Oioceros rothii (Wagner, 1857) from the late Miocene of Pikermi (Greece): cranial and dental morphology, comparison with related forms

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ABSTRACT
Until now, the species *Oioceros rothii* (Wagner, 1857) was known only by isolated horn-cores, frontlets and skull fragments, but its skull structure and dentition were poorly known. In this article, an almost complete skull of *O. rothii* with associated mandibles, plus isolated dentitions and frontlets from Pikermi, the type locality, are described and compared. The species *O. rothii* has many characters in common with *O. atropatenes* (Rodler & Weithofer, 1890) and *Samotragus praecursor* Bouvrain & Bonis, 1985. It has a relative short face, slightly inclined in relation to the braincase, which is relatively long. Its dentition is characterised by a premolar series, which is longer relatively to the molars than in *O. atropatenes* and *S. praecursor*. "*Oioceros*" *wegneri* Andree, 1926 probably represents a different genus, characterised by a longer and strongly inclined face in relation to the braincase, short braincase and horn-cores placed almost entirely behind the orbits.

KEY WORDS
Mammalia, Artiodactyla, Bovidae, *Oioceros*, *Samotragus*, *Samodorcas*, late Miocene, Pikermi, Greece, Eurasia.

RÉSUMÉ
Oioceros rothii *(Wagner, 1857) du Miocène supérieur de Pikermi (Grèce) : morphologie crânienne et dentaire, comparaison avec les formes voisines.*
L'espèce *Oioceros rothii* (Wagner, 1857) n'était connue jusqu'à maintenant avec certitude que par des chevilles isolées, des massacres et des fragments de crâne. La structure crânienne et la dentition d'*O. rothii* restaient malheureusement inconnues. Dans cet article, un crâne presque complet d'*O. rothii* avec ses mandibules en connexion, des dentures isolées et des massacres qui proviennent de Pikermi,

MOTS CLÉS
Mammalia,
Artiodactyla,
Bovidae,
Oioceros,
Samotragus,
Samodorcas,
Miocène supérieur,
Pikermi,
Grèce,
Eurasie.

localité type d'*O. rothii*, sont décrits et comparés. L'espèce *O. rothii* présente plusieurs caractères que l'on retrouve chez *O. atropatenes* (Rodler & Weithofer, 1890) et *Samotragus praecursor* Bouvrain & Bonis, 1985. Elle possède un crâne à face relativement courte, peu inclinée par rapport à l'arrière-crâne, et un arrière-crâne non raccourci. La dentition est caractérisée par une rangée prémolaire plus longue par rapport aux molaires de *O. atropatenes* et *S. praecursor*. "*Oioceros*" *wegneri* Andree, 1926 représente probablement un genre différent, caractérisé par une face plus longue et très inclinée par rapport à l'arrière-crâne, un arrière-crâne court et des chevilles en grande partie en arrière des orbites.

INTRODUCTION

The species *Oioceros rothii* (Wagner, 1857) is one of the relatively rare bovids of the Pikermi fauna. Its first remains were found in Pikermi and described by Wagner (1857) as *Antilope rothii*. Later Gaudry (1865) named it *Antidorcas*? *rothii*, and finally Gaillard (1902; *fide* Pilgrim & Hopwood 1928) erected for this species the new genus *Oioceros*. The holotype of "*Antilope*" *rothii* is a frontlet from Pikermi described and figured by Wagner (1857: pl. 8, fig. 20) and its most important diagnostic character is the inverse torsion of the horn-cores. Most of the subsequently found specimens do not display more diagnostic characters, as they are horn-cores and skull fragments. The poor knowledge of the species *O. rothii* and the genus *Oioceros* resulted in the referral of a lot of fossil antelopes with inverse torsion of the horn-cores to *Oioceros*. Nevertheless, Pilgrim & Hopwood (1928) and Pilgrim (1934) had already mentioned that some of these forms could represent separate genera. During the last decades a great effort has been made (Solounias 1981; Bouvrain & Bonis 1985; Köhler 1987; Chen 1988; Masini & Thomas 1989; Azanza *et al.* 1998) to clarify the status of the genus *Oioceros*, as well as its relationships to other genera with inverse torsion of horn-cores. Middle Miocene species with inverse torsion of the horn-cores as *Oioceros tanyceras* Gentry, 1970 from Fort Ternan (Kenya), *O.*? *grangeri* Pilgrim, 1934 and *O.*? *noverca* Pilgrim, 1934 from Tung Gur (Mongolia) have been removed from *Oioceros* by Köhler (1987). Consequently, the number of the species of the genus *Oioceros* has been much reduced. *O. rothii*, however, remained poorly known, since neither a complete skull, nor mandibles in connection to the skull had been found until now.

The subject of this paper is the description of an almost complete skull of *O. rothii* found with its associated mandibles in the Pikermi collection of the AMPG. In order to provide as many information as possible for this species we have also included all the *O. rothii* specimens of the AMPG Pikermi collection, as well as specimens of the Pikermi collections of the MNHN and the NHML.

ABBREVIATIONS

AMPG	Athens Museum of Palaeontology and Geology;
LGPUT	Laboratory of Geology and Palaeontology, University of Thessaloniki;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHML	Natural History Museum, London.

METHODS

All measurements are given in mm, with an accuracy of one decimal digit. Slightly inaccurate measurements (in case of badly preserved specimens) are given in parentheses. In some cases (missing teeth, doubtful craniometric points) the measurements are given approximately, with the indication "*c.*". The measurements of the horn-cores are taken at the bases of the horn-cores. The anteroposterior diameter (DAP) corresponds to the large diameter of the horn-core base and it may not be parallel to the sagittal plane. The mediolateral diameter (DT) is perpendicular to the DAP. The dental lengths (L) were measured on the occlusal surface. The tooth width (W) is the maximum width. Uppercase letters are for upper teeth and lowercase letters for lower teeth. The height (H) of the mandibular ramus was measured lingually under the middle of the m3.

SYSTEMATICS

Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Subfamily ANTILOPINAE Gray, 1821
Tribe OIOCERINI Pilgrim, 1934

Genus *Oioceros* Gaillard, 1902

TYPE SPECIES. — *Antilope rothii* Wagner, 1857.

ADDITIONAL SPECIES. — *O. atropatenes* (Rodler & Weithofer, 1890).

DIAGNOSIS. — Small to medium sized antelopes; short face (M3 below the orbit), slightly bent in relation to the braincase; nasal bones widening posteriorly; prominent orbital rims; frontals between the horn-cores almost at the same level as the supraorbital margins; frontal depression between the posterior part of the nasals and the horn-core bases; supraorbital foramina close to the bases of the horn-cores; infraorbital foramen above P3; postcornual fossa present; horn-cores inserted above the posterior part of the orbits, with inverse torsion, and a main keel that starts from a postero-lateral position; horn-core axis almost straight in lateral view; anteroposterior and transverse diameter of the horn-cores that diminish gradually from the base upwards; braincase not shortened.

Oioceros rothii (Wagner, 1857)

Synonymy: see Pilgrim & Hopwood (1928: 24).

HOLOTYPE. — Frontlet (Wagner 1857: pl. 8, fig. 20), Palaeontological Museum, Munich.

MATERIAL EXAMINED. — AMPG Pikermi collection: almost complete skull with the left and right horn-cores (partly preserved), the left P3-M3, and the right P2-P3 and M1-M3 (PG 95/1502a); right maxilla fragment with the P2-M2 (PA 3509/91); right mandibular ramus with the p3-m3 (PA 3519/91); right mandibular ramus with the p4-m3 (PG 95/1502b); left mandibular ramus with the p4-m3 (PG 95/1502c); frontlets with the left and right horn-cores (PG 95/1509, PG 95/1510, PG 95/1514, PA 1412/91); right horn-cores (PA 909/91, PA 3553/91, PG 88/1583); left horn-cores (PA 2990/91, PG 88/1540). The mandibles PG 95/1502b & c were found connected to the skull PG 95/1502a by matrix. The frontlet PA 1412/91 brings also the code PA 3031/91.
MNHN Pikermi collection: frontlets (PIK. 2244, PIK. 2246, PIK. 2247, PIK. 2249). PIK. 2249 has been figured by Gaudry (1865: pl. 52, figs 2, 3).
NHML Pikermi collection: frontlet with the left and right horn-cores (M 11461). This specimen is mounted on a plaster base and according to Pilgrim & Hopwood (1928: 25) it is not certain that the two horn-cores were derived from the same individual.

LOCALITY. — Pikermi, Greece.

AGE. — Late Miocene, middle Turolian (MN 12).

DIAGNOSIS. — Medium sized *Oioceros*; lyrate horn-cores with elliptical cross section throughout their length; postero-lateral keel that runs almost the whole horn-core; horn-core torsion of one gyre; interfrontal and parietofrontal sutures open and complicated; interfrontal suture only slightly elevated between the horn-core bases; ethmoid fissure present; occipital face in obtuse angle to the braincase roof; basioccipital slightly wider posteriorly than anteriorly, without median groove; premolar series long relatively to the molars (LP2-P4/LM1-M3) × 100 = *c.* 78.

DIFFERENTIAL DIAGNOSIS. — *O. rothii* differs from *O. atropatenes* by the larger general size; the larger dimensions of the horn-cores, their more important torsion (less than one gyre in *O. atropatenes*), and their more elliptical cross section at their bases; the larger dentition, the more advanced degree of molarization on the lower premolars, and the larger premolar series relative to the molars.

DESCRIPTION

Skull

The available skull (PG 95/1502a) is almost completely preserved (Fig. 1). The face is short (M3 at the level of the anterior third of the orbit) and slightly bent relative to the braincase. Because of the preservation status it is not clear whether there is a lachrymal fossa, but there is an ethmoid fissure. The premaxillary bones are in contact with the nasals. The width of the

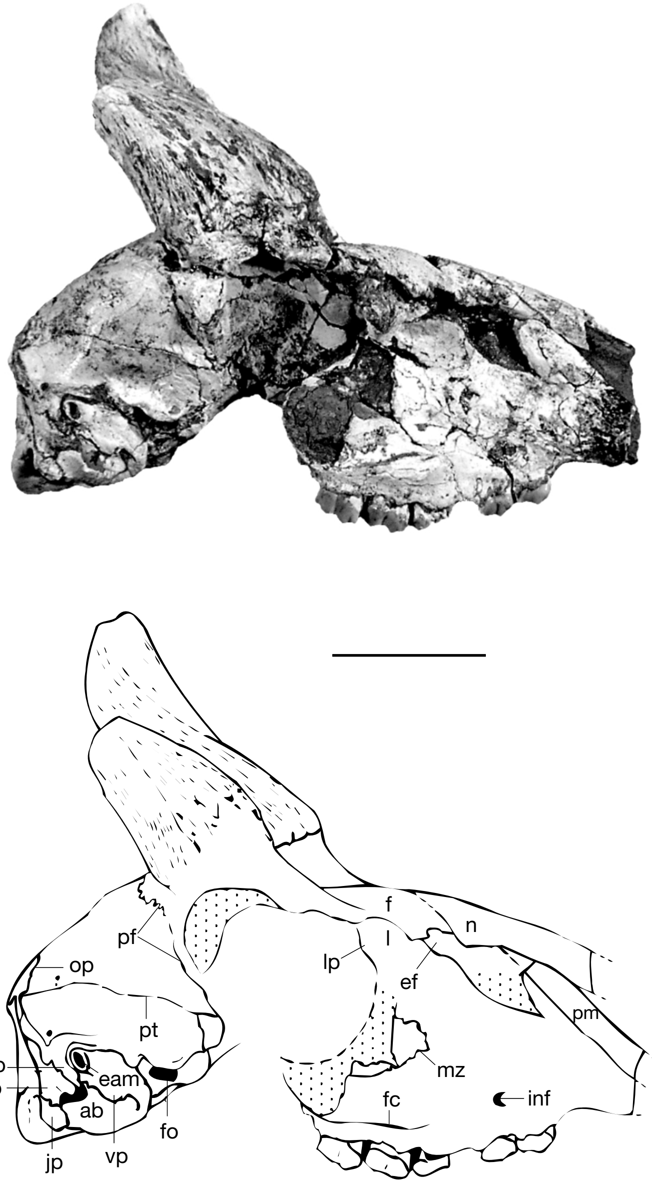

FIG. 1. — *Oioceros rothii* (Wagner, 1857) from Pikermi, skull (PG 95/1502a); **A**, right lateral view; **B**, sketch-drawing showing the most important anatomical characters. Abbreviations: **ab**, auditory bulla; **eam**, external auditory meatus; **ef**, ethmoid fissure; **f**, frontal; **fc**, facial crest; **fo**, foramen ovale; **inf**, infraorbital foramen; **jp**, jugular process; **l**, lachrymal; **lp**, lachrymal process; **mp**, mastoid process; **mz**, maxillozygomatic suture; **n**, nasal; **op**, occipitoparietal suture; **pf**, parietofrontal suture; **pm**, premaxillar; **pp**, post-tympanic process; **pt**, parietotemporal suture; **vp**, vaginal process. Scale bar: 40 mm.

premaxilla is 8 mm and its contact with the nasal measures about 20 mm. The posterior end of the premaxillary bone is above the P3. The nasals widen posteriorly, their maximum width occurs at about 20 mm before their posterior end which is above the anterior margin of the orbits. Most probably there is no contact between the nasal and the lachrymal. The infraorbital foramen

FIG. 2. — *Oioceros rothii* (Wagner, 1857) from Pikermi, skull (PG 95/1502a), palatinal view. Scale bar: 40 mm.

opens above the anterior half of P3. The maxillo-lachrymal suture is not clearly visible. The most anterior point of the maxillozygomatic suture is above the posterior part of the M1, and there is a facial crest that extends anteriorly to the M1. The frontals are depressed between the nasals and the horn-core bases.

The interfrontal and parietofrontal sutures are open and complicated. The former is slightly elevated between the horn-cores. The parietofrontal suture has a slight forward central indentation, forming a large obtuse angle in dorsal view. The frontals between the horn-cores are almost at the same level as the supraorbital margins, and their thickness behind the horn-cores is small (about 5 mm). The supraorbital foramina are small, and open above the centre of the orbits almost level with the supraorbital margins, very close to the bases of the horn-cores. The maximum distance between the supraorbital foramina ranges from 32.3 mm to 40.2 mm (AMPG and MNHN, Pikermi, n = 7). The orbital margins are not completely preserved but the orbits look large in relation to skull size. The maximum width over the horn-core bases ranges from 58.4 to 68.8 mm (AMPG and MNHN, Pikermi, n = 8). The supraorbital margins project laterally. In PA 1412/91 for example, the greatest width at the supraobital margins is estimated to at least 84 mm, while the width at the bases of the horn-cores and laterally is only 65.4 mm. The anterior margin of the orbits lies above the M3/M2 contact. The maxillopalatine suture cannot be traced clearly, its likely anterior limit, however, is level with the M1/M2 contact.

The braincase is relatively long, almost as long as the preorbital region (Fig. 1), its greatest width is at its mid-length, and there are no temporal lines. The width of the skull behind the horn-cores (at the parietofrontal suture) ranges from 53.1 to 58.1 mm (AMPG, Pikermi, n = 5). The top of the braincase, close to the centre of the parietal bone, is slightly swollen. The supraoccipital bone has the form of a transversely elongated trapezium. The occipital face forms an obtuse angle with the roof of the braincase (Fig. 1). The nuchal crest is not prominent. The external occipital crest is slightly developed and the two surfaces laterally of this crest form a wide obtuse angle. The foramen magnum is slightly higher (16.8 mm) than broad (14.6 mm). The mastoid bone is not in contact with the parietal. The angle formed by the level of the nasals and the line that connects the nuchal crest with the meeting point of the interfrontal and parietofrontal sutures is about 127°. The angle formed between the previously mentioned meeting point, the nuchal crest and the dorsal margin of the foramen magnum is about 118° (parameters measured on a sagittal profile of the skull).

The auditory bulla is laterally compressed, strongly connected to the jugular process and the basioccipital, and its occipital face lies level with the posterior limit of the posterior tuberosities of

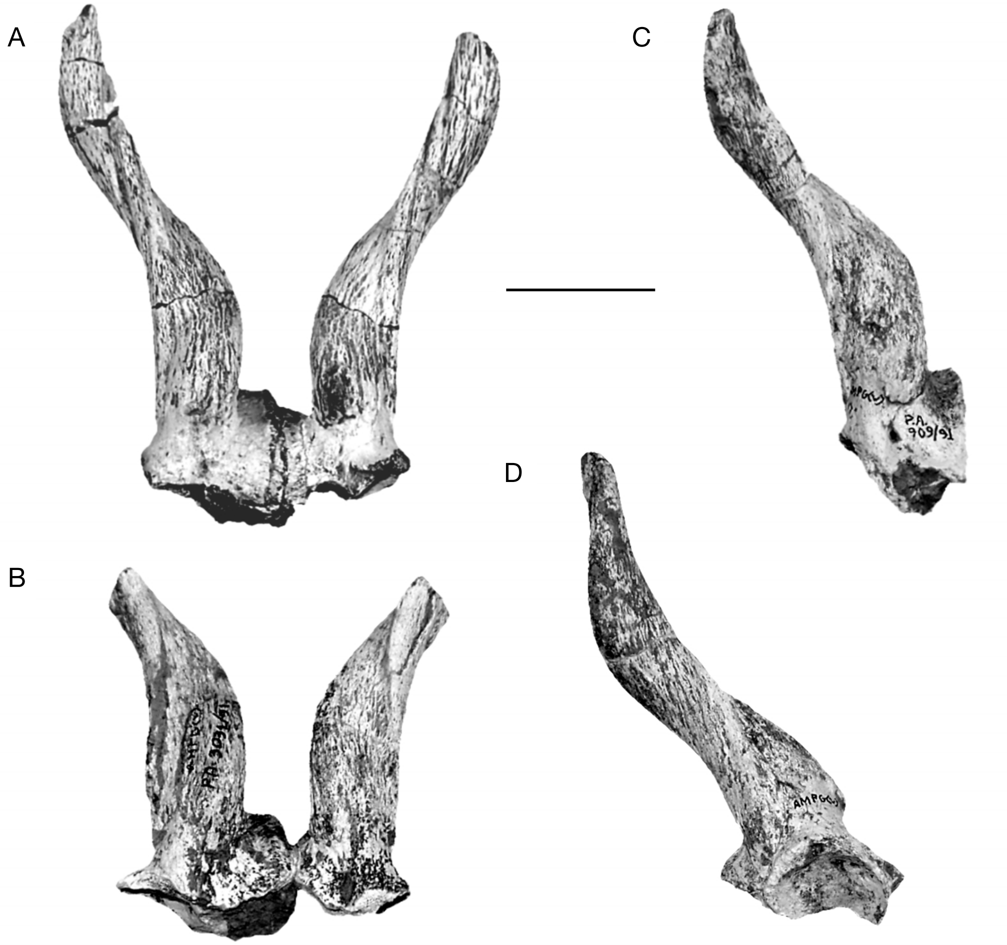

FIG. 3. — *Oioceros rothii* (Wagner, 1857) from Pikermi; **A**, frontlet (PG 95/1514), anterior view; **B**, frontlet (PA 1412/91), anterior view; **C**, **D**, right horn-core (PA 909/91); **C**, anterior view; **D**, lateral view. Scale bar: 40 mm.

the basioccipital (Fig. 2). The external auditory meatus directs postero-dorsally (Fig. 1). The jugular processes are broken ventrally and the degree of their downward extension cannot be estimated. The post-tympanic process directs ventrally and anteriorly, passing under the external auditory meatus (Fig. 1). The basioccipital is rectangular, its transverse section at its central area is convex and the posterior tuberosities are slightly wider than that the anterior ones (Annexe: Table 1). The latter are anteroposteriorly elongated and extend anteriorly beyond the level of the oval foramina, which are small (larger diameter about 5 mm).

Horn-cores

None of the available horn-cores is completely preserved. The most completely preserved horn-cores are the right one of PG 95/1514, and PA 909/91. The left horn-core of PG 95/1502a shows a pathological possibly thickening at the base of its postero-lateral keel. The horn-cores of *O. rothii*, characteristic for their inverse torsion (counter-clockwise in the right horn-core from the base upwards when observed in dorsal view), are inserted above the orbits, so that, in lateral view and with the tooth row horizontal, the anterior part of their bases is above the centre of the orbits. The posterior part of their bases is slightly behind the posterior margin of the orbits (Fig. 1). In frontal view the bases of the horn-cores are almost parallel to each other, but they diverse upwards and finally their tips are sub-parallel to each other (Fig. 3A, B). In lateral view the horn-core axis does not curve but remains almost straight (Fig. 3D). There is a main keel that starts postero-laterally and runs almost the whole horn-core. In some of the less massive horn-cores (PG 95/1514, PG 95/1510, PG 95/1509), this keel is less acute and less distinct than in the more massive horn-cores (PG 95/1502a, PA 909/91, PA 1412/91). Anterior to this keel there is a wide groove, variable in development, but always clearly distinct at the base of the horn-core. In some specimens there is another narrow groove, posterior to the keel. The horn-cores taper gradually distally and their section is ovoid throughout their length (Fig. 4). The pedicels are short and they almost disappear posteriorly. The horn-cores (especially the more massive ones) protrude anteriorly over the pedicels, forming an anterior V-shaped extension over them. There is a deep postcornual fossa, independent in development from the horn-core robustness. Two almost complete horn-cores (the right horn-core of PG 95/1514, and PA 909/91) trace one complete gyre, and their total length (in straight-line) can be estimated to 120-130 mm. Two horn-cores (PG 88/1540, PG 88/1583) are broken at their bases and show that the pedicels are not hollowed.

Upper dentition

The upper tooth row is characterised by the long premolar series relative to the molars (Annexe: Table 4; Figs 5A; 6C). P2 is moderately elongated, its parastyle is very small and does not project labially, and its paracone rib is thick, situated just behind the parastyle. The protocone is less developed than the hypocone and less projected lingually. The protocone and the hypocone are separated lingually by a slight groove, situated almost opposite the rib of the paracone. On the occlusal surface, the anterior fossa is very reduced and situated at the anterior part of the protocone, very close to the enamel. P3 is similar to P2 but less elongated (Annexe: Table 4), while its parastyle is more developed. The paracone rib is very thick. As in P2, a slight groove separates lingually the protocone from the more developed hypocone. The position and the development of its anterior fossa resemble those of P2. A trace of the posterior fossa can be observed on the left P3 of PG 95/1502a. The P4 has a thick parastyle while its paracone rib is only slightly developed. A very clear groove separates lingually the protocone from the hypocone. The protocone extends lingually more than the hypocone. Its anterior fossa is like that of P2 and P3, but a small posterior fossa is also visible. The metastyle is thinner than the parastyle. The molars have a thick parastyle, the rib of the labial wall of the paracone is moderately developed, and the labial wall of the metacone is only slightly convex. The M1 and M2 of PG 95/1502a have faint entostyles (absent in PA 3509/91). The metastyles and the mesostyles are thinner than the parastyles. The M1 and M2 have a central fossa. A fold at the posterior fossa, or a small additional fossa at the posterior part of the hypocone can be seen on the occlusal surface of some molars.

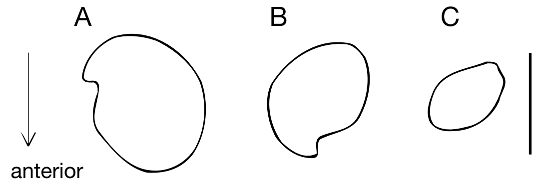

Fig. 4. — *Oioceros rothii* (Wagner, 1857) from Pikermi, sections of the right horn-core (PA 909/91); **A**, section of the horn-core about 1 cm above its base; **B**, section of the horn-core at the middle of its total length; **C**, section of the horn-core about 2 cm from its tip. The arrow shows approximately the anterior direction. Scale bar: 20 mm.

Lower dentition

Besides the two mandibles (PG 95/1502b & c) found in connection with the skull, we refer to *O. rothii* another mandible (PA 3519/91). Despite their slightly smaller dimensions (Annexe: Table 5), the teeth of this mandible show many morphological similarities to PG 95/1502b & c, even in details. Because of the lack of a complete mandible the length of the tooth row and that of the premolar row cannot be calculated with accuracy. These parameters are given approximately (Annexe: Table 5). As in the upper tooth row, the lower premolar row is long relative to the molars (Annexe: Table 5; Figs 5B-D; 6A, B). The mandibular corpus is not especially deep below m3, and its depth decreases gradually anteriorly. On the labial surface of the mandibular corpus and slightly behind m3 there is a well developed angular tuberosity (rugose area) for the masseter muscle. The p3 is slightly smaller than the p4 (Annexe: Table 5). The paraconid is not distinct from the parastylid, and the metaconid is obliquely directed and connected to the posterior part of the tooth. The valley between the paraconid and the metaconid remains wide and open down to the base of the crown. There is a groove in front of the hypoconid. The p4 is similar to p3, but the metaconid has anteroposterior direction and the groove in front of the hypoconid is more distinct. The lower molars have thick parastylid, but the metastylid and the entostylid are weakly developed. The lingual wall of the metaconid and the entoconid are simple and slightly convex without strong ribs. There are no goat folds. There is a vertical groove on the labial wall of the posterior lobe of m1. The ectostylids are more developed on the anterior molars. There is a second ectostylid in front of the third lobe of m3 in PG 95/1502c, but not in PG 95/1502b. In PA 3519/91, the m3 is slightly broken in this area, but a trace of an ectostylid in front of the third lobe is still present. The third lobe of m3 is relatively large and has a central fossa.

COMPARISONS AND DISCUSSION

As we mentioned earlier, some of the available horn-cores (PG 95/1509, PG 95/1510, PG 95/1514) have less distinct and acute keel, and smaller dimensions (Annexe: Table 2). It is not known if such differences could represent sexual dimorphism, as observed by Gaudry (1865: 298). In addition to Pikermi, the species *O. rothii* is also known from the localities Ravin X and Ravin R.Ar. of Vathylakkos (Arambourg & Piveteau 1929). Bernor (1978; *fide* Bouvrain & Bonis 1985) on the contrary referred the Vathylakkos specimens to the species *Oioceros atropatenes*. However, the horn-core MNHN SLQ. 794 figured by Arambourg & Piveteau (1929: pl. 8, fig. 5) is not different in morphology or dimensions (Annexe: Table 2; Fig. 7) from the Pikermi specimens of *O. rothii*. In my opinion, the latter authors and Bouvrain & Bonis (1985) were right in assigning it to this species.

The species *O. rothii* is not known from Samos. Gentry & Heizmann (1996) and Gentry *et al.* (1999) regarded *Samotragus crassicornis* Sickenberg, 1936 from Samos as a synonym of *O. rothii* and stated that it represents the male of the latter species. Such an opinion, however, is not sufficiently supported since in Pikermi no horn-core with the characters of *S. crassicornis* has been found so far. In Samos on the other hand, no horn-cores resembling *O. rothii* are known.

Outside Greece specimens of *O. rothii* are also known from Maragha in Iran (Mecquenem 1924; Bouvrain & Bonis 1985; Watabe 1990; Bernor *et al.* 1996). Bernor *et al.* (1996) mention the existence of *O. rothii* in the Middle Maragha fauna. A frontlet from Maragha (MNHN MAR. 1320) referred by Mecquenem (1924: pl. 7, fig. 4) to *O. rothii* is not different from the Pikermi specimens of this species (Annexe: Table 2). Except horn-cores, Mecquenem (1924) referred also to *O. rothii* a skull preserving the upper molar series, but with its horn-cores broken close to their bases. This specimen has been considered a different species, *Oioceros*? *mecquenemi*, by Pilgrim (1934), but Solounias (1981) and Gentry *et al.* (1999) referred it to *O. rothii*, an identification which is very likely. Watabe (1990: pl. 2, figs 1, 2) referred also two skulls from the site III of Maragha to *O. rothii*. Both skulls, however, do not preserve the dentition. Watabe (1990: table 1) referred also some horn-cores from the same locality to *O. rothii*. These horn-cores have no important differences from the Pikermi specimens in absolute dimensions, but they seem to have larger DT/DAP ratio (Annexe: Table 3; Fig. 7). Unfortunately, it is not known if these differences correspond to different technique of measurements or/and to the preservation status of the Maragha (site III) specimens.

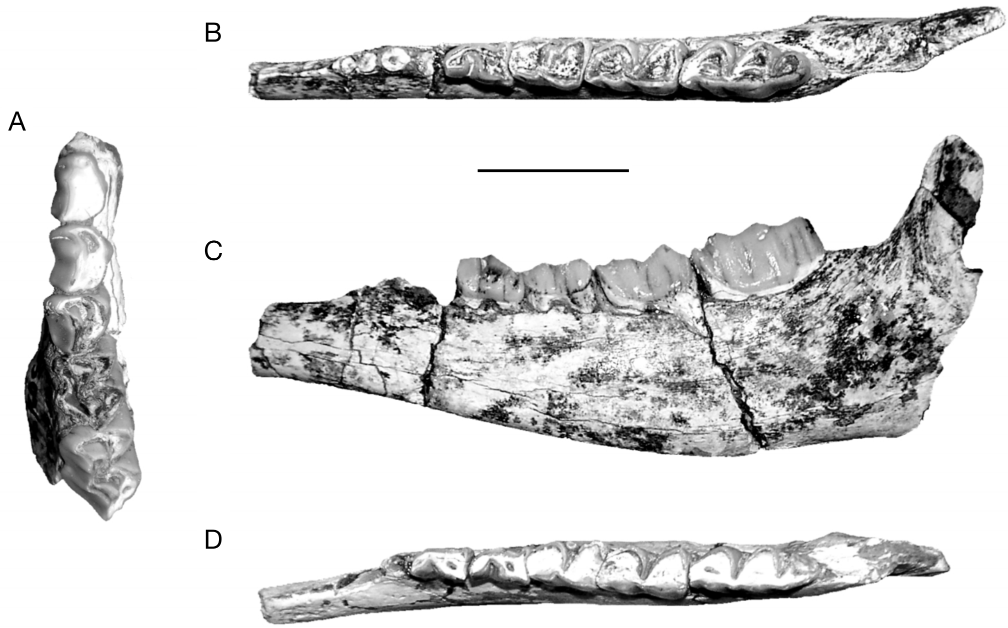

FIG. 5. — *Oioceros rothii* (Wagner, 1857) from Pikermi; **A**, right maxilla fragment (PA 3509/91), occlusal view; **B**, **C**, right mandible (PG 95/1502b); **B**, occlusal view; **C**, lingual view; **D**, right mandible (PA 3519/91), occlusal view. Scale bar: 20 mm.

In Turkey, *O. rothii* has been reported from Gökdere (Senyürek 1952) and Çorak Yerler (Köhler 1987), and only mentioned in a faunal list at Küçükyozgat (Senyürek 1953). The specimens from Gökdere are two horn-core fragments described by Senyürek (1952: figs 58-61). As already pointed out by Bouvrain & Bonis (1985), it is not clear if these specimens belong to *O. rothii* or *Samotragus* Sickenberg, 1936. Judging from the figures, it seems that one of the Gökdere horn-cores (Senyürek 1952: figs 59, 60) shows a stronger curvature in lateral view than *O. rothii*. The horn-cores of *O. rothii* from Çorak Yerler are not particularly different from the Pikermi specimens in dimensions (Annexe: Table 3; Fig. 7), especially if we consider that in the Çorak Yerler sample a juvenile horn-core is also included (Köhler 1987).

COMPARISON WITH INDIVIDUAL DENTITIONS REFERRED TO *OIOCEROS ROTHII* OR OTHER SPECIES

Until now no mandible had been found in connection to the skull of *O. rothii* and the lower dentition of *O. rothii* was not definitely known. The mandible MNHN MAR. 8031 from Maragha referred by Mecquenem (1924: pl. 6, fig. 2) to *O. rothii* cannot be referred to it since it is clearly different in morphology from the available specimens from Pikermi. Its dimensions are not very different (Annexe: Table 5) but the molars have well developed goat folds and the third valley of the p3 is open. On this specimen, the p4 seems not to have erupted normally, which affects the size of the premolar series and the corresponding premolar to molar ratio. Erdbrink (1976: pl. 2, fig. b) has referred another mandible from Mordaq, near Maragha, to *O. rothii*. This specimen has the same characters as MAR. 8031 (presence of goat folds, open third valleys in p3, p4) and cannot be referred to *O. rothii*. Moreover it has slightly larger molars (Erdbrink 1976: 48) and its depth below the m1/m2 contact measures 22.5 mm, contrary to 17-18 mm on the available specimens from Pikermi. It is important to notice here that Erdbrink (1976) accepts three different species of *Oioceros* in Maragha, *O. rothii*, *O. atropatenes* and *O. boulei* Mecquenem, 1924, and does not seem to be aware of Heintz's opinion who considered *O. boulei* a junior synonym of *O. atropatenes* (Heintz 1963). Moreover, Erdbrink (1976) referred to *O. rothii* the species *Oioceros*? *proaries* Schlosser, 1904, originally based on a hornless skull from Samos (Schlosser 1904: pl. 13, fig. 10a-c). According to Erdbrink (1976), *O.*? *proaries* has only minor differences from *O. rothii*, perhaps of subspecific significance, but Köhler (1987) synonimized *O.*? *proaries* with *Pseudotragus parvidens* (Gaudry, 1861). According to the measurements given by Schlosser (1904), *O.*? *proaries* has larger upper tooth series compared to *O. rothii* and relatively shorter premolar series. The dimensions, as well as the morphological characters of the upper dentition of "*O.*? *proaries*" are similar to those of a skull from Pikermi referred to *P. parvidens* by Roussiakis (1996).

Among the mandibles from Maragha, the specimen that appears closer in morphology to the Pikermi specimens of *O. rothii* is the mandible MNHN MAR. 1829 described by Mecquenem (1924: pl. 7, fig. 5-5a) as "*Helicophora rotundicornis*". The dimensions (Annexe: Table 5), the morphology of the molars (absence of goat folds, presence of a central cavity on the back lobe of m3), and the structure of the p3 and p4 (closed third valleys) of this specimen are in agreement with the present specimens.

A mandible from Ravin X in Thessaloniki (MNHN SLQ. 1035) attributed in *O. rothii* by Arambourg & Piveteau (1929: pl. 8, fig. 4-4a) has slightly shorter premolar series than the available specimens (Annexe: Table 5) and less developed parastylids. Moreover there is a goat fold at least in m3. The p4 has no important differences from the Pikermi specimens, except its less developed groove in front of the hypoconid. Another mandible from Thessaloniki (MNHN SLQ. 793), described as "*Helicotragus rotundicornis*" by Arambourg & Piveteau (1929: pl. 8, figs 3-3a), displays some similarities with our specimens. This specimen has a closed third valley in p3 and p4, and comparable total length but slightly shorter premolar length.

A maxilla fragment from Pikermi referred by Schlosser (1904: 72, fig. 3) to *O. rothii*? is only slightly smaller than the present upper teeth of *O. rothii* and its premolar to molar ratio could be similar (the M3 is missing), according to Schlosser's figure. Its upper molars also have central fossae as *O. rothii*. Nevertheless, the P3 of this specimen is more elongated and its hypocone does not project lingually, and the fossae on the occlusal surface of the premolars are not anteriorly situated as in the present specimens of *O. rothii*.

The available dental remains of *O. rothii* are inadequate in number to give us an appropriate image of their size range. It seems, however, that the dentition of *O. rothii* is intermediate in size between *Gazella capricornis* (Wagner, 1848) and *Palaeoreas lindermayeri* (Wagner, 1848). Unfortunately, comparison of *O. rothii* with *Prostrepsiceros rotundicornis* (Weithofer, 1888), a species also found in Pikermi, cannot be made since the dentition of *P. rotundicornis* is not definitely known. A mandible from Pikermi thought to belong to *P. rotundicornis* according to Gentry (1971: pl. 6, fig. 2 bottom) has larger teeth than *O. rothii* and lower molars with goat folds.

COMPARISON WITH *OIOCEROS ATROPATENES*

The species *O. atropatenes*, known from Maragha, has been revised by Heintz (1963) and includes *O. boulei* Mecquenem, 1924, a form that was also based on specimens from Maragha. *O. atropatenes* has many characters in common with *O. rothii*. Both species have slightly bent braincase relatively to the face, prominent orbits, a depression at the frontals between the posterior part of the nasals and the bases of the horn-cores, infraorbital foramen that opens above P3, M3 below the anterior part of the orbit, straight horn-core axis in lateral view and horn-core dimensions that decrease gradually upwards, and transversely convex basioccipital. Moreover, they have upper premolars with anterior fossae situated anteriorly close to the enamel, P2 and P3 with lingually projected hypocone, and reduced parastyle in P2. The braincase of the skull of *O. atropatenes*, figured by Mecquenem (1924: figs 10, 11), is not completely preserved. Judging from the preserved part of the braincase roof, however, that measures about 25 mm in length

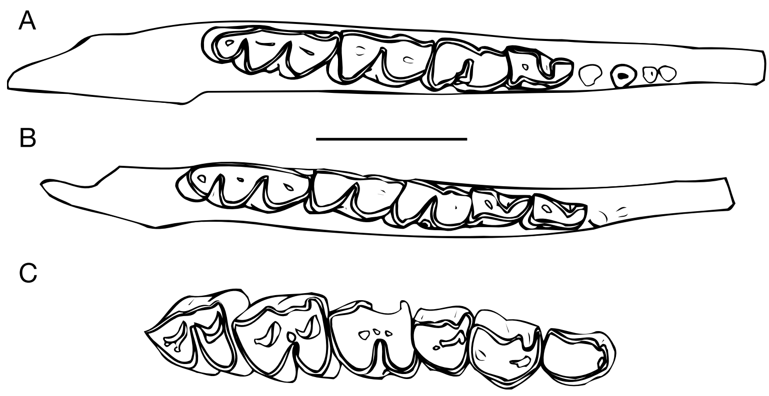

FIG. 6. — *Oioceros rothii* (Wagner, 1857) from Pikermi; **A**, right mandible (PG 95/1502b), occlusal view; **B**, right mandible (PA 3519/91), occlusal view; **C**, right upper tooth-row (composite from the left and right preserved teeth of PG 95/1502a), occlusal view. Scale bar: 20 mm.

behind the horn-cores, the braincase was not particularly shortened in relation to the face.

The horn-cores of *O. atropatenes*, however, are smaller in dimensions than those of *O. rothii* (Annexe: Table 3; Fig. 7), their basal section is almost circular, and their torsion is less than one gyre. Heintz (1963) demonstrated also that in *O. atropatenes* both the males and the females have horn-cores, but the horn-cores of the females are less massive and straighter than those of the males, a difference not observed in *O. rothii*. In *O. atropatenes* the teeth are smaller than in *O. rothii*, the total length of the upper tooth row is 45 mm (Heintz 1963: table 2), contrary to approximately 62 mm in *O. rothii* (Annexe: Table 4). Moreover, the upper premolar row is more reduced relative to the molars in *O. atropatenes* than in *O. rothii*. The ratio (LP2-P4/LM1-M3) × 100 in *O. atropatenes* is 60.7 according to Heintz (1963) and 66.6 according to Bouvrain & Bonis (1985). In *O. rothii* on the other hand, the corresponding ratio is approximately 78. Besides its smaller size, the lower dentition of *O. atropatenes* differs from *O. rothii* in the structure of p4 that has a narrow but open valley between the metaconid and the entoconid (Heintz 1963), and in the presence of faint goat folds on the lower molars (Mecquenem 1924).

The specimens from the early Turolian (MN 11) locality of Nikiti-1 referred by Kostopoulos & Koufos (1996) to *Oioceros* cf. *atropatenes* unfortunately are not in a good state of preservation, but their characters seem intermediate between *O. atropatenes* and *O. rothii*. The horn-cores from Nikiti-1 have dimensions close to the highest values of *O. atropatenes* from Maragha (Annexe: Table 3; Fig. 7). They are slightly smaller than *O. rothii* from Pikermi, but their DT/DAP index is especially larger (Annexe: Table 3). The teeth of the Nikiti-1 specimens (Kostopoulos & Koufos 1996: tables 19, 20) are larger than in *O. atropatenes* from Maragha (Heintz 1963: table 2), but comparable to *O. rothii*. The molarization of the lower premolars looks intermediate between *O. atropatenes* from Maragha and *O. rothii* from Pikermi, as the third valley of p3 and p4 is closed near the base of the crown (Kostopoulos & Koufos 1996). In *O. atropatenes* from Maragha the p3 is not definitely known, but the p4 has a narrow but completely open third valley (Heintz 1963). In *O. rothii* the third valley is completely closed in p3 and p4. The lower molars of the Nikiti-1 species, however, are more similar to *O. atropatenes* since they possess goat folds.

COMPARISON WITH *OIOCEROS WEGNERI*

The species *O. wegneri* was originally based on an almost complete skull from Samos (Andree 1926: pl. 15, figs 3, 6) preserving its upper tooth rows. The lower dentition is not known with certainty

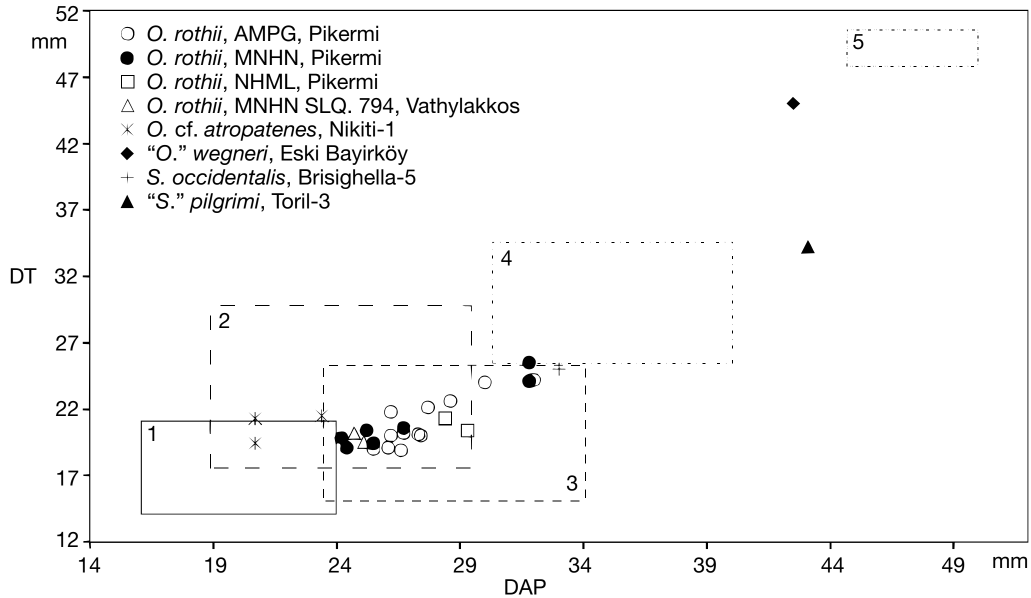

FIG. 7. — Scatter diagram of the anteroposterior (DAP) and transverse diameter (DT) of the horn-cores of several inverse spiralled antelopes. The numbered squares represent the measurement ranges for: *Oioceros atropatenes* (Rodler & Weithofer, 1890) from Maragha (**1**); *O. rothii* (Wagner, 1857) from Maragha, site III (**2**); *O. rothii* from Çorak Yerler (**3**); *Samotragus praecursor* Bouvrain & Bonis, 1985 from Ravin de la Pluie (**4**) and "*O.*" *wegneri* Andree, 1926 from Samos (**5**). Data from Tables 2 and 3 (see Annexe).

but Solounias (1981: fig. 50D-G) referred to the same species, besides some frontlets and palates, a mandible that he believed to come from the type skull. All these specimens come from Samos, but *O. wegneri* has also been recorded in the early Turolian (MN 11) of Eski Bayirköy, Garkin and Mahmutgazi, in Turkey (Köhler 1987), and in the middle Turolian (MN 12) of Düzyayla, also in Turkey (De Bruijn *et al.* 1999). Furthermore, some specimens from the middle Turolian (MN 12) of Kemiklitepe (KTA and KTB) are referred by Bouvrain (1994) as ?*Oioceros wegneri*.

The horn-cores of *O. wegneri* have many keels and longitudinal grooves, are larger in dimensions than those of *O. rothii*, and have almost circular section close to their base (Annexe: Table 3; Fig. 7). Moreover, they seem to diverge laterally more than in *O. rothii* and *O. atropatenes* (Andree 1926: pl. 15, fig. 6; Köhler 1987: fig. 100). The horn-core axis, however, is almost straight in lateral view and the dimensions decrease gradually distally, as in *O. rothii* and *O. atropatenes*. The length of the upper tooth row of *O. wegneri* is 65.5 mm in the holotype (Andree 1926), almost similar with that of *O. rothii*. Its premolar row, however, is shorter than in *O. rothii* and the ratio (LP2-P4/LM1-M3) × 100 is 68.4 in the holotype (Andree 1926: 171). The same ratio, according to Solounias (1981: table 35), ranges from 61-70 (Samos, n = 6) in *O. wegneri*. The mandible referred by Solounias (1981: fig. 50D) to *O. wegneri* differs from *O. rothii* on the presence of goat folds on the molars, and the open valley between the metaconid and the entoconid of p4. Concerning the skull morphology, *O. wegneri* does not have many characters in common with *O. rothii*, *O. atropatenes* and *S. praecursor* Bouvrain & Bonis, 1985 (some characters are not known in *S. crassicornis*). It differs from the above species because it has short braincase and longer face (facial portion about twice as long as the braincase, M3 below the anterior margin of the orbit or even more anteriorly), horn-cores almost entirely behind the orbits despite their very short pedicels, infraorbital foramen above P2, and interfrontal suture that forms a crest on the frontals anterior to the horn-core bases as well as between the supraorbital foramina. Unfortunately, the face of *S. crassicornis*, type species of *Samotragus*, is not known but its braincase is not shortened (Solounias 1981: fig. 52A). Additionally, *O. wegneri* differs from *O. rothii* and *O. atropatenes* on the particularly elevated frontals above the supraorbital margins, the more anterior position of the supraorbital foramina (above the anterior part of the orbits) and the strongly bent braincase relative to the face. In the last character *O. wegneri* differs also from *S. praecursor*. It is not known whether the orbital rims of *O. wegneri* are prominent, as in *O. rothii*, *O. atropatenes* and *Samotragus*, or not. *O. wegneri* is more derived than *O. rothii*, *O. atropatenes* and *S. praecursor* in most of its characters as the longer face, the shorter braincase and the more posterior insertion of the horn-cores. In these characters, the strongly bent braincase and the position of the infraorbital foramen, it resembles *Samodorcas kuhlmanni* (Andree, 1926) from Samos. This last species, however, has horn-cores strongly inclined backwards, anteroposteriorly compressed at their bases, with an acute keel. A frontlet from Eski Bayirköy referred by Köhler (1987: fig. 100) to *O. wegneri* shows also very thick frontals behind the horn-cores, character also derived compared to the thin frontals of *O. rothii*. *O. rothii*, *O. atropatenes* and *S. praecursor* appear more derived than *O. wegneri* in the position of the infraorbital foramen, difference, however, small as the infraorbital foramen in these species opens above the P3, while in *O. wegneri* it opens only slightly more anteriorly, above the P2. Furthermore, *Samotragus* can be considered more derived on the horn-core morphology, described in the following section. From the above comparison it seems that *O. wegneri* does not share many characters with *O. rothii*, *O. atropatenes* and *Samotragus*. In my opinion, Andree's species differs significantly from *Oioceros* and *Samotragus* on the skull morphology, and its characters could be of generic rank and not of specific only.

Comparison with *Samotragus*

Samotragus crassicornis, the type species of the genus, is known from three specimens only, all from Samos. Solounias (1981) transferred *S. crassicornis* to the genus *Sinotragus* Bohlin, 1935, but as shown by Bouvrain & Bonis (1985) the name *Samotragus* is valid. The type specimen of *S. crassicornis* is a skull fragment with the horn-cores, lacking the braincase and the face (Sickenberg 1936: pl. 3, figs 1, 2). Moreover, Solounias (1981: fig. 52A-D) referred to the same species two more specimens, one preserving the braincase. The preorbital region and the dentition are unknown. The horn-cores of this species are especially larger in dimensions than those of *O. rothii* (Annexe: Table 3), their dimensions decrease abruptly above their mid-height and they diverge strongly laterally in their distal part. In lateral view, the horn-cores bend strongly backwards after their mid-height (Sickenberg 1936: pl. 3, fig. 2). There is no postcornual fossa and the occipital face looks backwards, forming an obtuse angle with the roof of the braincase (Solounias 1981: fig. 52A).

Samotragus praecusror, from the Vallesian of Ravin de la Pluie and Ravin des Zouaves-1 in Macedonia (Greece), is one of the best known species, since complete skulls, mandibles associated with skulls and numerous limb bones have been found. The females of *S. praecursor* have no horn-cores, while the horn-cores of the males are similar to those of *S. crassicornis* but smaller. The dimensions and the DT/DAP index are larger than those of *O. rothii* (Annexe: Table 3; Fig. 7). The teeth of *S. praecursor* are smaller than in *O. rothii* (Bouvrain & Bonis 1985: tables 1, 2) and the premolars of this species are smaller relatively to the molars. Bouvrain & Bonis (1985) give for the index (LP2-P4/LM1-M3) $\times$ 100, a value of 59. According to personal measurements taken on the holotype (LGPUT RPl 480), however, this index has been found equal to 72-73. The skull of *S. praecursor* is similar to that of *O. rothii* in many respects. The face is equally bent in relation to the braincase and equally elongated (M3 below the anterior third of the orbit), and the infraorbital foramen opens above P3 as in *O. rothii*. The postcornual fossa, however, is faint and present only in the males. Despite these similarities, the horn-cores of *S. praecursor* have large dimensions at their bases that decrease abruptly above their mid-height, diverge strongly laterally in their distal part, and bend backwards in lateral view as in *S. crassicornis*. Furthermore, the posterior limit of the premaxillar bone is anterior to P2 in *S. praecursor* (LGPUT RPl 480), above P3 in *O. rothii*, difference probably related with the smaller tooth row of *S. praecursor*. The basioccipital of *S. praecursor* is also different from that of *O. rothii*. The basioccipital is concave medially at the area between the anterior and the posterior tuberosity instead of having a convex transverse section as in *O. rothii*. The basioccipital of the females of *S. praecursor* (LGPUT RPl 211) is smaller than that of the males (LGPUT RPl 480-481), but the structure remains the same.

Samotragus occidentalis Masini & Thomas, 1989 is known from the late Turolian (MN 13) of the karst fissures of Brisighella-5 (Italy). It is known from horn-cores, lower and upper dentitions, a juvenile skull fragment and parts of the skeleton. Its horn-cores have the same morphological characters as *S. crassicornis* and *S. praecursor*, but their distal parts diverge laterally in a smaller degree. They are comparable in dimensions to *S. praecursor*, slightly only larger than the Pikermi *O. rothii* (Annexe: Table 3; Fig. 7), and there is a postcornual fossa. The horn-cores of *S. occidentalis*, however, curve backwards stronger than in *O. rothii* and their section is elliptical close to the base as in *O. rothii* but almost circular upwards (Masini & Thomas 1989: text-fig. 1). Its teeth have the same dimensions as *O. rothii*, and the molars have feeble goat folds. The p3 and p4 have a distinct parastylid and the third valley of p4 remains open for half of its height at least (Masini & Thomas 1989: fig. 3). Kostopoulos & Koufos (1996) argue that the generic attribution of this species to *Samotragus* is doubtful and that it can not be distinguished clearly from "*O.*" *wegneri*. The horn-cores of the Italian species, however, does not show the many keels and longitudinal grooves as "*O.*" *wegneri*, and their backward bending looks stronger (Masini & Thomas 1989: pl. 1, fig. 1b).

Samotragus pilgrimi Azanza, Nieto & Morales, 1998 was described from the middle Miocene (MN 7-8) of Toril-3 in Spain. According to Azanza *et al.* (1998) this species is related to *Samotragus* because the section of its horn-cores narrows abruptly on the upper half, their axis is not as straight as in *Oioceros*, they have an anterior V-shaped extension over the pedicels and their helix is open. Unfortunately, complete horn-cores of this species are not known. Judging from the figured holotype, however, it seems that the horn-core axis does not bend strongly backwards as in *S. crassicornis* or *S. praecursor*, neither does the section narrow abruptly above the mid-height as its large diameter diminishes but slightly (Azanza *et al.* 1998: fig. 1A, B). Moreover, the V-shaped extension of the horn-cores over the pedicels can not be considered a definite character of *Samotragus* since it is present in some of the available *O. rothii* specimens. Concerning their dimensions, they are larger than *S. praecursor*, while their compression index is inside the range of *O. rothii* from Pikermi (Annexe: Table 3; Fig. 7). Thus, the horn-cores of the Spanish species are closer in morphology to *O. rothii* than to *Samotragus*. The braincase of the holotype of *S. pilgrimi* is badly damaged. According to Azanza *et al.* (1998) it has thickened frontal bones contrary to the thin ones of *O. rothii*, and occipital surface almost vertical or slightly inclined forwardly (Azanza *et al.* 1998: fig. 1B). On the contrary in *O. rothii*, *S. crassicornis* and *S. praecursor* the occipital face forms an obtuse angle with the roof of the braincase. From the above it seems that the Toril-3 species cannot be referred to *Oioceros* or *Samotragus* without hesitations.

CONCLUSION

The species *O. rothii* remained poorly known until now because most specimens referred to it were isolated horn-cores and frontlets. Moreover, its skull structure and dentition were unknown.

In the context of the present study the genus *Oioceros* comprises the species *O. rothii* and *O. atropatenes*. The species "*Oioceros*" *wegneri*, originally founded by Andree (1926) on the basis of a skull from Samos, is proposed here to be excluded from the genus *Oioceros*. "*O.*" *wegneri* differs significantly from *O. rothii* and *O. atropatenes* on its skull characters, as the longer face, the shorter and strongly bent braincase, the more posterior insertion of the horn-cores, the strongly raised frontals above the supraorbital margins, and the presence of a crest on the frontals anterior to the horn-core bases that extends anteriorly between the supraorbital foramina. *Oioceros* is closely related to *Samotragus*, a genus that includes the species *S. crassicornis*, *S. praecursor* and *S. occidentalis*. The generic determination of "*S.*" *pilgrimi* from the middle Miocene of Toril-3 in Spain, originally attributed to *Samotragus* by Azanza *et al.* (1998), is debatable.

Gaudry (1865), referring *O. rothii* to the genus *Antidorcas*, supposed relationships with the Antilopini. Gaillard (1902; *fide* Bouvrain & Bonis 1985), however, attributed the Pikermi species to the new genus *Oioceros*, implying relationships to *Ovis*, and the Caprinae. Gaillard is followed in this view by many authors as Gentry (1970). Later, Solounias (1981) classified *Oioceros* in the Antilopini, and Bouvrain & Bonis (1985) in the Antilopinae and the tribe Oiocerini. Gentry (1970) listed numerous characters on which *Oioceros* is similar to the Caprinae. It is not necessary to comment these characters here, since they are discussed by Bouvrain & Bonis (1985). It is useful to mention, however, that the *Oioceros* characters used by Gentry (1970), as well as the diagnosis of this genus given by the same author, were based mainly on "*Oioceros*" *tanyceras*, "*O.*" *grangeri* and "*O.*" *noverca*, species subsequently removed from *Oioceros*. Moreover, some of the Caprinae characters stated by Gentry (1970), as the hollow horn-cores, the shortened braincase, the pronounced bending down of the braincase, the narrowing of the braincase towards the rear and the raising of the frontals between the horn-cores are absent from *Oioceros* as defined here. Some other characters mentioned by Gentry (1970), as the premolar to molar ratio and the presence or not of goat folds are more variable and can reflect dietary adaptations. Later, Gentry (2000; Gentry pers. comm.) grouped *Oioceros* and *Urmiatherium* Rodler, 1889 under the heading "Tribe Antilopini or ?Oiocerini".

The present skull of *O. rothii* shows that the external auditory meatus directs postero-dorsally as in *Gazella* (Bouvrain & Bonis 1988), and the post-tympanic process directs anteriorly and ventrally, and passes under the external auditory meatus as in the Antilopini (Bouvrain & Bonis 1985). Following Bouvrain & Bonis (1985), the genera *Oioceros*, *Samotragus* and *Samodorcas* constitute the tribe Oiocerini inside the subfamily Antilopinae.

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ANNEXE

TABLE 1. — Skull measurements (in mm) of *Oioceros rothii* (Wagner, 1857) from Pikermi (PG 95/1502a).

Braincase width behind the horn cores	53.8
Greatest braincase width	56.1
Width at the mastoids	60.5
Width, anterior tuberosities of the basioccipital	21.5
Width, posterior tuberosities of the basioccipital	25.6
Width at the occipital condyles	41.7
Supraorbital foramens-external occipital tuberosity	87.3
P2-intercondylar notch	128.3
Length of the interfrontal suture	*c*. 60.0
Length, frontonasal-occipitoparietal suture	*c*. 89.0
Length, frontonasal suture-external occipital tuberosity	*c*. 106.0
Length, parietofrontal-occipitoparietal suture	36.1
Length, parietofrontal suture-external occipital tuberosity	56.0
Highest point of nuchal crest-highest foramen magnum	29.3
Highest point of nuchal crest-lower foramen magnum	43.5
Highest point of nuchal crest-occipital condyles	45.6

TABLE 2. — Horn-core dimensions (in mm) of *Oioceros rothii* (Wagner, 1857) from Pikermi, Thessaloniki and Maragha. Abbreviations: **DAP**, anteroposterior diameter; **DT**, mediolateral diameter; inaccurate measurements in parentheses.

	DAP		**DT**		**DT × 100/DAP**	
	sin.	**dext.**	**sin.**	**dext.**	**sin.**	**dext.**
PA 909/91, Pikermi	-	30.0	-	24.0	-	80.0
PA 1412/91, Pikermi	27.7	28.6	22.1	22.6	79.8	79.0
PA 3553/91, Pikermi	-	26.0	-	18.9	-	72.7
PG 95/1502a, Pikermi	-	(32.0)	26.5	24.2	-	(75.6)
PG 95/1509, Pikermi	26.1	27.4	19.1	20.0	73.2	73.0
PG 95/1510, Pikermi	27.3	26.2	20.1	20.0	73.2	76.3
PG 95/1514, Pikermi	26.6	25.5	18.9	19.0	71.1	74.5
PG 88/1540, Pikermi	26.7	-	20.2	-	75.7	-
PG 88/1583, Pikermi	-	26.2	-	21.8	-	83.2
MNHN PIK. 2244, Pikermi	25.2	24.4	20.4	19.1	80.9	78.3
MNHN PIK. 2246, Pikermi	26.7	25.5	20.6	19.4	77.2	76.1
MNHN PIK. 2247, Pikermi	24.2	-	19.8	-	81.8	-
MNHN PIK. 2249, Pikermi	31.8	31.8	25.5	24.1	80.2	75.8
NHML M 11461, Pikermi	29.3	28.5	20.4	21.3	69.6	74.7
MNHN SLQ. 794, Vathylakkos	25.1	24.7	19.5	20.2	77.7	81.8
MNHN MAR. 1320, Maragha	30.0	30.0	22.6	-	75.3	-

TABLE 3. — Horn-core dimensions (in mm) of various inverse spiralled antelopes. Abbreviations: **DAP**, anteroposterior diameter; **DT**, mediolateral diameter.

	DAP	DT	DT × 100/DAP
Oioceros rothii, Pikermi (AMPG, MNHN, NHML)	24.2-32.0 (n = 21)	18.9-26.5 (n = 22)	69.6-83.2 (n = 21)
O. rothii, Maragha, site III (Watabe 1990)	18.8-29.4 (n = 10)	17.5-29.7 (n = 10)	78.9-118.5 (n = 10)
O. rothii, Çorak Yerler (Köhler 1987)	23.5-34.0 (n = 7)	15.2-25.3 (n = 7)	64.7-78.3 (n = 7)
O. atropatenes, Maragha (Heintz 1963; males & females included)	16.0-24.0 (n = 33)	14.0-21.0 (n = 33)	-
O. cf. *atropatenes*, Nikiti-1 (Kostopoulos & Koufos 1996)	20.7-23.4 (n = 3)	19.4-21.5 (n = 3)	91.9-102.9 (n = 3)
"*Oioceros*" *wegneri*, Samos (Solounias 1981)	44.7-50.0 (n = 2)	47.8-50.5 (n = 2)	-
"*Oioceros*" *wegneri*, Eski Bayirköy (Köhler 1987)	42.5 (n = 1)	(45.0)-45.1 (n = 2)	106.1 (n = 1)
Samotragus crassicornis, Samos (Solounias 1981)	66.4-73.0 (n = 3)	57.0-60.1 (n = 3)	-
S. praecursor, Ravin de la Pluie (Masini & Thomas 1989)	30.3-40.0 (n = 7)	25.4-34.5 (n = 7)	82.5-104.8 (n = 7)
S. occidentalis, Brisighella-5 (Masini & Thomas 1989)	33.0 (n = 1)	25.0 (n = 1)	75.8 (n = 1)
"*Samotragus*" *pilgrimi*, Toril-3 (Azanza *et al*. 1998)	43.1 (n = 1)	34.2 (n = 1)	79.4 (n = 1)

TABLE 4. — Upper teeth measurements (in mm) of *Oioceros rothii* (Wagner, 1857) from Pikermi. Abbreviations: **L**, length; **W**, width; inaccurate measurements in parentheses.

	PG 95/1502a, sin.	PG 95/1502a, dext.	PA 3509/91
(L × W) P2	-	10.0 × 7.8	9.1 × 7.5
(L × W) P3	9.4 × 9.7	9.1 × (9.5)	9.0 × 8.7
(L × W) P4	7.7 × 9.5	-	7.6 × 9.5
(L × W) M1	(10.2) × -	10.4 × 10.6	(10.7) × -
(L × W) M2	(13.4) × -	12.8 × 12.1	12.8 × 11.4
(L × W) M3	(12.8) × -	12.9 × 11.5	-
LP2-P4	-	(27.5)	26.2
LP3-P4	16.8	-	16.8
LM1-M3	35.0	(35.1)	-
LP2-M3	-	61.8	-
LP3-M3	50.9	51.1	-
(LP2-P4/LM1-M3) × 100	-	(78.3)	-
(LP3-P4/LM1-M3) × 100	48.0	-	-
(LP2/LP2-P4) × 100	-	(36.4)	34.7

TABLE 5. — Lower teeth measurements (in mm) of *Oioceros rothii* (Wagner, 1857) from Pikermi, compared to various lower dentitions from Thessaloniki and Maragha. Abbreviations: **H**, height; **L**, length; **W**, width; inaccurate measurements in parentheses.

	O. rothii		***O. rothii***	**"*O. rothii*"**		**"*Helicophora rotundicornis*"**	
	PG 95/1502b-c Pikermi		**PA 3519/91** Pikermi	**SLQ. 1035** Thessaloniki	**MAR. 8031** Maragha	**MAR. 1829** Maragha	**SLQ. 793** Thessaloniki
(L × W) p2	-	-	-	5.6 × 3.3	5.7 × 3.7	5.7 × 3.8	4.8 × 3.4
(L × W) p3	-	-	7.9 × 5.2	8.2 × 4.3	8.2 × 5.0	9.0 × 5.6	8.4 × 4.5
(L × W) p4	9.0 × 5.9	9.4 × 6.0	8.4 × 5.2	8.7 × 4.8	-	10.0 × 6.2	8.4 × 5.1
(L × W) m1	10.6 × 7.3	10.1 × 7.4	10.0 × 6.9	(9.7) × 7.9	10.7 × 8.1	9.8 × 6.5	9.4 × 6.5
(L × W) m2	12.1 × 7.7	12.5 × 7.7	12.2 × 6.9	11.8 × 8.8	13.1 × 9.5	12.6 × 7.5	12.0 × 6.6
(L × W) m3	16.8 × 7.4	16.4 × 7.5	16.0 × 6.3	18.0 × 8.8	17.0 × -	16.8 × 7.2	17.0 × 6.6
Lp2-p4	*c.* 23.0	-	*c.* 21.5	21.8	19.2	23.6	20.5
Lp3-p4	-	-	16.0	17.0	13.7	18.7	15.6
Lm1-m3	38.5	38.8	37.2	40.8	40.5	39.4	38.0
Lp2-m3	*c.* 61.0	-	*c.* 58.0	62.6	59.8	62.0	57.7
Lp3-m3	-	-	52.7	57.7	54.1	56.7	53.0
(Lp2-p4/ Lm1-m3) × 100	(59.7)	-	(57.8)	53.4	47.4	59.9	53.9
(Lp3-p4/ Lm1-m3) × 100	-	-	43.0	41.7	33.8	47.5	41.0
Hm3	20.4	(20.5)	19.6	(18.6)	-	20.2	17.7