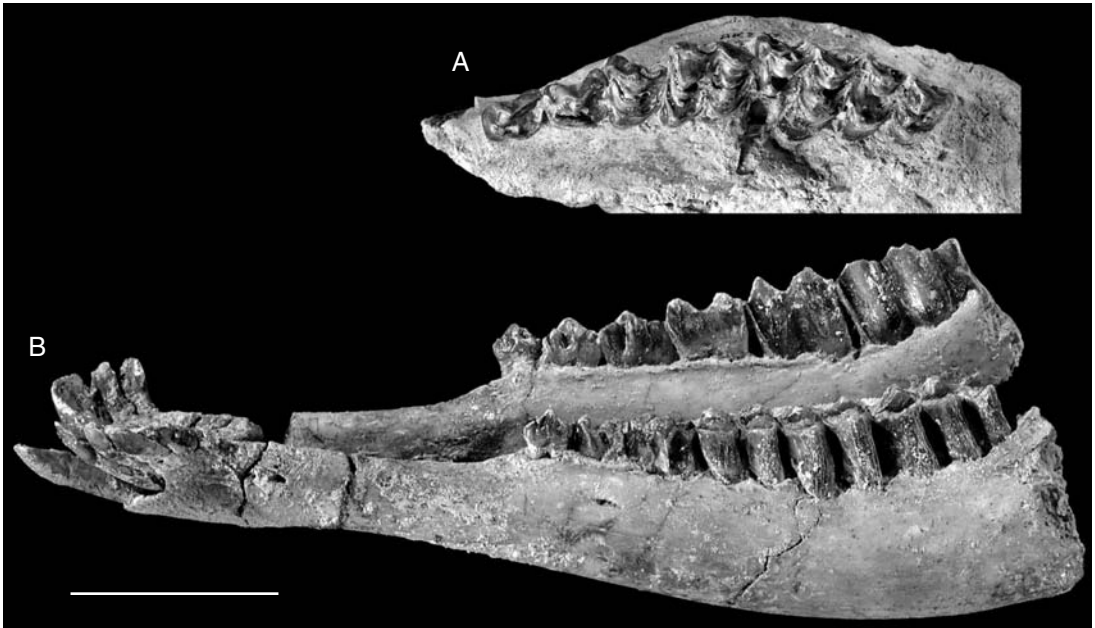
Fig. 21. — *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı; **A**, upper toothrow AK2-312, occlusal view; **B**, lower toothrow AK2-63, lateral view. Scale bar: 4 cm.

row is stronger. The lower molars have strong stylids, especially metastylid. There is no goat fold or basal pilar ("ectostylid"). The talonid of m3 is single-tubercled with strong postero-lingual stylid.

One of the most impressive characters of the dentition is its hypsodonty. Considering unworn or slightly worn specimens, the hypsodonty index ("Height of posterior lobe/Occlusal length") is estimated as follows: 113.5 for M1 (n = 1), 91.9-97.7 for M2 (n = 2), 103.4-121.9 for M3 (n = 3), 122.4-126.9 for m2 (n = 2) and 82-100.4 for m3 (n = 3).

COMPARISON

The morphological features of the Akkaşdağı skull and frontlets, such as the strong cranio-facial angle, the long and relatively narrow opisthocranium, the sabre-like horn-cores with strong mediolateral compression, the large sinus extending into the pedicle, the small supraorbital foramina not sunken into depressions, the short premolar row and the advanced hypsodonty, clearly align them with the large late Miocene antelopes referred to *Protoryx/Pachytragus* group. I follow Köhler (1987), Roussiakis (1996), Gentry *et al.* (1999), and Gentry (2000) in considering *Pseudotragus* Schlosser, 1904 (synonyms: *Microtragus* Pilgrim & Hopwood, 1928; *Sporadotragus* Kretzoi, 1941) as a valid and distinct genus.

Protoryx enanus Köhler, 1987 from the middle Miocene (MN7) of Turkey and the slightly later *Protoryx solignaci* Robinson, 1972 from MN8-9 of Tunisia, are quite different from the Akkaşdağı form, being more primitive either in the horn-core or dental morphology and rather smaller in dimensions (Köhler 1987; Gentry 2000).

In comparison with *Protoryx carolinae* Forsyth-Major, 1891 from Pikermi, the Akkaşdağı form differs in the smaller size, longer and narrower opisthocranium, more posteriorly directed condyles, more laterally projected mastoids, more triangularly shaped basioccipital (rather rectangular in *P. carolinae*) with less marked groove and bulbous posterior tuberosities (crest like in *P. carolinae*), more developed pterygoid process
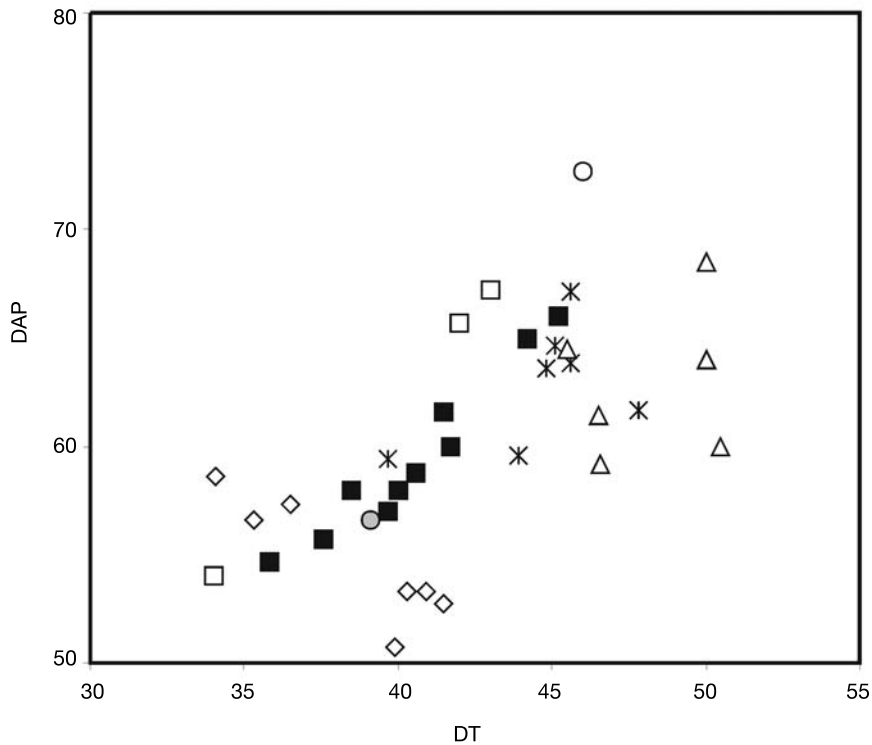
Fɪɢ. 22. — *Pachytragus* horn-core distribution of basal measurements; ■, *P. crassicornis* Schlosser, 1904, Akkaşdağı; ○, BMNH M3878, Maragha; □, *P. ?crassicornis*, KTA; ●, *Pachytragus* sp., Kınık; △, *Protoryx carolinea* Forsyth-Major, 1891, Pikermi; ✳, *P. laticeps* Andree, 1926, Samos; ◇, *P. crassicornis*, Samos. Abbreviations: **DAP**, anteroposterior diameter; **DT**, transverse diameter. Data from Gentry 1971; Köhler 1987; Bouvrain 1994a; and pers. data.

of the sphenoid, flat cranial roof and shorter and more uprightly inserted and almost uncurved horn-cores. Moreover, the horn-cores of *P. carolinae* show a weaker mediolateral compression (Fig. 22), increasing slightly toward the apexes; the index DT/DAP at the base varies between 70.5 and 84 in *P. carolinae* versus 65. and 69.7 in Akkaşdağı, while at 10 cm from the base the same index becomes 69.5-74 versus 60.7-70 respectively.

I do not believe *Protoryx carolinae* exists in Samos; all the material from the island I have seen is definitely different from the Pikermi one. Therefore, I come closer to Gentry's (1971) thoughts in placing the forms from Samos (as well as those from Maragha) in a different genus, *Pachytragus* Schlosser, 1904. The morphology of the Akkaşdağı form also matches the diagnostic char-

acters of this genus (Gentry 1971: 244). The recent study of the rich *Pachytragus* collection from Samos housed in the AMNH (October 2004) let me clarify my previous opinion (exposed in the manuscript reviewed by the referees) and I finally follow Gentry (1971, 2000) in accepting the occurence of two *Pachytragus* species in Samos. I think *Pachytragus latifrons* (Andree, 1926) and *Pachytragus crassicornis* Schlosser, 1904 are well distinct chrono-stratigraphically: the former is known from the early-middle Turolian levels of Samos (?Qx, Q4, Q1) while *P. crassicornis* is exclusively identified from a certainly younger fossil level (Q5; see also Kostopoulos *et al.* 2003); the specimen AMNH 20708 from Q1, for which Gentry (1971: 255) suggests stronger similarities with *P. crassicornis*, belongs with confidence to a young mature male individual of *P. laticeps*.

Interestingly, the braincase dimorphism exhibited in *P. latifrons* (see discussion in Gentry 1971; Bosscha-Erdbrink 1988) has been bequeathed in *P. crassicornis* too (but in a lesser degree): six crania of *P. crassicornis* from Q5 have a shorter and broader braincase than the remaining three specimens, which show a long-brained aspect. The character appears to me strongly related to the mechanical response of the skull to the degree of lengthening and backward curvature of the horns and it is worth to be further studied. I do not think the presence of an anterodistal keel is a species related character as suggested by Gentry (1971); although the presence of keel varies significantly (even in the same individual; AMNH 20579), it seems that the character occurs preferencially (or more frequently) in the short-horned individuals of both species (e.g., *Pachytragus laticeps*, specimen MGL S30 figured in Gentry 1971: pl. III, figs 1, 2; *P. laticeps* AMNH 22857, 20612, PIM 4, 8, 9; *P. crassicornis* Schlosser, 1904: pl. 11, fig. 11; *P. crassicornis*, AMNH 22943, 22938, 22939).

Both *P. laticeps* and *P. crassicornis* populations from Samos comprise rather exclusively male individuals (the female morphology AMNH 20687 [Gentry 1971: 252] is much less recognized into the worldwide Samos sample), suggesting gregarious bovids living in large segregated herds. Hence, it seems quite logical to accept that the keel development is more closely linked to the behavioural ecology of these animals, substituting the attractiveness of a long horn.

Pachytragus laticeps and *P. crassicornis* are very closely related species with the former representing the direct ancestor of the latter. The relatively short and diverged horn-cores, the so-called "mesocephalic" skull structure and the size proportions detected in Akkaşdağı (Fig. 22) fit pretty well with *P. crassicornis*. According to Gentry (1971) a distinction of the premolar shortness into the Samos sample is impossible. The premolar/molar ratio of the Akkaşdağı form varies between 60 and 68 in the upper dentition and 56 and 58 in the lower one. These values are placed safely into the variation of the Samos *Pachytragus* (the ratio varies between 56 and 69 in the upper toothrow, n = 16 and between 56.6 and 65.7 in

the lower, n = 16), being rather larger than in *P. carolinae* (the upper dentition ratio is about 49 in one of the three known Pikermian specimens; BMNH M11415). Interestingly *P. carolinae* shows a shorter premolar row indicating more advanced dentition than the Samos and Akkaşdağı forms.

The Maragha *Pachytragus*, at least the cranium BMNH M3878 (which by the way is the same specimen mentioned and figured by Pilgrim & Hopwood 1928: pl. III, fig. 2 under the register number M3841) shows numerous common features with several Samos specimens but it has certainly stronger horn-cores, more expanded anteroposteriorly. These two characters, as well as the smaller degree of horn-core's divergence, differentiate it from the Akkaşdağı form. Among the Maragha material described by Bosscha-Erdbrink (1988) there are, however, several specimens approaching the Akkaşdağı form both in morphology and dimensions.

Bouvrain (1994a) describes *P. laticeps* from Kemiklitepe A/B (Turkey) and Köhler (1987) *Protoryx* sp. from Kınık (Turkey). Although the available material from these two localities is quite restricted (some isolated horn-cores and dentitions) the horn-core morphology and proportions (Fig. 22) as well as the dental structure and hypsodonty (Bouvrain 1994a: 186) indicate close affinity with the Akkaşdağı form.

A lot of words have been spent on the relationships of *Pachytragus* to the recent representatives of Caprini and/or Hippotragini (Gentry 1971, 2000; Bosscha-Erdbrink 1988). Among other characters, Gentry (1971: 279) emphasizes the importance of the size of the central incisor as distinguishing Eurasian from African antelopes. In a general scheme (Gentry 1970, 1987) i1 is slightly larger than other incisors and canine in Bovini, *Panthalops* and Caprini, while a significantly large i1 (associated perhaps with a reduced i3 and c) characterizes Tragelaphini, Boselaphini, Hippotragini and Antilopini. Hitherto, the incisor morphology and size of *Pachytragus* was unknown but the Akkaşdağı material provides the first evidence on this feature, indicating a relation

FIG. 23. — *Palaeoryx majori* Schlosser, 1904 from Akkaşdağı, skull AK3-130; **A**, lateral view; **B**, dorsal view. Scale 5 cm.

of the type i1 > i2 = i3 < c. Although relatively worn, the first incisor of the Akkaşdağı *Pachytragus* is larger than i2, a character that is also attested by its larger root (Fig. 21B). In the restricted mandible sample of living Caprini I have examined, i1 is equal in size to i2 and i3. It is the same in several fossil forms related to Caprini (cf. Gentry 1970: pl. 9, fig. 6, pl. 14, fig. 3), while late Miocene Antilopini show a significantly larger i1 in comparison to the rest incisors and the canine. Although the size difference between the Perivolaki i1 and i2 is not as sharp as that shown in Antilopini, it indicates closer relations to the "African" pattern than to the "Eurasian" one (cf. Gentry 1970: pl. 9, fig. 5). Thus, the case for *Pachytragus* being related to Caprini (Gentry 2000) would be weakened.

Genus *Palaeoryx* Gaudry, 1861

Palaeoryx majori Schlosser, 1904

Palaeoryx majori Schlosser, 1904: 38, pl. VII, fig. 5.

Palaeoryx laticeps Andree, 1926: 161, pl. XIII, figs 4, 6.

MATERIAL EXAMINED. — Frontlet: AK3-130; P3-M3: AK5-643 (LM1-M3 = 60.7); P4-M3: AK5-426 (LM1-M3 = 62.0); P3-P4: AK4-191; P3: AK5-609; M2: AK5-369; m2-m3: AK4-199.

DESCRIPTION
Skull
The braincase is wide (Appendix: Table 10) and the cranial roof slightly convex (Fig. 23A). The opisthocranium is short and moderately low. The mid-frontal suture is raised slightly and is rather
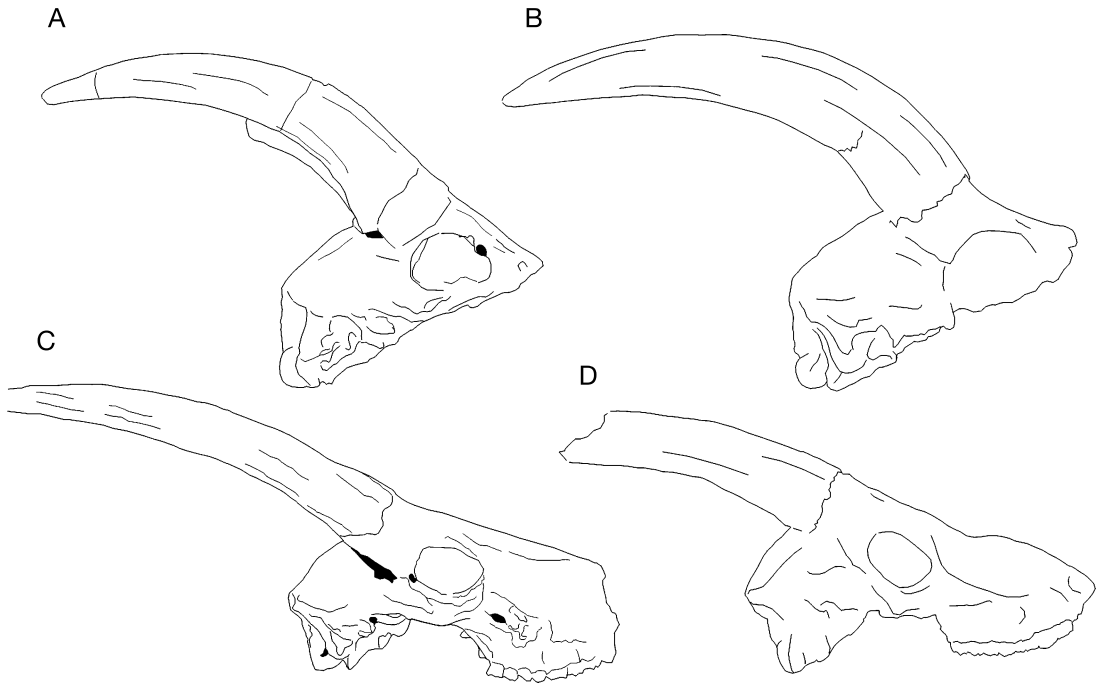
FIG. 24. — Drawings of the skull specimens of *Palaeoryx majori* Schlosser, 1904 (**A**, **B**) and *Palaeoryx pallasi* (Wagner, 1857) (**C**, **D**); **A**, MTLB-160 (AeMNH); **B**, PIM-121; **C**, MTLA-113 (AeMNH); **D**, M10831 (BMNH) from Samos and Pikermi (approximately at the same scale).

open (Fig. 23B). The frontals are not elevated between the horn-cores. Ahead of them the frontals incline smoothly, forming an angle of about 105° with the cranial roof. The orbits are rather rounded and well projected laterally. The width of the skull at the dorsal orbital rims accounts 155 mm. The supraorbital foramens are sunken into elongated and narrow pits. There are no postcornual grooves. The anterior tuberosities of the preserved basioccipital are strong, widely separated and slightly oblique comparatively to the sagittal plane. Between them and the posterior tuberosities a wide furrow runs along the basioccipital axis. The oval foramen is large, placed well in front of the anterior tuberosities. The horn-cores are elongated (≈ 300 mm along the anterior surface) and placed just above the orbits and laterally (Fig. 23A, B). Their basal part forms an angle of about 80° with the cranial roof. They are placed well apart at the base (internal basal distance at about 57 mm) and widely divergent toward the

apexes. In their uppermost part they re-curve inwards (Fig. 23). In lateral view they appear strongly inclined backwards and curved posteriorly (Fig. 23A). Thin discontinuous longitudinal grooves run along their surface. They do not bear any keel. Their cross-section is elliptical with weak mediolateral compression at the base, becoming stronger towards the tips (Appendix: Table 10).

Dentition
The few dental specimens assigned to this form, cannot give a complete idea on the tooth morphology. They differ from the previously described dentition of *Miotragoceus valenciennesi* and *Tragoportax* aff. *amalthea* in the longer molar row and the stronger hypsodonty. The P3 is lingually bi-lobed, while both the P3, 4 bear a hypoconal spur. The upper molars are wide with well developed basal pillar, which in some specimens (mainly in M2) appears double. The lobes fuse

slowly together, giving rise to a strong central islet. The m3 has a clear goat fold, a strong "ectostylid" and a well developed-rounded talonid.

COMPARISON

The morphological characters of the skull AK3-130 leave no doubts about its attribution to the genus *Palaeoryx* Gaudry, 1861, according to the diagnoses given by Pilgrim & Hopwood (1928) and Gentry (1971). Although early authors distinguished several species into this genus (Schlosser 1904; Andree 1926; summarized and reviewed by Pilgrim & Hopwood 1928), later authors simplify its taxonomy and recognize a single species *Palaeoryx pallasi* (Wagner, 1857) (Gentry 1971; Solounias 1981; Bosscha-Erdbrink 1988). Solounias (1981) accepts the monospecificity of the genus, but he also recognizes four varieties based on some dental and horn-core differences.

My observations on the *Palaeoryx* material from Pikermi (BMNH, MNHN) and Samos (MGL, BMNH, AMNH, PIM, AeMNH) allow a slightly different approach, recognizing *Palaeoryx majori* Schlosser, 1904 as a valid species. Indeed, the differences between *Palaeoryx pallasi* (Wagner, 1857) and *Palaeoryx woodwardi* Pilgrim & Hopwood, 1928 do not merit a specific value, since they do not exceed population variability observed in other late Miocene bovids. It seems that these two forms are correctly regarded as conspecific, meaning that *P. pallasi* is equally present in Pikermi and Samos. Nevertheless, the fossil record of Samos offers strong evidences on the occurrence of a second species on the island.

Recent excavations in Samos (Koufos *et al.* 1997) brought into the light two skull specimens of *Palaeoryx* from the middle Turolian fossiliferous horizons, labeled MTLA-113 and MTLB-160 (AeMNH) (Fig. 24). Although similar in their general morphology, these two skulls differ in a large set of secondary characters summarized in the appendix (Table 14). These differences obviously exceed those of intraspecific variability. The cranial and dental characters of MTLA-

113 are very close to those of other specimens from Samos and Pikermi attributed to *Palaeoryx pallasi* (Fig. 24). MTLB-160 seems however identical to the specimen figured by Schlosser (1904: pl. VII, fig. 5) under the name *Palaeoryx majori*. Most of the characters observed in MTLB-160 reappear in the holotype of *Palaeoryx laticeps* Andree, 1926 stored in the Münster collection with the serial number PIM-121 (Fig. 24). The braincase structure of this specimen also differs from that of another specimen in the same collection PIM-118, attributed to *Palaeoryx pallasi*. NHMW A4779 (Solounias 1981: fig. 61D, E) looks very similar to the specimen MTLB-160 and to the type skull of *P. majori* Schlosser, 1904 and it should be included into this species.

Most of the features distinguishing *P. majori* from *P. pallasi* can also be observed in the skull AK3-130, which therefore is placed in the former species. The single significant difference that can be observed concerns the setting of the horn-cores on the frontals, which appears wider in the Akkaşdağı form, reflecting probably intraspecific variation.

The dentition of *P. majori* is not certainly known. Schlosser (1904) ascribed to his new species some isolated dentitions that however could belong to *P. pallasi* as well. Since both species are present in Samos, the dental characters of each form need a more careful approach. The Akkaşdağı data are also poor to solve the issue. Judging from the Akkaşdağı toothrows it seems that *P. majori* has a shorter molar row than *P. pallasi*. The available M1-M3 lengths from Akkaşdağı range from 60.7 to 62 being smaller than that of MGL S200, MGL S199, PIK 2456, PIK 2459, BMNH M10831 (range: 65.5-69.5). Similar values occur on the specimens MGL S327 (61.8 mm) and BMNH M10832 (61.3 mm) that, however, cannot be distinguished from *P. pallasi*.

The coexistence of two *Palaeoryx* species is also manifested in Halmyropotamos, Greece (Melentis 1967), where both *P. pallasi* (= *P. woodwardi*) and *P. majori* are present. On the contrary, the presence of the genus in Turkey

is badly documented. Köhler (1987) refers some isolated teeth from Kayadibi and Eski Bayırköy and a few horn-core fragments and a mandible from Mahmutgazi to *Palaeoryx pallasi*. Bouvrain (1994a) describes from KTA some dentitions and one horn-core as ?*Palaeoryx* sp. The morphology of the described toothrows is quite similar to that from Akkaşdağı, certifying the presence of the genus in this locality.

CONCLUSION

The quite rich bovid material of Akkaşdağı includes the following taxa: *Gazella* cf. *capricornis*, *Gazella* aff. *pilgrimi*, *Prostrepsiceros rotundicornis*, *Miotragocerus valenciennesi*, *Tragoportax* aff. *amalthea*, *Pachytragus crassicornis* and *Palaeoryx majori*. In this balanced bovid assemblage, *Gazella* is the main representative, prevailing over *Pachytragus* and *Prostrepsiceros*, while the presence of boselaphins and *Palaeoryx* is rather minor. The mentioned bovid association indicates strong similarities at species level with Pikermi, Samos and Kemiklitepe A/B, all dated to the middle-upper part of MN 12. Four of the seven identified bovid species occur in Pikermi (*G. capricornis*, *P. rotundicornis*, *M. valenciennesi*, *T. amalthea*) and four of seven in the middle-late Turolian faunal assemblages of Samos (*G. pilgrimi*, *M. valenciennesi*, *P. crassicornis*, *P. majori*), while five of the six bovids mentioned in Kemiklitepe A/B are also present in Akkaşdağı. A similar bovid community is also present in the Turkish faunas of Mahmutgazi (MN11/12) and Kınık (MN12) (e.g., Köhler 1987). *Gazella* cf. *capricornis* from Akkaşdağı shows more advanced features than the typical sample from Pikermi, suggesting a younger age. In addition, the presence of *Pachytragus crassicornis* indicates chronological relations with the upper fossil levels of Samos (Q5), dated to late middle Turolian (e.g., Kostopoulos *et al.* 2003). The somewhat archaic features preserved in *P. rotundicornis* from Akkaşdağı cannot allude to an older age, as similar characters have been also seen in some other middle Turolian populations from Turkey

(Kemiklitepe, Gökdere); it seems more possible that the evolutionary process of Pikermi *P. rotundicornis* was different than the eastern populations of the species because of local ecological factors. Thus, according to the bovids, a middle Turolian age (late MN 12) seems convenient for the Akkaşdağı, matching also with the radiometric dating of the underlying tuffs (Karadenizli *et al.* 2005).

The co-occurrence of two *Gazella* species in the Akkaşdağı fauna seems to follow the general rule of early-middle Turolian mammal assemblages, as well as, that of the modern African faunas. It looks strange that from a cluster of middle-late Turolian faunas only Pikermi appears to include a single species, but the study shows that this situation could be also fictitious. In any case, the systematic of late Miocene gazelles remains unresolved and a general revision is needed.

Prostrepsiceros occurs more or less continuously in a wide geographic area from Saudi Arabia-North Africa up to the Black Sea-Caspian region and from Greece to the western margin of the Tibetan Plateau (Bouvrain 1982; Bouvrain & Thomas 1992; Gentry 1999, 2003). The radiation and distribution of the genus, as well as the phylogenetic relationships among the quite numerous affiliated taxa are not yet clear enough. Evidently the genus appeared as early as in Vallesian (MN9, Gentry 2003) and exists hereafter with a variety of forms. Except for *P. vallesiensis* (MN 10), early representatives of *Prostrepsiceros* are mentioned from Middle Sinap (Turkey, MN9-MN10), Nikiti-1 (Greece, late MN10) and Jebel Hamrin (Iraq, MN10/11) (Bouvrain & Thomas 1992; Kostopoulos & Koufos 1996; Bonis & Koufos 1999), suggesting a fast radiation and distribution.

Early representatives of *Prostrepsiceros* share in common a weak cranio-facial angle, a long basioccipital with a wide central groove, small supraorbital foramens not into pits and away from the frontal base, small postcornual grooves and slender horn-cores comparatively to the skull size, inserted on the posterior part of the orbital roof, strongly inclined backwards and widely separated on the frontals. Some of these apparently

primitive features can also be seen in the poorly known *Sinapodorcas* Bouvrain, Sen & Thomas, 1994 from Middle Sinap, Turkey (Bouvrain *et al.* 1994; Gentry 2003), a genus that seems to me very closely related to *Prostrepsiceros*.

Hence, Bouvrain's (1982) suggestion in dividing *Prostrepsiceros* in two distinct subgenera might indeed reflect an early division in two distinct lineages that evolved independendly from late Vallesian onwards. The first one includes *P. vallesiensis*, *P. houtumschindleri*, *P. lybicus* and *P. vinayaki* and the second *Sinapodorcas*, *P. syridisi*, *P. rotundicornis*, *P. fraasi*, *P. zitteli* and *P. axiosi*. According to Lehmann & Thomas (1987) a relationship between *P. lybicus* and the Jebel Hamrin form seems undeniable while Gentry (1999) looks for the possible ancestor stock of Sahabi form in *P. fraasi* from Samos. Judging from the new discoveries in Molayan, I think that a possible relation between *P. lybicus*, *P. vinayaki* and *P. vallesiensis* should not be excluded.

In the frame of this work an effort has been made to delineate the status of Turolian Boselaphini in Eastern Mediterranean. We restore *Miotragocerus valenciennesi* over *Tragoportax gaudryi* and we recognize the priority of *Miotragocerus* over *Graecoryx*, *Pikermicerus* and *Dystychoceras*. *Tragoportax* is represented in the area by two species *T. amalthea* and *T. rugosifrons*, while the European genus *Miotragocerus* seems to extend into Western Asia and India, since *Sivaceros* looks very similar in order to be distinct. The ontogenetic growth of boselaphin horns does not confirm previous suggestions (Bohlin 1935; Solounias 1981, 1990) in distinguishing them from Bovidae. The basic split into the tribe predates the Siwaliks record (middle Miocene) producing two lineages that lead to *Sivaceros-Miotragocerus* and *Strepsiportax-Tragoportax*. The suggested rareness of boselaphines in the middle-upper Turolian of Turkey is slightly modified. The presence of *Tragoportax-Miotragocerus* in the Akkaşdağı fauna might indicate that their absence elsewhere is partly due to a taphonomical or artificial bias.

The study of the large antelope material from Akkaşdağı allows us to adopt Gentry's (1971, 2000) proposal in accepting *Pachytragus* as a valid genus, distinct from the Pikermi *Protoryx* and to recognize *Pachytragus crassicornis* outside Samos. The central incisor character of *Pachytragus* does not confirm however Gentry's (1971, 2000) phylogenetic proposal in relating the genus with Eurasian Caprini. Finally, reassessment of the available fossil record allows the recognition of *Palaeoryx* as a polyspecific genus and the reinstatement of *Palaeoryx majori* as a valid species that co-occurred with *Palaeoryx pallasi* in the eastern middle Turolian faunas.

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APPENDIX

TABLE 1. — Skull measurements (in mm) of *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı. Abbreviations: **DAP**, anteroposterior diameter; **DT**, transverse diameter.

	AKB-29	AK5-598	AK2-443	AK12-72
Height foramen magnum	13.2			
DT foramen magnum	14.0			
DT bi-condylar	36.4	36.0		
Height occiput	25.0	(34.5)		
Width bi-mastoid	59.5	57.6		
DT ant. tuberosities of basioccipital	17.0	14.0		
DT post. tuberosities of basioccipital	26.3	22.0		
DT horn-core base	23.7/24.2		19.8/20.4	18.8/18.9
DAP horn-core base	25.2/25		25.2/26.3	25.0/25.7
DT supraorbital pits	30.4		37.0	38.8
Width braincase	58.0	51.9		
Chord Bregma-nuchal crest	53.0	51.0		
Width skull in the posterior part of orbits	≈ 85.0		(73.0)	85.2
Height orbit			34.5	
DT orbit			34.8	
P2-M3		55.7		
M1-M3		32.5	30.3	
Width palate at M3		27.7		

TABLE 2. — Horn-core measurements (in mm) of *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı. Abbreviations: **7**, at 7 cm from the base; **b**, base; **d**, dex; **DAP**, anteroposterior diameter; **DT**, transverse diameter; **s**, sin.

	DTb	DAPb	DT7	DAP7	Length	DT/DAPb	DT/DAP7
AK2-153d	21.0	26.7				78.65	
AK2-154d	21.6	25.7	13.6	15.3	110.0	84.05	88.89
AK2-443d	20.4	26.3	12.8	15.0	118.5	77.57	85.33
AK2-443s	19.8	25.2	12.0	15.0	116.0	78.57	80.00
AK2-444d	21.3	27.6	15.0	15.5	111.0	77.17	96.77
AK2-444s	21.0	25.6				82.03	
AK2-446d	21.8	26.0				83.85	
AK2-447d	22.0	26.1				84.29	
AK2-450d	18.6	23.8				78.15	
AK2-455s	20.9	27.0	14.4	16.8		77.41	85.71
AK2-66d	23.1	26.7	14.5	16.3	105.0	86.52	88.96
AK2-67s	22.2	26.2	14.9	16.0	117.0	84.73	93.13
AK2-68d	20.1	26.1	12.5	14.8	125.0	77.01	84.46
AK2-68s	20.7	26.7	13.3	15.2	117.0	77.53	87.50
AK2-71s	18.1	24.4	13.5	16.5	119.0	74.18	81.82
AK2-72Bd	21.5	25.5	12.8	16.5	117.0	84.31	
AK2-72Bs	21.1	26.5	12.4	14.4	118.0	79.62	86.11
AK2-76d	18.5	24.2				76.45	
AK3-120s	17.8	24.4				72.95	
AK3-71s	18.5	24.9				74.30	
AK4-78d	23.5	29.1	15.7	18.0	122.0	80.76	87.22
AK4-78s	23.4	27.8	17.3	18.5	125.0	84.17	93.51
AK5-190d	18.5	24.5	11.7	14.8		75.51	79.05
AK5-603s	21.8	26.5				82.26	
AK6-293s	23.3	26.5	15.7	16.0	116.5	87.92	98.13
AK6-293d	24.4	26.0				93.85	

	DTb	DAPb	DT7	DAP7	Length	DT/DAPb	DT/DAP7
AK6-66s	19.5	26.2				74.43	
AK6-67d	19.4	26.7				72.66	
AK7-163d	20.0	26.0				76.92	
AK7-30d	20.3	26.3				77.19	
AK12-72d	18.8	25.0	13.1	16.8	117.0	75.20	77.98
AK12-72s	18.9	25.7	12.3	15.7	117.0	73.54	78.34
AK13-24d	22.6	25.5	14.8	?17.6	117.0	88.63	
AKB-29d	23.7	25.2				94.05	
AKB-29s	24.2	25.0				96.80	
AKK-193s	20.3	25.2				80.56	
AKK-76	22.1	26.0	16.0	18.4	125.0	85.00	86.96
GOK-188	19.5	22.7				85.90	
GOK-189	20.2	23.6				85.59	
Youngs							
AK5-599d	18.3	22.8	10.0	11.8		80.26	84.75
AK5-599s	19.4	23.0	10.6	11.7	100.0	84.35	90.60
AK5-600d	21.1	26.0				81.15	
AK5-600s	20.5	26.6	10.6	11.3	100.0	77.07	93.81
AK2-44Bs	17.0	22.9	9.3	11.6	97.0	74.24	80.17
AKK-98	19.5	23.1			90.0	84.42	
AK3-193d	17.1	22.0				77.73	
AK6-65s	20.5	23.0				89.13	
AK5-640d	18.0	22.2				81.08	

TABLE 3. — Upper toothrow measurements (in mm) of *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı. Abbreviations: **d**, dex; **L**, length; **s**, sin; **W**, width.

	PM	P	M	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
AK2-443s			30.3					7.2	8.5	6.9	9.7	10.7	10.6	11.7	10.1
AK3-169s	57.0	24.7	33.1	7.6	6.4	8.7	7.5	7.8	8.3	10.6	9.8	11.8	10.5	11.6	(8.5)
AK3-169d	56.7	24.0	32.5	7.4	6.4	8.7	7.0	7.5	8.3	10.3	9.7	11.4	9.6	11.3	
AK5-598s	55.7	23.0	32.5	7.3	6.7	8.7	7.4	7.9	8.0	10.8	9.5	11.2	10.3	11.5	9.5
AK6-224d			30.2			7.2	6.0	6.6	8.0	9.0	8.7			10.7	8.3
AK6-157s						7.9	6.4	6.9	8.0						
AK6-82s		23.0		7.1	6.5	7.2	7.1	7.4	8.2			11.7	10.7	10.7	10.1
AK12-74d	54.4	22.0	32.5	6.6	6.4	7.9	6.7	6.9	8.3	8.5	9.9	11.2	10.9	12.2	10.5
AK12-73s	54.0	22.6	32.0	7.5	6.3	7.9	6.7		7.4	10.5	9.6	11.9	9.9		
AK13-25d	50.0+		28.5			6.9	6.8	5.7	8.0	8.5	8.4	10.0	10.0	11.1	10.0

TABLE 4. — Lower toothrow measurements (in mm) of *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı. Abbreviations: **d**, dex; **L**, length; **s**, sin; **W**, width.

	pm	p	m	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
AK2-65s		21.5		5.5	3.2	8.0	4.3	8.0	4.3	8.8	5.3	10.9	6.1		
AK3-189d			33.9			7.6	4.0	8.1	5.0	9.0	6.6	11.0	6.8	15.0	6.6
AK3-77d		21.0		5.0	3.0	8.0	4.2	8.5	4.5			10.4	6.2	15.0	6.8
AK3-189s	58.8	21.2	38.4	4.7	3.0	7.2	4.2	8.7	5.5	10.0	5.9	11.9	6.3	15.5	6.2
AK3-301d		20.2		4.7	3.0	7.2	3.9	7.8	4.2						
AK4-89d	53.7	18.6	33.5	4.0	2.8	6.6	4.0	8.5	4.7	8.5	6.5	10.5	6.8	14.6	6.7
AK5-205s			34.6			7.7	4.2	8.0	4.7	8.8			6.4	14.8	6.5
AK5-206s			34.0			7.0	4.7	7.5	5.3	8.5	6.0	10.4	6.5	13.8	6.3
AK5-262d		19.5				7.7	4.4	7.7	4.7	9.5	5.4				
AK5-257s		23.8		6.0	3.5	8.3	4.7	9.6	5.0	8.9	6.4	11.5	6.5		
AK12-83s	54.0	19.3	34.2			6.4	4.0	8.0	4.9					15.3	6.0
GOK-211			32.9			6.1	4.2	8.0	4.7	7.5	6.0	10.5	6.1	14.6	6.0

TABLE 5. — Horn-core measurements (in mm) of *Gazella* aff. *pilgrimi* Bohlin, 1935 from Akkaşdağı. Abbreviations: **7**, at 7 cm from the base; **b**, base; **d**, dex; **DAP**, anteroposterior diameter; **DT**, transverse diameter; **L**, length; **s**, sin.

	DTb	DAPb	DT7	DAP7	L	DT/DAPb	DT/DAP7
AK5-642	24.0	28.4	17.0	24.0		84.51	70.83
AK5-601d	20.9	27.8	14.6	20.2	135	75.18	72.28
AK5-601s	21.1	28.1	14.5	21.5	135	75.09	67.44
GOK-184	20.8	26.5	12.4	17.1	130	78.49	72.51
GOK-183	20.8	25.3	14.2	17.0	137	82.21	83.53
AKA-42	20.8	26.9	13.8	17.0		77.32	81.18
AKA-49	20.1	27.5	12.7	17.0	110	73.09	74.71
AKB-45	20.2	26.1				77.39	

TABLE 6. — Comparison of *Gazella* cf. *capricornis* (Wagner, 1848) from Akkaşdağı with *G. capricornis* from Pikermi (Greece) and *G. deperdita* (Gervais, 1847) from Lubéron (France). Abbreviations: **7**, at 7 cm from the base; **b**, base; **d**, dex; **DAP**, anteroposterior diameter; **DT**, transverse diameter; **L**, length; **s**, sin; **W**, width. Numbers in italics represent the mean values of the appeared range.

	G. cf. *capricornis*	*G. capricornis*	*G. deperdita*	
	Akkaşdağı	Pikermi (MNHN, BMNH)	Cucuron (BMNH)	Lubéron (Heintz 1971)
DAPb × 100/DTb	103.3-137.6 *123.9* (n = 48)	102.5-139.2 *120.3* (n = 99)	119.8-145.7 *134.4* (n = 11)	123.0-150.8 *134.9* (n = 73)
DAP7 × 100/DT7	100.0-128.9 *116.2* (n = 24)	85.0-136.4 *110.4* (n = 55)	126.4-164.0 *143.8* (n = 5)	120.6-155.5 *142.6* (n = 30)
P2-M3	54.0-57.0	48.6-54.9 (n = 9)	57.0-60.5 (n = 2)	
Ratio P/M	67.7-74.6	75.4-78.4	70.5-73.2	
p2-m3	53.7-58.8	49.4-56.7 (n = 8)	51.5-60.7 (n = 6) (59.2 BMNH M34794)	
Ratio p/m	55.2-56.4	59.7-70.8	50.0-62.7	
"W/L × 100" p4	52.1-70.6 *58.5* (n = 12)	50.0-62.8 *56.0* (n = 16)	58.5-75.8 *64.5* (n = 26)	

TABLE 7. — Skull and horn-core measurements of *Prostrepsiceros rotundicornis* (Weithofer, 1888) from Akkaşdağı. Abbreviations: **7**, at 7 cm from the base; **b**, base; **d**, dex; **DAP**, anteroposterior diameter; **DEHc**, external horn-core distance (basal); **DIHc**, internal horn-core distance (basal); **DT**, transverse diameter; **s**, sin; **WOR**, width of the skull behind the horn-cores; **WSP**, width of the frontal at the supraorbital pits.

	AK2-75d	AK2-73d	AK2-74s	AK3-68s	AK3-70d	AK4-189s	AK5-641s	AK5-641d	AK5-152	AK6-64s	AK6-64d	AK no No.
WOR							(67.5)			(65.0)		
WSP							39.7		40.8	42.0		
DEHc							23.7			20.7		
DIHc							94.8			88.1		
DTpedicel	27.8	29.0			26.0	26.9	36.0			33.5		
DAPpedicel	33.6	29.6			30.0	28.6	33.0			30.5		
DTb	34.8	37.2	35.4	30.0	32.7	27.0	38.2	39.7	38.2	35.2	35.5	36.0
DAPb	30.4	32.0	32.0	27.0	28.3	25.5	34.0	33.9		30.7	32.2	30.0
DT7	26.0	25.6	24.4	21.0	22.5	19.4	31.5	29.3		29.6	26.0	
DAP7	28.6	26.0	26.2	22.0	23.5	20.0	31.8	31.4		30.2	28.2	
DTb/DAPb	114.5	116.2	110.6	111.1	115.5	105.9	112.3	117.1		114.6	110.2	120.0

TABLE 8. — Upper toothrow measurements (in mm) of *Prostrepsiceros rotundicornis* (Weithofer, 1888) from Akkaşdağı. Abbreviations: **d**, dex; **DAP**, anteroposterior diameter; **L**, length; **s**, sin; **W**, width.

	M	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
AK2-452d	42.5					13.5	12.6	15.2	13.8	14.0	13.0
AK3-220s	41.5			9.5	9.0	12.9	11.9	15.0	13.2	14.6	13.3
AK4-195s	40.2					13.0	11.5	15.0	13.5	14.0	13.5
AK5-51s	40.8	9.3	8.0	9.4	10.1	12.4	12.1	14.8	13.6	14.1	12.5
AK6-72d	39.1					12.4	11.7	14.5	13.5	13.8	13.0

TABLE 9. — Lower toothrow measurements (in mm) of *Prostrepsicerros rotundicornis* (Weithofer, 1888) from Akkaşdağı. Abbreviations: **d**, dex; **DAP**, anteroposterior diameter; **L**, length; **s**, sin; **W**, width.

	pm	p	m	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
AK2-323d	70.5	29.2	41.3	7.0	3.8	10.5	4.8	11.9	5.6	10.3	7.0	13.1	8.2	17.5	8.2
AK2-318s	70.2	28.5	41.0	6.4	3.6	10.5	5.1	11.5	5.6	10.1	7.1	13.1	8.2	17.3	8.2
AK2-459s	74.0	29.4	44.0	7.2	3.7	9.3	5.6	11.9	6.6	11.8	7.7	13.8	8.7	18.2	8.5
AK3-76s			42.8			10.2	5.8	11.8	6.2	10.9	7.3	12.7	8.0	18.3	8.5
AK4-200d			42.8					10.5	5.6	11.2	7.5	13.5	8.5	18.0	8.1
AK5-617s			43.2					10.7	6.3			13.7	8.2	18.0	8.6
AK5-639s			43.5			9.3		11.4		12.0	7.7	14.1	8.1	17.7	8.5
AK5-618s	68.8	26.8	40.5	7.0	3.7	9.4	4.7	10.5	6.0	9.0	7.8	12.5	9.0	18.8	9.1
AK6-191s			42.9					10.6	5.9			12.7	8.8	18.7	9.2
AK7-102s	75.1	28.1	45.0	7.3	3.4	10.0	5.4	11.0	6.0	10.6	7.5	13.6	8.9	19.3	8.6

TABLE 10. — Skull measurements (in mm) of *Miotragocerus valenciennesi* (Gaudry, 1861), *Pachytragus crassicornis* Schlosser, 1904 and *Palaeoryx majori* Schlosser, 1904 from Akkaşdağı. Abbreviations: **DAP**, anteroposterior diameter; **DT**, transverse diameter.

	Miotragocerus valenciennesi	*Pachytragus crassicornis*	*Palaeoryx majori*
	AK5-597	**GOK-181+182**	**AK3-130**
Height foramen magnum	23.8	22.2	
DT Foramen Magnum	20.3	25.3	
Width bi-condylar	60.7	57.5	
Height occiput	54.0	43.3	
Width bi-mastoid	92.5	91.7	
Width at ant. tub. of basioccipital	21.7	19.3	31.0
Width at post. tub. of basioccipital	38.5	31.0	
Length auditory bulla	29.4		
Width bi-zygomatic	119.0		
Length basion-median indent of palate	95.0		
DT horn-core base	42.4	37.5	45.8
DAP horn-core base	89.6		54.5
Width at supraorbital pits	(46.0)		
Width braincase	74.6	79.0	91.7
Chord Nasion-Bregma	117.5		
Chord Bregma-nuchal crest		67.3	≈ 58.0
Chord Nasion-Lambda	155.3		
Chord nuchal crest-anterior level of horn-cores	160.0		
Skull width at the orbits	133.7		(155.0)
Height orbit	48.1		
DT orbit	46.0		
P2-M3	92.0		
Width at facial crest	(105.0)		
Width palate at M3	51.3		

TABLE 11. — Skull and horn-core measurements (in mm) of *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı. Abbreviations: **10**, at 10 cm from the base; **b**, base; **d**, dex; **DAP**, anteroposterior diameter; **DEHc**, external horn-core distance (basal); **DIHc**, internal horn-core distance (basal); **DT**, transverse diameter; **L**, length; **s**, sin; **WOR**, width of the skull behind the horn-cores.

	WOR	DEHc	DIHc	DTb	DAPb	DT10	DAP10	L
AK2-503d	≈ 84.0	113.5	17.0	45.2	66.0	28.8	42.7	280
AK2-503s				44.2	65.0	28.9	43.2	270
AK3-200d		106.0	20.0	39.4		26.0	40.9	
AK3-200s				40.6	58.8	28.6	41.1	270
AK4-80				41.7	60.0			
AK4-190				40.0	58.0			
AK6-316				41.5	61.6			
AK7-126				38.5	58.0	24.9	41.0	
AK7-161				35.8	54.7			
AK12-70s		112.0	21.0	39.7	57.0	28.5	41.0	250
AK12-70d				37.6	55.7	28.0	40.0	

TABLE 12. — Upper toothrow measurements (in mm) of *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı. Abbreviations: **d**, dex; **L**, length; **s**, sin; **W**, width.

	PM	P	M	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1	LM2	WM2	LM3	WM3
AK2-312s	87.8	33.0	54.5	10.0	8.6	13.0	9.8	11.9	12.8	17.0	17.0	20.4	18.0	19.3	16.5
AK2-312d		36.7		11.5	8.1	12.5	10.1	12.0	12.6	16.9	16.8	20.5	18.4		
AK2-157d			63.6			13.2	11.2	12.0	14.5	20.1	17.7	22.2	17.9	21.9	15.0+
AK2-156s			57.0					12.1	13.5	16.7	15.8	20.3	18.3	20.5	17.2
AK5-204d						13.6		12.5		19.3	16.5	22.5	(15.0)		
AK5-253s										20.3	16.8	21.6	17.9		
AK5-455d		37.8		11.0	9.1	12.5	11.0	11.6	13.7	15.0+	16.0				
AKB-95d	99.7	39.5	63.5												
GOK-210s	90.0	37.0	54.3												

TABLE 13. — Lower toothrow measurements (in mm) of *Pachytragus crassicornis* Schlosser, 1904 from Akkaşdağı. Abbreviations: **d**, dex; **L**, length; **s**, sin; **W**, width.

	pm	p	m	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
AK2-63d	95.3	35.0	60.3	9.9	5.6	11.5	7.3	13.8	8.0	15.8	10.5	18.3	12.7	26.0	11.9
AK2-63s	94.5	(34.0)	59.5												
AK2-64d			61.1			11.0	7.2	13.5	7.6	16.0	11.4	19.3	11.8	26.7	11.5
AK2-155d		35.5		9.6	5.6	11.9	7.4	13.5	8.0	15.7	9.9	20.3	12.5		
AK4-123s	99.0	35.5	63.2	10.5	6.1	12.0	7.3		7.9	16.5	11.7	19.5	12.4	27.4	11.8
AK5-616d		36.2		10.2	5.5	12.1	7.0	13.3	8.0	15.2	11.6	18.9	12.8		
AK7-66s		37.5		10.0	6.0	11.8	7.2	14.5	8.2	17.5	9.9		11.8		
AK11-59s			61.6							16.8	11.0	19.5	11.4	25.5	10.1
AK12-79s		35.0		9.6	5.7	12.2	7.6	13.3	8.2	15.5	11.5				

TABLE 14. — Differentiate skull characters between *Palaeoryx pallasi* (Wagner, 1857) and *Palaeoryx majori* Schlosser, 1904 from Samos.

Skull characters	*Palaeoryx pallasi* MTLA-113	*Palaeoryx majori* MTLB-160
Opisthocranium	short	moderately long
Basioccipital	relatively short, strongly concave in lateral profile	longer, slightly concave in lateral profile
Anterior tuberosities of basoccipital	bulbous, vertical to the sagittal plane	crest-like, vertical to the sagittal plane
Posterior tuberosities of basioccipital	crest like to simply swelling, anteroposteriorly diverged	crest like, thin, vertically to the sagittal plane
Occiput profile	slightly concave more or less vertical to the cranial roof	flat, forming an obtuse angle with the cranial roof
Occipital condyles	not widely expanded, directed downwards	widely expanded, directed posteriorly
Mastoid	restricted posteriorly	expanded laterally
Paroccipital process	strong, slightly oblique to the sagittal plane	thiner, strongly oblique to the sag. plane
Cranial roof-face angle	obtuse (120°)	relatively acute (100°)
Horn-core insertion	on the postero-superior part of the orbits, slightly laterally, moderately diverged and posteriorly directed	above the orbits, strongly laterally and directed upwards in the basal part
Horn-core structure	long, slightly tilted backwardly, slightly re-curved inwards	moderately long, strongly tilted backwards, strongly re-curved inwards
Orbit	elliptical, in front of the horn-cores	rounded, beneath the horn-cores