Disponible en ligne sur www.sciencedirect.com
ScienceDirect
Annales de Paléontologie 95 (2009) 181–195
ANNALES DE PALÉONTOLOGIE
www.em-consulte.com

Original article

Prostrepsiceros and *Protragelaphus* (Artiodactyla, Mammalia) from the Late Miocene locality of Chomateri (Attica, Greece)

Prostrepsiceros et Protragelaphus (Artiodactyla, Mammalia) du Miocène supérieur de Chomateri (Attique, Grèce)

Socrates J. Roussiakis

National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Historical Geology and Palaeontology, Panepistimiopolis, 15784 Athens, Greece

Available online 22 October 2009

Abstract

The Late Miocene fossiliferous locality of Chomateri is located close to the classic locality of Pikermi, but unfortunately its faunal context is not sufficiently known. Some fossil remains of spiral-horned antelopes from Chomateri are assigned to *Prostrepsiceros rotundicornis* and *Protragelaphus skouzesi*. The co-existence of *P. rotundicornis* and *P. skouzesi* is relatively rare in the Late Miocene, but well-documented in Pikermi. Comparisons of the Chomateri material support a middle Turolian age for the Chomateri locality and suggest a close chronological relation to the Pikermi fauna.

Keywords: Late Miocene; Turolian; Bovidae; Chomateri; Pikermi; Greece

Résumé

Située près de la localité classique de Pikermi, la localité fossilifère du Miocène supérieur de Chomateri est malheureusement pauvrement connue. Quelques restes fossiles d'antilopes à chevilles spiralées découverts à Chomateri sont rapportés à *Prostrepsiceros rotundicornis* et *Protragelaphus skouzesi*. L'association de ces deux espèces est relativement rare au Miocène supérieur, mais bien connue à Pikermi. La comparaison du matériel de Chomateri permet de montrer que cette localité doit être rapportée au Turolien moyen et suggère une étroite relation chronologique avec la faune de Pikermi.

Mots clés : Miocène supérieur ; Turolien ; Bovidae ; Chomateri ; Pikermi ; Grèce

E-mail address: srousiak@geol.uoa.gr.

0753-3969/$ – see front matter © 2009 Published by Elsevier Masson SAS.
doi:10.1016/j.annpal.2009.09.002

1. Abbreviations

AMPG: Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens.
IPUW: Institut für Paläontologie der Universität Wien.
LGPUT: Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki.
MNHNP: Muséum national d'histoire naturelle, Paris.
NHML: Natural History Museum, London.
NHMW: Naturhistorisches Museum, Wien.
SMNS: Staatliches Museum für Naturkunde, Stuttgart.

2. Introduction

The site of Chomateri is located 2.6 km east of the classic Pikermi locality in a clay pit close to the Kisdari summit (Fig. 1; Marinos and Symeonidis, 1975). Discovered in 1971, this fossiliferous site became known from successive excavations that took place mainly in the 1970s and early 1980s. These excavations revealed a continuous fossiliferous plane, approximately 15.6 m in total length, where the bone deposits were artificially exposed to demonstrate the fossil bone accumulations as an *in situ* natural history monument. Consequently, only few specimens have been unearthed and described. The Chomateri fauna has been the subject matter of various publications (Marinos and Symeonidis, 1975; Symeonidis, 1973a, 1973b, 1978; Symeonidis et al., 1973; Bachmayer et al., 1982; Zapfe, 1991; De Bruijn et al., 1999; Koufos, 2006). Nevertheless, the faunal composition of this important site is still insufficiently known and some of the published data relevant to this fauna might need reconsideration. The fossil remains of *Prostrepsiceros* and *Protragelaphus* described in the present paper come from ossiferous blocks that were extracted during the field campaigns in 1970s and were stored in the Museum of Palaeontology and Geology in Athens.

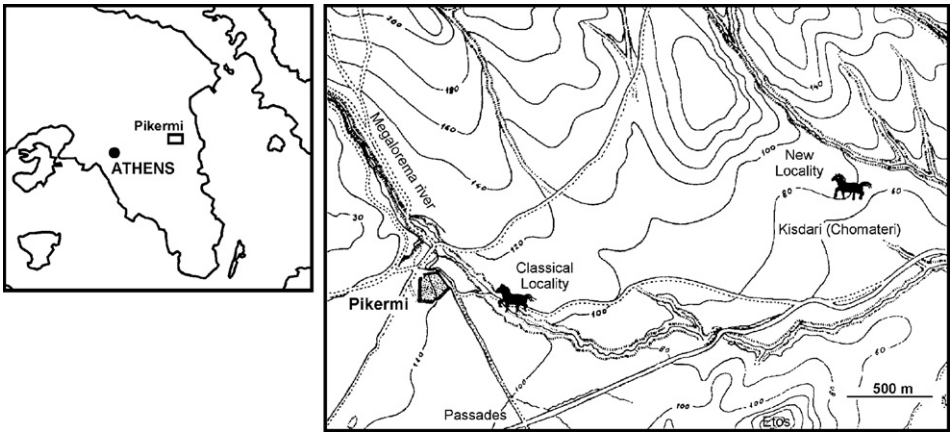

Fig. 1. Map indicating the fossiliferous localities of Chomateri and Pikermi.
Localisation géographique du gisement fossilifère de Chomateri et du gisement fossilifère classique de Pikermi.
Based on Symeonidis et al., 1973; Marinos and Symeonidis, 1975.

3. Systematic descriptions

Order: ARTIODACTYLA Owen, 1848
Family: BOVIDAE Gray, 1821

3.1. Genus Prostrepsiceros Major, 1891

Prostrepsiceros rotundicornis (Weithofer, 1888)

3.1.1. Material

Chomateri: AMPG NP25/91: frontlet with the left and the right horn-cores. The right horn-core is slightly damaged at its middle-length, but almost completely preserved.

Examined material from Pikermi: AMPG PA2910/91, PA3507/91, PG95/1513, PG88/1557, PG88/1559, PG88/1562 (young individual?); IPUW unnumbered frontlet figured by Weithofer (1888: Pl. 18, Figs. 3, 4); MNHNP PIK2160 (Gaudry, 1862–1867: Pl. 52, Fig. 5); NHML M10844, M11436, M11437 (Pilgrim and Hopwood, 1928: Pl. 1, Figs. 2 and 2a), M11438, M12999.

3.1.2. Description

The horn-cores are set moderately apart on the frontals and over the orbits (Table 1 and Fig. 2). They appear lyriform in anterior view and follow a moderately open spiral in clockwise sense (as defined by Pilgrim and Hopwood, 1928). In anterior view, their proximal parts form an angle of about 35° with the sagittal plane. Then they curve laterally and backwards, and at their distal part they turn upwards. Their basal transverse diameter is larger than the anteroposterior one (DT > DAP, Table 1) and their basal section is sub-elliptical with convex anterolateral surface but almost flat posteromedial. The pedicles are short, both laterally and medially. There are two faint keels. The "anterior" keel descends posteromedially, forms one complete revolution

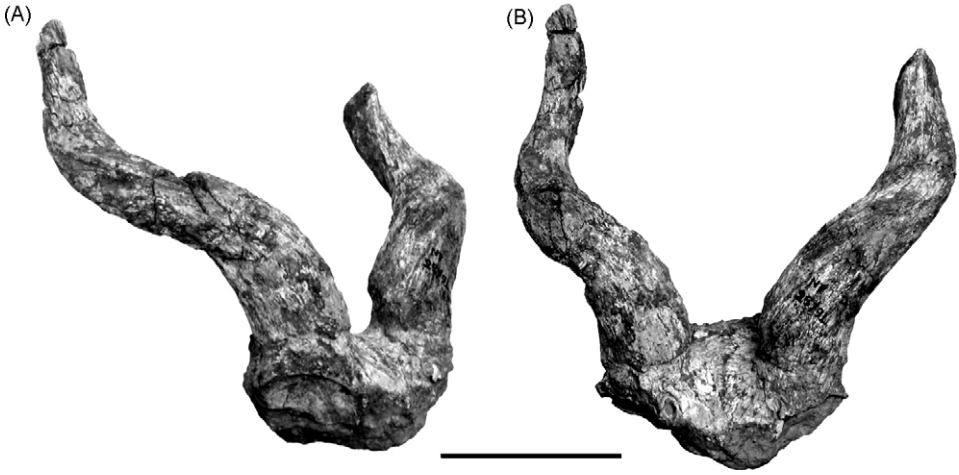

Fig. 2. *Prostrepsiceros rotundicornis* from Chomateri, Greece. Frontlet AMPG NP25/91. **A**. Anterolateral view. **B**. Anterior view. Scale bar 6 cm.
Prostrepsiceros rotundicornis de Chomateri, Grèce. Massacre AMPG NP25/91. **A**. *Vue antérolatérale.* **B**. *Vue antérieure. Échelle graphique 6 cm.*

Table 1
Skull and horn-core measurements (in millimetre) of *P. rotundicornis* from Chomateri, Pikermi and Akkaşdağı. DAP: anteroposterior diameter; DT: transverse diameter.
Mensurations (en millimètre) des crânes et des chevilles de P. rotundicornis de Chomateri, Pikermi et Akkaşdağı. DAP : diamètre antéropostérieur ; DT : diamètre transversale.

	Chomateri			Pikermi			Akkaşdağı		
	NP25/91			Mean	Range	*n*	Mean	Range	*n*
DAP (horn-core base)	28.1 (sin.)		28.6 (dext.)	28.9	23.8–36.8	16	30.5	25.5–34.0	11
DT (horn-core base)	32.9 (sin.)		31.7 (dext.)	33.8	28.6–40.5	16	35.0	27.0–39.7	12
DT × 100/DAP	117.1 (sin.)		110.8 (dext.)	117.0	103.0–129.8	16	113.5	105.9–120.0	11
Distance between the horn-cores' bases		22.9		25.5	21.3–(28.5)	4	22.2	20.7–23.7	2
Width laterally of the horn-cores' bases		81.2		85.6	81.7–90.9	5	91.5	88.1–94.8	2
Skull width behind the horn-cores		68.5		65.8	65.5–66.0	2	(66.3)	(65)–(67.5)	2
Width, medial edges of the supraorbital foramens		30.5		32.4	32.0–32.8	2	–	–	–
Width, lateral edges of the supraorbital foramens		37.0		37.5	–	1	–	–	–
Skull width at the supraorbital margins		$\geq$ 83.6		–	–	–	–	–	–

Data for Akkaşdağı according to Kostopoulos (2005); other data according to the author (the Pikermi sample is based on the AMPG, IPUW, MNHNP and NHML collections).

and is accompanied on the left horn-core by a shallow furrow. The "posterior" keel descends above the anterior margin of the postcornual fossa, it is very weak along most of its length, but becomes slightly more evident toward the distal part of the horn-core. The right horn-core is almost completely preserved and measures 150 mm in length (in straight line), with its total length estimated at about 160 mm. The parietofrontal suture is open, as is the interfrontal one which is slightly swollen. The interfrontal region between the horn-cores is only slightly higher than the supraorbital margins. The latter are not completely preserved, but judging from the better-preserved right supraorbital margin, they would have projected steeply. The postcornual fossa is rather shallow. The supraorbital foramens are relative small and open about 14 mm below the bases of the horn-cores and directly into the orbits, which indicates the absence of sinuses at this part of the frontals. The preorbital region and the region behind the parietofrontal suture are missing. Nevertheless, the sagittal profile at the interfrontal region is gently convex, suggesting that the face is slightly bent relative to the braincase. The frontal bones at the interfrontal-parietal junction measure about 6 mm in thickness.

3.1.3. Comparisons

The characters of the Chomateri frontlet indicate that it must be referred to the genus *Prostrepsiceros* Major, 1891. Various species are included in this genus, but *Prostrepsiceros rotundicornis* (Weithofer, 1888), *Prostrepsiceros zitteli* (Schlosser, 1904), *Prostrepsiceros fraasi* (Andree, 1926) and *Prostrepsiceros axiosi* (Kostopoulos, 2004) share with the Chomateri specimen the antero-posteriorly compressed horn-cores (DAP < DT).

The Chomateri frontlet agrees very well with *Prostrepsiceros rotundicornis* from Pikermi. Its horn-cores follow an equally open spiral, they are equally bent posteriorly in lateral view, and their basal dimensions and their compression indices fall inside the range of the Pikermi sample studied (Table 1). The Pikermi horn-cores exhibit important range on their basal dimensions. The specimen described and figured by Weithofer (1888: Pl. 18, Figs. 3, 4), stored in the IPUW collections, is larger in basal dimensions than other specimens examined and probably also in length (its preserved straight length measures about 170 mm). A specimen in Athens (AMPG PG88/1562), plotted on the left-most part of the Pikermi sample (Fig. 3), has a faster tapering horn-core with more porous surface and smaller basal dimensions, and could belong to a younger individual.

Apart from Pikermi, *P. rotundicornis* has also been referred from Halmyropotamos in Euboea (Greece), Ravin des Zouaves-5 (RZO) in Macedonia (Greece), and various Turkish localities. The occurrence of *P. rotundicornis* in Halmyropotamos is based on a left half frontlet described by Melentis (1970: Pl. 7, Fig. 5) as "*Helicotragus*" *rotundicornis*. Although only the proximal-most part of the left horn-core is preserved, all present characters indicate that this specimen is correctly attributed to *P. rotundicornis*. The locality of Ravin des Zouaves-5 (RZO) has yielded two frontlets of *P. rotundicornis* (LGPUT RZO-120, RZO-223). The RZO *Prostrepsiceros* is very similar to the Pikermi and Chomateri form, but it has larger supraorbital foramens.

Prostrepsiceros rotundicornis has been reported from various localities of Turkey. Senyürek (1952: Figs. 45–47) assigned to "*Helicotragus*" *rotundicornis* two horn-cores from Gökdere, comparable in dimensions to the Pikermi specimens (Fig. 3). Tekkaya (1969) referred to the same species a poorly informative horn-core fragment from Kayadibi, while Nicolas (1978) noted its presence in Küçûkçekmece, but no description, measurements and figures are provided. Gentry (2003) referred to *P. rotundicornis* a frontlet from the late Vallesian of Middle Sinap (Loc. 63) preserving the right horn-core. This specimen, however, could represent a different species. Its horn-core is mediolaterally compressed, contrary to the anteroposteriorly compressed horn-cores

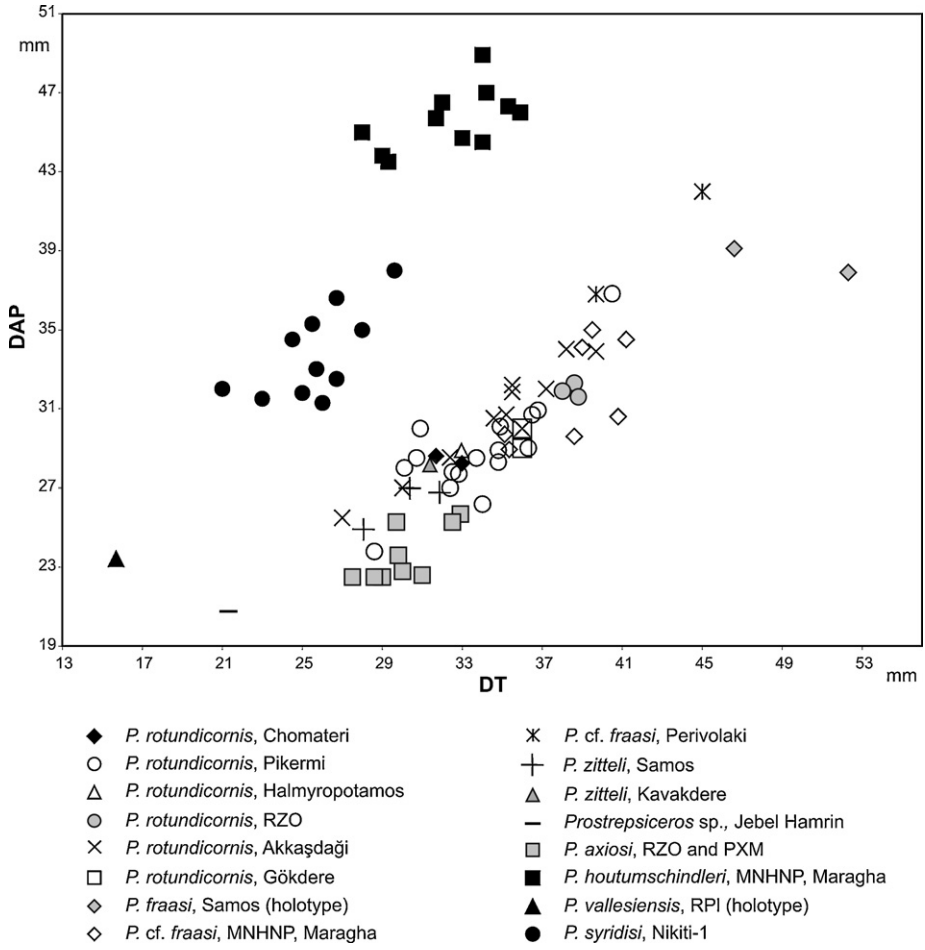

Fig. 3. Scatter diagram comparing the basal horn-core dimensions (DT vs DAP) in several species of *Prostrepsiceros*. *Prostrepsiceros rotundicornis* from Gökdere according to Senyürek (1952); *P. rotundicornis* from Akkaşdaği and *P. fraasi* from Perivolaki according to Kostopoulos (2005, 2006); *P. zitteli* from Samos according to Schlosser (1904) and personal data; *P. zitteli* from Kavakdere according to Geraads and Güleç (1999); *P. axiosi* and *P. syridisi* according to Kostopoulos (personal communication 2006). *Prostrepsiceros* sp. from Jebel Hamrin according to Bouvrain and Thomas (1992). Other data according to the author. PXM: Prochoma; RPl: Ravin de la Pluie; RZO: Ravin des Zouaves-5.
Diagramme de dispersion entre les dimensions de la base des chevilles (DT vs DAP) des diverses espèces de Prostrepsiceros.

of *P. rotundicornis* from Pikermi, and the interfrontal region seems to be raised (Gentry, 2003: Fig. 15.12A). The best available *P. rotundicornis* sample from Turkey comes from the middle Turolian locality of Akkaşdaği (Kostopoulos, 2005). Compared to *P. rotundicornis* from Chomateri and Pikermi, the Akkaşdaği *Prostrepsiceros* has larger supraorbital foramens, approaching on this character the RZO form, and probably wider separated also. Finally, Kostopoulos (2005) reported the presence of *P. rotundicornis* in the middle Turolian of Kemiklitepe (upper fossiliferous level).

Prostrepsiceros zitteli is based on a frontlet from Samos (Schlosser, 1904: Pl. 6, Fig. 5), and it was considered as a junior synonym of *Prostrepsiceros houtumschindleri* (Rodler and Weithofer, 1890) by Gentry (1971) and Solounias (1981), followed lately by Bibi and Güleç (2008). However,

contrary to *P. houtumschindleri*, that bears a strong posterior keel and mediolaterally compressed horn-cores (DAP > DT), *P. zitteli* has no posterior keel and its horn-cores are anteroposteriorly compressed (DAP < DT). Consequently, and following Bouvrain (1982), Gentry and Heizmann (1996), Gentry et al. (1999), Gentry (2003) and Kostopoulos (2004), *P. zitteli* is herein considered as a valid species. On the same species can also be referred another Samos specimen in Vienna (NHMW A4785, 1911 Samos, V130; Andree, 1926: p. 166; Gentry, 2003: p. 349). The horn-cores of *P. zitteli* are comparable in basal dimensions with the smaller *P. rotundicornis* specimens (Fig. 3), but more tightly spiralled and with a stronger anterior keel. Moreover, the supraorbital foramens are larger and there is no postcornual fossa. *Prostrepsiceros zitteli* is also referred to from Jebel Hamrin (Iraq) by Bouvrain and Thomas (1992), on the basis of a skull and various isolated horn-cores. However, the horn-cores of the Jebel Hamrin form (Bouvrain and Thomas, 1992: Table 2, Figs. 2 and 3) are smaller in dimensions and follow a more open spiral than those of *P. zitteli* from Samos. On the contrary, a frontlet of *P. zitteli* from Kavakdere in Turkey (Geraads and Güleç, 1999: Table 2, Fig. 2A, B) is almost identical to the type specimen of *P. zitteli* from Samos.

Prostrepsiceros fraasi was originally described from Samos (Andree, 1926: Pl. 11, Fig. 4, Pl. 15, Fig. 1), and unfortunately it is known from its type locality from a single skull specimen (SMNS 13278) preserving the horn-cores and the braincase. *Prostrepsiceros fraasi* was included in *P. rotundicornis* by Gentry (1971) and Solounias (1981), but Bouvrain (1982) considered it as a valid species, opinion followed subsequently by Gentry and Heizmann (1996) and Gentry et al. (1999). The type specimen of *P. fraasi* has much larger horn-cores than the Chomateri and Pikermi form (Fig. 3), more uprightly inserted above the orbits in lateral view, with stronger distal curvature and outward swing, whereas the frontals in front of the horn-cores are stronger angled on the braincase. Compared to the horn-cores, the braincase is relatively small, comparable in width (about 69 mm) to *P. rotundicornis* from Pikermi and Chomateri. The supraorbital margins, as far as they are preserved, do not project abruptly and there is no postcornual fossa. A form close in morphology to *P. fraasi*, but with more slender horn-cores, is also known from Maragha. This form is best represented by the frontlet MNHNP MAR1306 (described as *Helicophora rotundicornis* by Mecquenem, 1925: Pl. 7, Fig. 1) and the skull MNHNP MAR1310 (referred to *P. rotundicornis* by Gentry, 1971: Pl. 5, Fig. 2), but there are also many other frontlets and isolated horn-cores in the MNHNP collections, as well as some specimens (from Site III of Maragha) described by Watabe (1990: Pl. 3, Figs. 1, 2). Bouvrain (1982) included this form to *P. fraasi*, but correctly referred to that it has smaller horn-cores from the type skull from Samos (Fig. 3). In addition, at least the skull MAR1310 has postcornual fossae and less inclined face.

Prostrepsiceros axiosi is known from the early Turolian locality of Ravin des Zouaves-5 (RZO) and the earliest middle Turolian locality of Prochoma in Greece, as well as from Grebeniki and Titov Veles (Kostopoulos, 2004). It approaches the Chomateri form in the relatively open spiralling of the horn-cores, but the horn-cores possess a stronger anterior keel, the postcornual fossae are almost absent, and the supraorbital foramens are larger.

Prostrepsiceros includes many other species, which, contrary to the Chomateri form, are all characterised by mediolaterally compressed horn-cores (DAP > DT). *Prostrepsiceros houtumschindleri* (Rodler and Weithofer, 1890) is common in Maragha. It has larger (Fig. 3), more tightly twisted and closely spiralled horn-cores with a strong posterior keel, and larger supraorbital foramens. *Prostrepsiceros syridisi* (Kostopoulos and Koufos, 1996) from the late Vallesian locality of Nikiti-1 was originally described as a subspecies of *P. houtumschindleri* but has slenderer and more loosely torsioned horn-cores. *Prostrepsiceros vallesiensis* (Bouvrain, 1982) is another species, known from the late Vallesian locality of Ravin de la Pluie (Greece) and Turkey

(Gentry, 2003). It differs from the Chomateri *Prostrepsiceros* on its significantly smaller size (Fig. 3), more tightly spiralled horn-cores, and the presence of acute keels.

3.2. Genus ***Protragelaphus*** *Dames, 1883*

Protragelaphus skouzesi Dames, 1883

3.2.1. Material

Chomateri: frontlets with the left and right horn-cores partly or completely preserved (AMPG NP1/01, NP3/01, NP6/01, NP7/01, NP10/01, NP11/01), frontlet with the left horn-core (AMPG NP8/01), frontlet with the right horn-core (AMPG NP2/01). The supraorbital margins of NP11/01 are partly restored by plaster. NP3/01 is laterally compressed and deformed, and its horn-cores are not symmetrical to the sagittal level. Its horn-cores also bear tooth-marks at their distal parts, as well as at their bases.

Examined material from Pikermi: IPUW unnumbered frontlet preserving parts of both horn-cores; NHML M10840 (Pilgrim and Hopwood, 1928: p. 89), NHML M4068 (cast of the skull figured by Wagner, 1857: Pl. 7, Fig. 18).

3.2.2. Description

The horn-cores are moderately separated on the frontals and diverge from the sagittal plane by an angle that ranges from about 20 to 30° ($n = 6$). They are slightly compressed mediolaterally at their bases (Tables 2 and 3), mainly because of a posterior keel that adds to the anteroposterior diameter of the horn-core. There is no anterior keel. The torsion is clockwise (as defined by Pilgrim and Hopwood, 1928) and follows a relatively close spiralling, while the horn-core axis is almost straight. The right horn-core of NP11/01 is almost completely preserved, measures about 215 mm in length (in straight line) and its posterior keel traces two revolutions. There are sinuses at the bases of the horn-cores (NP7/01). The postcornual fossa is moderate in size and clearly defined. The frontals are bent between the horn-cores and higher than the supraorbital margins. Their thickness, at or close to the interfrontal-parietal junction, ranges from 12–16 mm ($n = 5$). The interfrontal and parietofrontal sutures are open and complicated, while the former is raised. The supraorbital margins do not project strongly laterally, but slope downwards gently. The supraorbital foramens are small, smaller than in *Prostrepsiceros*, not sunken in depressions and open about 31–37 mm ($n = 10$) below the horn-cores' bases.

3.2.3. Comparisons

The presence of a strong posterior keel, the absence of an anterior one, the almost straight axis of the horn-cores, the raised interfrontal region and the small supraorbital foramens are characters of *Protragelaphus* (Dames, 1883), a genus that includes two species: *Protragelaphus skouzesi* (Dames, 1883) and *Protragelaphus theodori* (Bouvrain, 1978). The Chomateri specimens are very similar in morphology and dimensions to *P. skouzesi* (Figs. 4 and 5), a relatively rare species originally described from Pikermi. The horn-cores' divergence varies. The specimen NP1/01 approaches more on the horn-core divergence the Pikermi specimen figured by Weithofer (1888: Pl. 17, Figs. 4–6) while NP11/01 has smaller divergence and agrees well with the specimen described by Wagner (1857: Fig. 18), a cast of which is stored in NHML.

Protragelaphus skouzesi has also been reported from Halmyropotamos by Melentis (1970: Pl. 20, Figs. 2–4), who assigned to this species an isolated right horn-core (AMPG HAL1967/85) and a frontlet preserving the bases of the horn-cores (AMPG HAL1967/89). Both specimens

Table 2
Skull and horn-core measurements (in millimetre) of *P. skouzesi* from Chomateri. DAP: anteroposterior diameter; DT: transverse diameter.
Mensurations (en millimètre) des crânes et des chevilles de P. skouzesi de Chomateri. DAP : diamètre antéropostérieur ; DT : diamètre transversale.

	Protragelaphus skouzesi, Chomateri											
	NP1/01		NP3/01		NP6/01		NP11/01		NP2/01	NP7/01	NP8/01	NP10/01
	Sin.	Dext.	Sin.	Dext.	Sin.	Dext.	Sin.	Dext.				
Horn-core length (straight line)	–	–	–	–	–	–	–	(215)	–	–	–	–
DAP (horn-core base)	46.4	46.8	49.1	45.9	44.7	–	47.2	47.8	49.6	47.8	46.2	40.3
DT (horn-core base)	39.1	37.2	38.4	36.3	36.5	35.0	38.7	38.8	44.1	40.6	40.7	34.9
DT×100/DAP	84.3	79.5	78.2	79.1	81.7	–	82.0	81.2	88.9	84.9	88.1	86.6
Distance between the horn-cores' bases	36.4		(21.0)		27.7		(25.1)		–	29.3	–	38.2
Width laterally of the horn-cores' bases	104.2		(92.8)		95.2		98.5		(99.7)	102.9	–	96.4
Skull width behind the horn-cores	77.4		70.4		66.6		72.9		(73.9)	–	–	66.6
Width, medial edges of the supraorbital foramens	37.0		–		29.8		36.8		–	34.3	–	33.6
Width, lateral edges of the supraorbital foramens	42.1		–		34.5		41.9		–	38.8	–	38.4
Skull width at the supraorbital margins	≥ 114.4		–		≥ 108.0		–		–	–	–	≥112.2

Table 3
Skull and horn-core measurements (in millimetre) of *Protragelaphus* from Chomateri and Pikermi. DAP: anteroposterior diameter; DT: transverse diameter.
Comparaison des mensurations (en millimètre) des crânes et des chevilles de Protragelaphus de Chomateri et Pikermi. DAP : diamètre antéropostérieur ; DT : diamètre transversale.

	Protragelaphus skouzesi					
	Chomateri			Pikermi		
	mean	range	*n*	mean	range	*n*
Horn-core length (straight line)	(214.6)	–	1	237.5	(225.0)–250.0	2
DAP (horn-core base)	46.5	40.3–49.6	11	47.4	41.3–51.3	7
DT (horn-core base)	38.4	34.9–44.1	12	41.9	38.1–45.9	7
DT×100/DAP	83.1	78.2–88.9	11	88.6	82.4–94.4	7
Distance between the horn-cores' bases	29.6	21.0–38.2	6	30.2	23.0–34.6	3
Width laterally of the horn-cores' bases	98.5	92.8–104.2	7	105.1	102.9–107.6	3
Skull width behind the horn-cores	71.3	66.6–77.4	6	80.0	73.0–80.0	3
Width, medial edges of the supraorbital foramens	34.3	29.8-37.0	5	34.3	31.6–36.9	2
Width, lateral edges of the supraorbital foramens	39.1	34.5–42.1	5	37.2	–	1

Data according to the author (the Pikermi sample is based on the IPUW and NHML collections) and Weithofer (1888).

are eroded and their morphological characters are not clearly visible. Even though the specimen HAL1967/85 shows traces of an anterior keel we refer this to *P. skouzesi* since vestiges of an anterior keel are occasionally present in this species, as for example on the specimen from Maragha figured by Mecquenem (1925: Pl. 6, Fig. 6; Gentry and Heizmann, 1996: p. 382). On the contrary, the assignment of HAL1967/89 in *P. skouzesi* is debatable because its parietofrontal and interfrontal sutures appear closed (preservation status?). In *P. skouzesi*, however, it could be attributed another skull portion from Halmyropotamos (AMPG HAL1967/84; not referred to by Melentis, 1970) preserving the horn-cores' bases and the braincase. The absence of an anterior keel and the presence of a posterior one, the horn-core and braincase dimensions, the raised interfrontal region, the open interfrontal and parietofrontal sutures, the small and not sunken in depressions supraorbital foramens, the presence of postcornual fossae, and the gently sloping supraorbital margins indicate that this specimen can be assigned to *P. skouzesi*.

The only indication for the presence of *P. skouzesi* in Samos is a frontlet referred to this species by Andree (1926: Pl. 15, Figs. 4, 5). This specimen (SMNS 13279) is comparable metrically to the Pikermi and Chomateri *Protragelaphus* (Fig. 5), but there is a very strong ridge that connects the posterior keel of the horn-core to the orbital margin (Gentry, 1971). Of greater importance probably is the fact that, whereas the supraorbital foramens are equally separated from each other as in Pikermi and Chomateri *Protragelaphus*, they open much lower, about 55 below the horn-cores' bases. Likewise, the horn-cores' bases are far higher the supraorbital margins.

Protragelaphus skouzesi is also known from Maragha. In the NHMW collections, I have seen two specimens of *P. skouzesi* from Maragha, a skull fragment preserving the left horn-core (NHMW A4898, labelled as "*Palaeoreas lindermayeri*, Maragha, Kopran") and an unnumbered frontlet (labelled as "*Protragelaphus skouzesi* Maragha, Kopran II, coll. Polak"), both very similar to the Pikermi and Chomateri form. Unfortunately, I have not seen the Maragha specimens referred by Mecquenem (1925) to *P. skouzesi*, stored in the MNHNP collections. However, according to the data provided by Bouvrain (1978), some of these specimens exhibit a tendency toward wider separated supraorbital foramens.

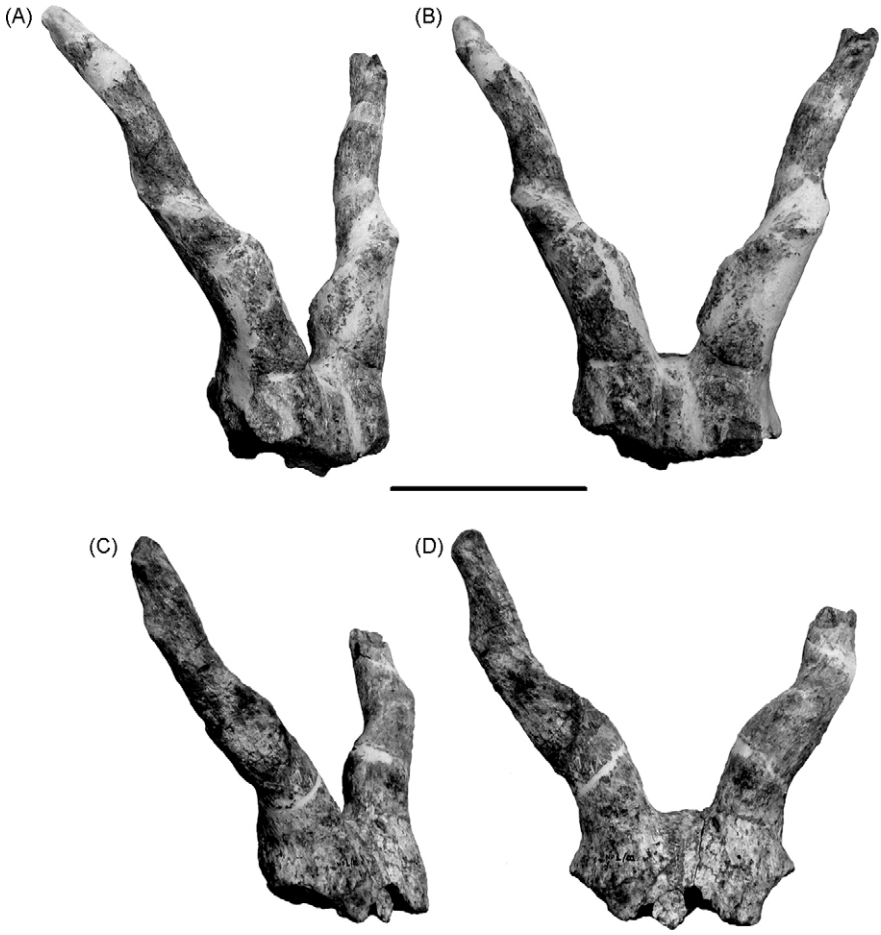

Fig. 4. *Protragelaphus skouzesi* from Chomateri, Greece. **A, B**. Frontlet AMPG NP11/01; anterolateral view (A), anterior view (B). **C, D**. Frontlet AMPG NP1/01; anterolateral view (C), anterior view (D). Scale bar 10 cm.
Protragelaphus skouzesi de Chomateri, Grèce. A, B. Massacre AMPG NP11/01 ; vue antérolatérale (A), vue antérieure (B). C, D. Massacre AMPG NP1/01 ; vue antérolatérale (C), vue antérieure (D). Échelle graphique 10 cm.

The occurrence of *P. skouzesi* in Turkey is not clearly demonstrated. *Prostrepsiceros skouzesi* is mentioned by Thenius (1949) at Ilhan, but no figures or measurements are provided. Geraads and Güleç (1999) referred to *Protragelaphus* some specimens from Bayir, Gülpinar, Serefköy and Manisa. The majority of these specimens could be assigned to *P. skouzesi* since they are almost identical with it in horn-core morphology, although some of these are smaller than *P. skouzesi* from Pikermi, Chomateri and Maragha (Fig. 5) approaching in basal dimensions *Ouzoceros* (Bouvrain and Bonis, 1986). Unfortunately, most of these specimens are isolated horn-cores and their poorly informative state of preservation does not allow a precise determination.

Protragelaphus theodori is known from the late Turolian localities of Dytiko-1 and Dytiko-3 only (Bouvrain, 1978; Koufos, 2006). Similarly to the Chomateri *Protragelaphus*, *P. theodori* has open inter- and parietofrontal sutures, gently sloping supraorbital margins and lacks anterior keels. However, *P. theodori* has larger horn-cores (Fig. 5), the postcornual fossa is

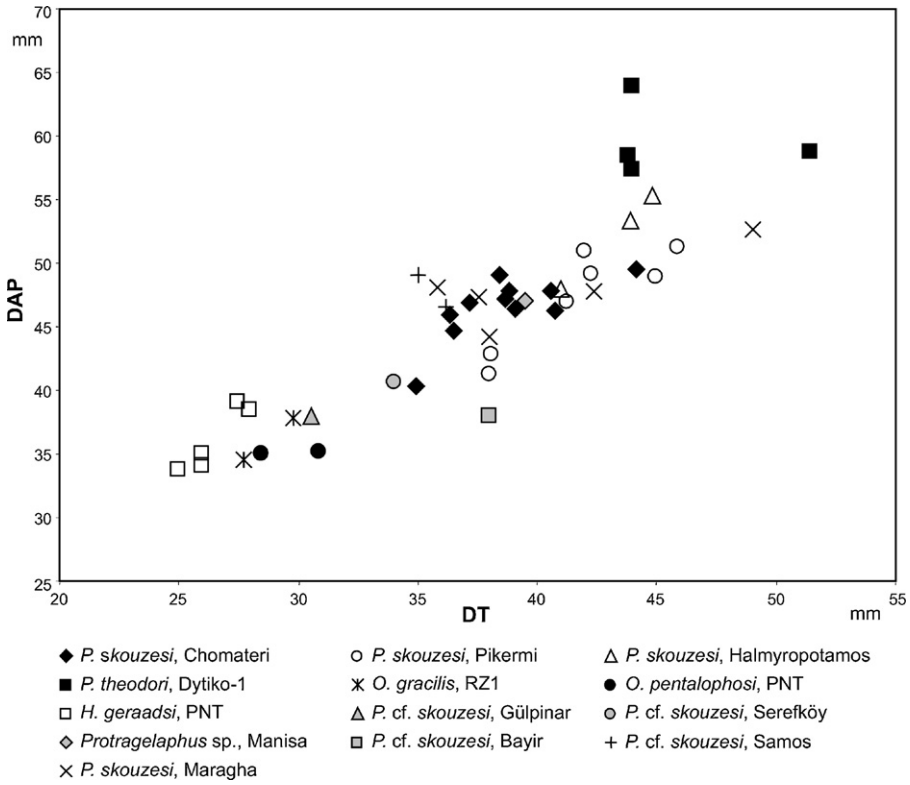

Fig. 5. Scatter diagram comparing the basal horn-core dimensions (DT *vs* DAP) in *Protragelaphus*, *Helladorcas* and *Ouzoceros*. *Protragelaphus skouzesi* from Pikermi according to the author and Weithofer (1888); *P. skouzesi* from Maragha and *H. geraadsi* from Pentalophos according to the author and Bouvrain (1978, 1997). *Protragelaphus* sp. from Manisa and *P.* cf. *skouzesi* from Gülpinar, Serefköy and Bayir according to Geraads and Güleç (1999). Other data according to the author. PNT: Pentalophos-1, RZ1: Ravin des Zouaves-1.

Diagramme de dispersion entre les dimensions de la base des chevilles (DT vs DAP) de Protragelaphus, Helladorcas et Ouzoceros.

faint or absent, the interfrontal suture is more elevated, and the supraorbital foramens are larger.

Helladorcas (Bouvrain, 1997) is a Late Miocene genus known until now exclusively from Greece and is probably related to *Protragelaphus* (Kostopoulos, 2006). It resembles the Chomateri form on the absence of an anterior keel and the presence of a posterior one, the gently projected supraorbital margins and the presence of postcornual fossae. Nevertheless, *Helladorcas* has not raised interfrontal region, its horn-cores are smaller in basal dimensions (Fig. 5) and lack sinuses at their bases, and the supraorbital foramens open in deep pits.

4. Conclusions

Prostrepsiceros is known from a wide geographic area, from the Balkan Peninsula and Ukraine to Pakistan and Afghanistan through Turkey, Iraq, Saudi Arabia and Iran (Bouvrain, 1982, 1992; Bouvrain and Thomas, 1992; Gentry, 1999, 2003; Geraads and Güleç, 1999; Kostopoulos, 2005; Spassov et al., 2006). *Prostrepsiceros* was also referred to from the latest Miocene/earliest Pliocene

of Sahabi in Libya with the species *Prostrepsiceros libycus* (Lehmann and Thomas, 1987). However, Bouvrain and Bonis (2007) transferred this species to *Dytikodorcas*, based mainly on the general morphology of its horn-cores that is very similar to *D. longicornis* from Dytiko. Other referred or probable occurrences of *Prostrepsiceros* in Africa, that remain however uncertain, are in Qued el Atteuch in Algeria (Thomas et al., 1982) and in Djebel Krechem el Artsouma in Tunisia (Geraads, 1989). According to the current knowledge, *Prostrepsiceros* appeared in the early Vallesian of Sinap in Turkey, where it persisted at least until the late Vallesian (Gentry, 2003). At the late Vallesian, *Prostrepsiceros* made its first appearance in the Balkan Peninsula, where it is known from the localities of Ravin de la Pluie and Nikiti-1 in Northern Greece with the species *P. vallesiensis* and *P. syridisi* respectively. During the Turolian, *Prostrepsiceros* became more widespread and it is known from various localities in the Balkan Peninsula, as well as from Ukraine, Turkey, Iran and Iraq. Up to the present, the species *Prostrepsiceros rotundicornis* is known with certainty only from Greece and Turkey. In Greece, it is known from the early Turolian locality of Ravin des Zouaves-5 as well as from the middle Turolian of Pikermi and Halmyropotamos. In Turkey, *P. rotundicornis* is mainly known from the middle Turolian localities of Akkaşdağı, Gökdere and Kemiklitepe-A (Kostopoulos, 2005).

Protragelaphus is less well-known than *Prostrepsiceros*. Remains referred to this genus are known from Greece, FYROM, Iran, Turkey and Ukraine (Bouvrain, 1978, 1992; Gentry et al., 1999; Geraads and Güleç, 1999). *Protragelaphus* includes two species, *P. theodori* and *P. skouzesi*, the former being exclusively known from the late Turolian localities of Dytiko-1 and Dytiko-3 (Axios valley, Greece). *Protragelaphus skouzesi* is an uncommon element of the Late Miocene large mammal faunas, but it has been recorded from localities distributed over a wide geographic area. It is known mainly from the middle Turolian of Pikermi, Halmyropotamos (Greece) and Maragha (Iran), but it is also reported from the early Turolian locality of Novoelisavetovka-2 in Ukraine (Gentry et al., 1999), while closely related or identical forms occurred also in Samos, and the western coast of Turkey (Andree, 1926; Geraads and Güleç, 1999).

Apart the *Prostrepsiceros* and *Protragelaphus* described herein, the bovid collection from Chomateri is up to now poor and, unfortunately, it consists mainly from fragmentary remains while the cranial remains are few. However, some observations concerning other bovid remains from Chomateri can be provided. The mandible referred to as "*Tragocerus amaltheus*" by Marinos and Symeonidis (1975: Pl. 11, Fig. 2) is very similar in morphology, dimensions and dental proportions to *Miotragocerus vallenciennesi* (Gaudry, 1862–1867). Similarly, the mandibular fragment referred by Marinos and Symeonidis (1975: p. 8) to *Gazella deperdita* appears more similar to *Gazella capricornis*. We could also refer to that the available Chomateri material indicates the presence of *Palaeoreas lindermayeri*, and probably of a second Boselaphine species, larger than *M. vallenciennesi*.

The co-existence of the genera *Prostrepsiceros* and *Protragelaphus* in the Late Miocene faunas is not very common, while the co-existence of *P. rotundicornis* and *P. skouzesi* is even rarer and not documented so far but only from Pikermi and Halmyropotamos in Greece. Their co-existence in Chomateri and the fact that the Chomateri *P. rotundicornis* is more similar to the Pikermi population of this species than to the Ravin des Zouaves-5 or Akkaşdağı populations indicate close chronological relation to the middle Turolian (MN12) fauna of Pikermi. *Protragelaphus skouzesi* is rarer. Nevertheless, the Chomateri *P. skouzesi* is very similar to the middle Turolian Pikermi form and different from the late Turolian *P. theodori* from Dytiko. Interesting, in the very rich in number of specimens NHML and MNHNP Pikermi collections, *P. skouzesi* is represented from a relatively small number of specimens. On the contrary, in the comparatively poor in number of specimens Chomateri collection in the Athens Museum this species is represented

from more specimens, indicating that *P. skouzesi* was probably more frequent in Chomateri than in Pikermi. Although it is very early to test and interpret such a hypothesis, this could reflect ecological differences between the Chomateri and Pikermi palaeobiocoenoses, without rejecting the possibility of slight differences in age.

Acknowledgments

The author is grateful to those persons who provided him access to collections in their care: Dr. A. Currant (Natural History Museum, London), Dr. L. Ginsburg† (Muséum national d'histoire naturelle, Paris), Dr. G. Koufos and Dr. D. Kostopoulos (Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki), Dr. E. Heizmann (Staatliches Museum für Naturkunde, Stuttgart), Dr. U. Göhlich (Naturhistorisches Museum, Wien), Dr. D. Nagel and Dr. K. Rauscher (Institüt für Paläontologie der Universität Wien). Part of this work was financially supported by the Naturhistorisches Museum, Wien, through SYNTHESYS project (AT-TAF-32831). The author also wishes to thank the anonymous referees in acknowledgment of their contribution.

References

Andree, J., 1926. Neue Cavicornier aus dem Pliocän von Samos. Palaeontographica 67, 135–175.

Bachmayer, F., Symeonidis, N., Zapfe, H., 1982. Die Ausgrabungen in Pikermi-Chomateri bei Athen. Eine Dokumentation. Annalen des Naturhistorischen Museums in Wien 84/A, 7–12.

Bibi, F., Güleç, E.S., 2008. Bovidae (Mammalia: Artiodactyla) from the Late Miocene of Sivas, Turkey. Journal of Vertebrate Paleontology 28, 501–519.

Bouvrain, G., 1978. *Protragelaphus theodori* n. sp. (Mammalia, Artiodactyla, Bovidae) du Miocène de Macédoine (Grèce). Géologie Méditerranéenne 5, 229–236.

Bouvrain, G., 1982. Révision du genre Prostrepsiceros Major, 1891 (Mammalia, Bovidae). Paläontologische Zeitschrift 56, 113–124.

Bouvrain, G., 1992. Antilopes à chevilles spiralées du Miocène supérieur de la province gréco-iranien : nouvelles diagnoses. Annales de Paléontologie 78, 49–65.

Bouvrain, G., 1997. Les Bovidés du Miocène supérieur de Pentalophos (Macédoine, Grèce). Münchner Geowissenschaftliche Abhandlungen 34, 5–22.

Bouvrain, G., de Bonis, L., 1986. *Ouzocerus gracilis* n. g., n. sp., bovidae (Artiodactyla, Mammalia) du Vallésien (Miocène supérieur) de Macédoine (Grèce). Geobios 19, 661–667.

Bouvrain, G., de Bonis, L., 2007. Ruminants (Mammalia, Artiodactyla : Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). Annales de Paléontologie 93, 121–147.

Bouvrain, G., Thomas, H., 1992. Une antilope à chevilles spiralées : *Prostrepsiceros zitteli* (Bovidae). Miocène supérieur du Jebel Hamrin en Irak. Geobios 25, 525–533.

De Bruijn, H., Saraç, G., van den Hoek Ostende, L., Roussiakis, S., 1999. The status of the genus Parapodemus Schaub, 1938; new data bearing on an old controversy. Deinsea 7, 95–112.

Gaudry, A., 1862–1867. Animaux fossiles et géologie de l'attique. F. Savy, Paris.

Gentry, A., 1971. The earliest goats and other antelopes from the Samos *Hipparion* fauna. Bulletin of the British Museum (Natural History) Geology 20, 231–296.

Gentry, A., 1999. Fossil pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: Whybrow, P., Hill, A. (Eds.), Fossil Vertebrates of Arabia. Yale University Press, New Haven, pp. 290–316.

Gentry, A., 2003. Ruminantia (Artiodactyla). In: Fortelius, M., Kappelman, J., Sen, S. (Eds.), Geology and Paleontology of the Miocene Sinap Formation. Columbia University Press, New York, pp. 332–379.

Gentry, A., Heizmann, E., 1996. Miocene ruminants of the central and eastern Tethys and Paratethys. In: Bernor, R., Fahlbusch, V., Mittmann, H.-W. (Eds.), The evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp. 378–391.

Gentry, A., Rössner, G., Heizmann, E., 1999. Suborder Ruminantia. In: Rössner, G., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Pfeil, München, pp. 225–258.

Geraads, D., 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie Centrale). Comparaisons biostratigraphiques. Geobios 22, 777–801.

Geraads, D., Güleç, E., 1999. On some spiral-horned antelopes (Mammalia: Artiodactyla: Bovidae) from the Late Miocene of Turkey, with remarks on their distribution. Paläontologische Zeitschrift 73, 403–409.

Kostopoulos, D., 2004. Revision of some late Miocene spiral horned antelopes (Bovidae, Mammalia). Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen 231 (2), 167–190.

Kostopoulos, D., 2005. The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdaği, Turkey. Geodiversitas 27, 747–791.

Kostopoulos, D., 2006. The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 9. Cervidae and Bovidae. Palaeontographica. Abhandlungen A 276, 151–183.

Kostopoulos, D., Koufos, G., 1996. Late Miocene Bovids (Mammalia, Artiodactyla) from the locality "Nikiti-1" (NKT), Macedonia, Greece. Annales de Paléontologie 81, 251–300.

Koufos, G., 2006. The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. Hellenic Journal of Geosciences 41, 183–214.

Lehmann, U., Thomas, H., 1987. Fossil Bovidae (Mammalia) from the Mio-Pliocene of Sahabi, Libya. In: Boaz, N., El-Arnauti, A., Gaziry, A., Heinzelin, J., Boaz, D. (Eds.), Neogene Palaeontology and Geology of Sahabi. A. Liss, New York, pp. 323–335.

Marinos, G., Symeonidis, N., 1975. Neue Funde aus Pikermi (Attika, Griechenland) und eine allgemeine geologische übersicht dieses paläontologischen Raumes. Annales Géologiques des Pays Helléniques 26 (1974), 1–27.

Mecquenem, R. de, 1925. Contribution à l'étude des fossiles de Maragha. Annales de Paléontologie 14, 1–34.

Melentis, J., 1970. Studien über fossile Vertebraten Griechenlands, 19. Die Pikermifauna von Halmyropotamos (Euböa - Griechenland). 1. Teil: Odontologie und Kraniologie. Annales Géologiques des Pays Helléniques 19 (1968), 285–411.

Nicolas, J., 1978. Un nouveau gisement de Vertébrés dans le Chersonien : Kutchuk-Tchekmedjè Ouest (Thrace turque). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris 287, 455–458.

Pilgrim, G., Hopwood, A., 1928. Catalogue of the Pontian Bovidae of Europe in the Department of Geology. British Museum (Natural History) Geology, 1–106.

Schlosser, M., 1904. Die fossilen Cavicornia von Samos. Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients 17, 21–118.

Senyürek, M., 1952. A study of the Pontian fauna of Gökdere (Elmadaği), south-east of Ankara. Belleten 16, 449–492.

Solounias, N., 1981. The Turolian fauna from the island of Samos, Greece, with special emphasis on the hyaenids and bovids. Contributions to Vertebrate Evolution 6, 1–232.

Spassov, N., Tzankov, T., Geraads, D., 2006. Late Neogene stratigraphy, biochronology, faunal diversity and environments of South-West Bulgaria (Struma River Valley). Geodiversitas 28, 477–498.

Symeonidis, N., 1973a. *Chalicotherium goldfussi* Kaup (Perissodactyla, Mammalia) aus dem Altpliozän von Pikermi (Griechenland). Annales Géologiques des Pays Helléniques 25, 301–307.

Symeonidis, N., 1973b. Ein bemrkenswertes Geweih von *Pliocervus pentelici* (Gaudry) aus dem Altpliozän von Pikermi (Griechenland). Österreichische Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse 10, 134–137.

Symeonidis, N., 1978. Ein Schädel von *Metailurus parvulus* (Hensel) aus Pikermi (Attica, Griechenland). Annales Géologiques des Pays Helléniques 29, 698–703.

Symeonidis, N., Bachmayer, F., Zapfe, H., 1973. Ausgrabungen in Pikermi bei Athen, Griechenland. Annalen des Naturhistorischen Museums in Wien 77, 125–132.

Tekkaya, I., 1969. Preliminary report on the Bovidae fauna from Kayadibi, Konya. Bulletin of the Mineral Research and Exploration Institute of Turkey 73, 140–144.

Thenius, H., 1949. Über die Säugetierfauna aus dem Unterpliozän von Ilhan bei Ankara (Türkei). Sitzungsberichte der Österreichischen Akademie der Wissenschaften (I) 158, 656–661.

Thomas, H., Bernor, R., Jaeger, J.-J., 1982. Origines du peuplement mammalien en Afrique du Nord durant le Miocène terminal. Geobios 15, 283–297.

Wagner, A., 1857. Neue Beiträge zur Kenntniss der fossilen Säugthier-Ueberreste von Pikermi. Abhandlungen der Bayerischen Akademie der Wissenschaften 8, 111–158.

Watabe, M., 1990. Fossil Bovids (Artiodactyla, Mammalia) from the Maragheh (Turolian, Late Miocene), Northwest Iran. The Annual Report of the Historical Museum of Hokkaido 18, 19–55.

Weithofer, A., 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. Beiträge zur Paläontologie Österreich-Ungarns 6 (3), 225–292.

Zapfe, H., 1991. *Mesopithecus pentelicus* Wagner aus dem Turolien von Pikermi bei Athen, Odontologie und Osteologie (Eine Dokumentation). Neue Denkschriften des Naturhistorischen Museums in Wien 5, 1–203.