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Taxonomic re-assessment and phylogenetic relationships of Miocene homonymously spiral-horned antelopes

DIMITRIS S. KOSTOPOULOS



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A morphological reappraisal of Middle Miocene and Early Pliocene antelopes with homonymously twisted horncores (i.e., with the left horncore twisted clockwise from the base up) and an additional re-description of some critical Greek specimens allows a revision of the current taxonomy at the species and genus level. A parsimony analysis recognizes *Hispanodorcas*, *Oioceros*, *Samodorcas*, *Samotragus*, *Paraoioceros*, and *Urmiatherium* as distinct lineages of the subtribe Oiocerina. The latter emerged during the Astaracian (ca. 14–11.5 Ma), and radiated in Eurasia during the mid–late Vallesian (ca. 10–9 Ma), resulting in a great variety of genera with unique combinations of morpho-ecological adaptations. The suprageneric relationships of Oiocerina are poorly understood, but their closest ancestors possibly lie within or close to the Middle Miocene "hypsodontines", and inside Antilopinae.

Key words: Mammalia, Bovidae, Oiocerina, systematics, phylogeny, zoogeography, ecology, Miocene, Greece.

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Introduction

Bovids are unique among mammals in having horns, i.e., permanent bony horncores covered by keratinous sheaths, which are never shed (Janis and Scott 1987; Davis et al. 2011). Studies on extant bovids imply that horn morphology is an extremely plastic character weakly linked to the environment, but strongly correlated with body size and intraspecific behavior (Geist 1966; Jarman 1974; Lundrigan 1996; Caro et al. 2003). Nontheless, the impact of phylogeny on the morphology of the horns cannot be ruled out completely, as particular living and fossil bovid tribes or suprageneric assemblages exhibit diagnostically stable horn shapes (e.g., tragocerines, gazelles, Cephalophini, Tragelaphini, Hippotragini).

One of the most striking horn features of both living and fossil bovids is twisting (including torsion and/or spiraling; see methodology), developed in either homonymous (i.e., with the left horncore twisted clockwise from the base up as in sheep) or heteronymous (i.e., with the left horncore twisted anticlockwise from the base up as in impala) form. The functional or phylogenetic significance of twisting has yet to be explained, though Köhler (1993) suggested that it does not play any role in fighting style. Heteronymous twisting appears to be a highly convergent character occurring repeatedly in nine out of thirteen living bovid tribes (or in 34% of extant bovid species). By contrast, bovid species with homonymously twisted horns only constitute about 13% of the living record, but are the rule in Alcelaphini, Caprini, and some Bovini, all of which display ramming as their predominant fighting behavior (Lundrigan 1996). Outside these three tribes, the presence of homonymous twisting is rather randomly distributed. While most Reduncini show no or weak heteronymous twisting, the Plio-Pleistocene African genus *Menelikia* Arambourg, 1941 exhibits horncores with homonymous spiraling, along with some other skull features resembling Alcelaphini. Similarly, homonymous twisting is usually absent in extant species of Antilopini, though it may be seen in the springbok and its forerunners, and exceptionally in some individuals of living gazelles.

In the Eurasian Neogene, homonymous twisting is frequently seen in taxa clustering with *Hypsodontus* Sokolov, 1949, *Urmiatherium* Rodler, 1889, and *Oioceros* Gaillard, 1902, with each of these representing an "archetype" of a particular taxonomic assemblage (here referred to as "hypsodontines", "urmiatheriines", and "oiocerines", respectively) of unclear phylogenetic affinities (see discussions in Köhler 1987; Gentry and Heizmann 1996; Gentry et al. 1999; Chen and Zhang 2004, 2009; Dmitrieva 2007; Gentry 2010). As currently understood, "oiocerines" (Oiocerini Pilgrim, 1934 sensu Bouvrain and Bonis 1985) are characterized by homonymously twisted horncores with keels or grooves (Bouvrain and Bonis 1985; Azanza et al. 1998). However, this set of

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characters is not exclusive to this group, raising doubts regarding both its monophyly and its taxonomic composition. "Oiocerines" presently comprise eight small to medium-sized antilopine-like species allocated to the three extant Eurasian genera *Oioceros*, *Samotragus* Sickenberg, 1936, and *Samodorcas* Bouvrain and Bonis, 1985, spanning the Late Miocene to Early Pliocene. However, the systematics of this group remain uncertain, with *Oioceros* and *Samotragus* sometimes considered synonyms (e.g., Gentry and Heizmann 1996; Gentry et al. 1999), and the generic attribution of *Oioceros wegneri* Andrée, 1926, *Samotragus pilgrimi* Azanza, Nieto, and Morales, 1998, and *Samotragus occidentalis* Masini and Thomas, 1989 still open to discussion (e.g., Kostopoulos and Koufos 1996; Gentry and Heizmann 1996; Roussiakis 2003). Furthermore, re-examination of the fossil record allows the recognition of more bovid taxa as potential "oiocerines". In particular, *Hispanodorcas* Thomas, Morales, and Heintz, 1982, and the scarcely known *Paraoioceros* Meladze, 1985 may provide further insights into the phylogenetic history of this group. Finally, the relationships of "oiocerines" with "urmiatheriines", and "hypsodontines" still have to be assessed, along with the possible phylogenetic links between them and the extant bovid tribes.

This paper provides an in-depth systematic revision of all the above-mentioned genera and species, as well as redescriptions of some critical Greek material and a discussion of the phylogenetic relationships, monophyly, and origin of "oiocerines" based on morphological, ecological, and zoogeographic criteria.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; AMPG, Athens Museum of Paleontology and Geology, Greece; BSPM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; CSIC, Museo Nacional de Ciencias Naturales Madrid, Spain; EMUU, Evolutions Museet Uppsala Universitet, Sweden; GNMT, Georgian National Museum, Tbilisi, Georgia; IPPS, Instituto Provincial de Paleontologia Sabadell, Barcelona, Spain; LGPUT, Laboratory of Geology and Paleontology of Thessaloniki University, Greece; MCSNF, Museo Civico di Scienze Naturali di Faenza, Italy; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMI, Natural History Museum of Ege University Izmir, Turkey; NHMUK, the Natural History Museum of London, UK; NHMW, Naturhistorisches Museum Wien, Austria; PIM, Institut für Geologie und Paläontologie Universität Münster, Germany; SMF, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Germany.

Other abbreviations.—APD, anteroposterior basal diameters; HCC, crown Caprini with homonymously twisted horncores; MMTT, Maragheh (Iran) fossil collection of Lake Rezaiyeh Expedition, deposited either in Tehran or in Washington, DC; MN, European land mammal Neogene zones; NKT, Nikiti-1; RPl, Ravin de la Pluie; RZ1, Ravin de Zouaves 1; TD, transverse basal diameters.

Material and methods

The crania of living bovids referred to in this study were from the NHMUK and the "Anatomie Comparée" collection of the MNHN, with further information taken from "Walker's Mammals of the World" (Nowak 1999). The morphological terminology for horncores and crania follows Bouvrain and Bonis (1985, 1988), Gentry (1992) and Kostopoulos (2006, 2009), while the dental terminology follows Heintz (1970). Horncore measurements included transverse (TD) and anteroposterior (APD) basal diameters. Twisted horncores were separated into torsioned (i.e., exhibiting a "screw" type of twisting) and spiraled (i.e., helicoidally twisted), as both ontogenetic and paleontological data seem to indicate that torsion predates true spiraling in an evolutionary sense (personal observation). Emended generic diagnoses were divided into plesiomorphic and apomorphic traits. The phylogenetic relationships among the genera discussed in this paper were investigated using a parsimony analysis including 13 taxa and 60 horncore, cranial and dental morphological characters (Appendix 1), 29 of which were adopted from Gentry (1992). The analysis was carried out using the branch and bound algorithm and Fitch optimization criterion implemented in the free software PAST v. 2.12 (Hammer et al. 2001), with *Eotragus* Pilgrim, 1939, considered the most archaic member of the family (Solounias and Moelleken 1992; Gentry et al. 1999; Bibi et al. 2009), used as outgroup.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Subfamily Antilopinae Gray, 1821 (sensu Kingdon, 1982)

Subtribe Oiocerina Pilgrim, 1934

Diagnosis.—Small to medium sized bovids with homonymously twisted horncores inserted above the orbits and occasionally extended over the short or absent pedicles; well-developed lateral notch present on the crown of the cornual process (i.e., the pedicle–horncore contact), and continuous with a basolateral sulcus on the horncore variously dividing the lateral surface of the latter into an anterior and a posterior portion; horncores parallel to subparallel in their proximal part, and moderately to strongly divergent distally; postcornual groove positioned laterally or absent; supraorbital foramina located within pits; temporal ridges reduced or absent; basioccipital relatively short and usually bearing a medial groove, as well as closely spaced anterior tuberosities.

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Genus *Hispanodorcas* Thomas, Morales, and Heintz, 1982

Type species: *Hispanodorcas torrubiae* Thomas, Morales, and Heintz, 1982; see below.

Emended diagnosis (modified from Thomas et al. 1982; Bouvrain and Bonis 1988).—Plesiomorphic traits: small-sized bovids with short, thin, and gradually tapering horncores; horncores inserted above the orbits, weakly inclined posteriorly with a straight or gently curved posterior edge, and situated relatively far apart on the frontals; frontals without sinuses and not raised above the level of the orbits; basioccipital narrowing anteriorly. Apomorphic traits: weakly developed homonymous twisting (1/2 coil) of the horncores; anterior keel poorly developed; horncores more strongly divergent distally than proximally, and bearing a variably wide and shallow lateral depression (i.e., a broad sulcus) dividing them into a smaller anterior and a larger posterior portion; horncores transversely compressed at the base (compression index 70–85%; Fig. 1), with a flattened lateral surface and a strongly convex medial surface; frontals moderately thick anterior to the horncores, and moderately to strongly flexed in lateral profile; pedicles very short; postcornual fossae situated laterally; small to moderately-sized supraorbital foramina located within pits; basioccipital with a variably developed medial groove.

Remarks.—*Hispanodorcas* is presently known from three species ranging from the middle Turolian to the early Ruscinian (MN12–MN14) (Thomas et al. 1982; Bouvrain and Bonis 1988; Alcalá and Morales 2006). Gentry et al. (1999) furthermore suggested that several Ukrainian specimens of early Turolian age usually referred to "*Gazella*" *rodleri* Pilgrim and Hopwood, 1928 might be allocated to *Hispanodorcas* (but see discussions in Bouvrain and Bonis 1988; Kostopoulos and Bernor 2011), whereas Kostopoulos (2006: 148) indicated that some bovid material from the latest Vallesian locality of Nikiti-1 (Greece), previously ascribed to *Oioceros* (Kostopoulos and Koufos 1996), may in fact represent *Hispanodorcas*.

A character frequently used for defining *Hispanodorcas* is the presence of a lateral longitudinal groove on the horncore extending on to the pedicle and reaching the postcornual fossa. This feature, originally described by Thomas et al. (1982), became part of the emended generic diagnosis provided by Bouvrain and Bonis (1988). Although this groove is well marked on both the holotype of *H. torrubiae* (Thomas et al. 1982: fig. 1, pl. 1: 1), and the left horncore of the holotype of *H. orientalis* (Bouvrain and Bonis 1988: fig. 2), it is much less evident in some of the paratypes of *H. torrubiae* (Thomas et al. 1982: pl. 1: 2), and almost absent in *H. heintzi* (Alcalá and Morales 2006) and the material from Nikiti-1 described here. Furthermore, the same feature is also present in some specimens of *Oioceros atropatenes* (Rodler and Weithofer, 1890), as well as in the holotype of *Samotragus occidentalis* Masini and Thomas, 1989, thus indicating that this groove may not be diagnostic at the genus level. However, all known specimens of *Hispanodorcas* show a rather characteristic flattening on the lateral surface of the horncores. In most cases, this flattening appears as a wide and shallow depression (Fig. 2A) with a blunt anterior and a more pronounced posterior edge, with the latter forming a faint crest. In *H. torrubiae* and *H. orientalis* at least, this depression develops distally into a rather deep furrow (Fig. 2B).

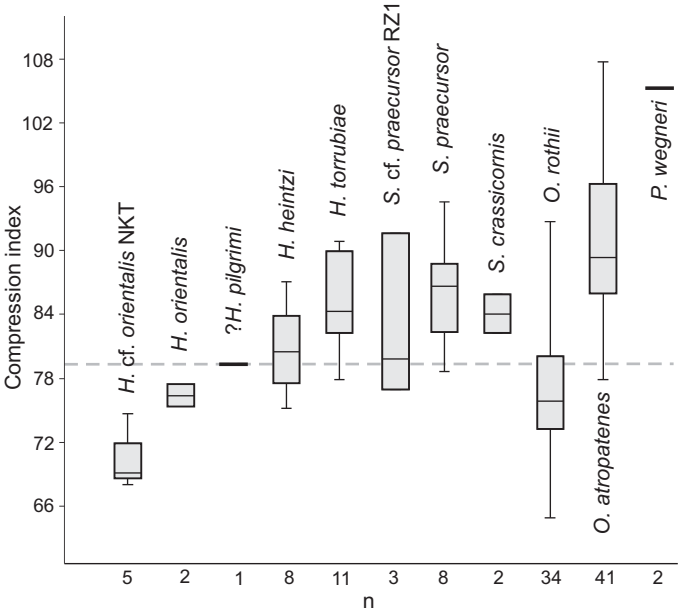


Fig. 1. Box-plots of the horncore basal compression index (i.e., TD*100/ADP) for several species and genera of Oiocerina, showing the medial (horizontal line inside the boxes), the 25–75% quartiles (gray boxes) and the minimum and maximum range of values (short horizontal lines). NKT-1, Nikiti-1; RZ1, Ravin des Zouaves 1.

Hispanodorcas torrubiae Thomas, Morales, and Heintz, 1982

Holotype: Isolated left horncore, IPPS-CC20502 (Thomas et al. 1982: fig. 1).

Type locality: Concud-Cerro de la Garita, Teruel Basin, Spain.

Type horizon: Late middle Turolian (MN12; ca. 6.9 Ma), Late Miocene.

Diagnosis.—As in Thomas et al. (1982).

Differential diagnosis.—*H. torrubiae* differs from other members of the genus in its longer horncores, with the latter being more evenly divergent from the bases upwards, lacking an anterior keel, and occasionally showing weak transverse ridges.

Remarks.—This species is known only from its horncore. In addition to the type locality, it has also been reported from the contemporaneous Spanish locality of Los Mansuetos, which yielded a single horncore (Thomas et al. 1982). Some teeth and postcranials from Crevillente 15–16, Spain, described as cf. *Hispanodorcas* (Montoya and Alberdi 1995), may also belong to this taxon, though the lack of horncores prevents any direct comparisons.

Geographic and stratigraphic range.—Middle to late Turolian (Late Miocene) of Spain.

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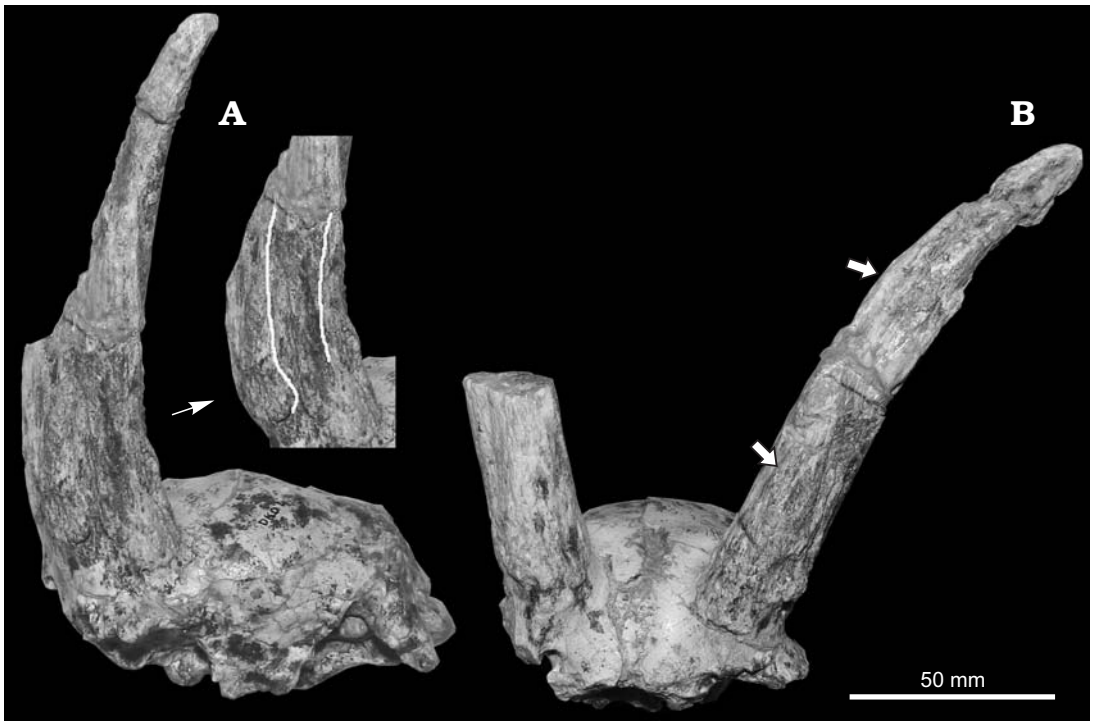


Fig. 2. Oiocerin antelope *Hispanodorcas orientalis* Bouvrain and Bonis, 1988, from the late Turolian locality of Dytiko-3 (DKO), Axios Valley, Northern Greece, in lateral (**A**) and anterior (**B**) views of the holotype cranium LGPUT DKO-4. The arrow in A indicates an enlarged version of the same view, where the white lines indicate the extent of the lateral depression; the arrows in B mark the trace of the anterior keel.

Hispanodorcas orientalis Bouvrain and Bonis, 1988

Fig. 2.

Holotype: partial skull with horncores and associated parts of maxillae and mandible, LGPUT DKO-4 (Fig. 2; Bouvrain and Bonis 1988: figs. 1, 2).

Type locality: Dytiko-3, Axios Valley, Greece.

Type horizon: Late Turolian (MN13; Koufos 2006), Late Miocene.

Diagnosis.—As in Bouvrain and Bonis (1988).

Differential diagnosis.—*H. orientalis* differs from other members of the genus in its slightly smaller size, as well as its more transversely compressed and more strongly distally diverging horncores, with the latter bearing a blunt anterior keel (Fig. 2). It additionally differs from *H. torrubiae* in having shorter horncores without transverse ridges.

Remarks.—Contrary to Bouvrain and Bonis (1988), I suggest that the anterior surface of the horncore of *H. orientalis* is marked by a moderately developed, proximally blunt and anteromedially descending keel (Fig. 2B). The lateral groove on the horncore of *H. orientalis* is much less developed than in the holotype of *H. torrubiae*, appearing only on the proximal third of the horncore as part of the characteristic shallow depression developed along the entire anterolateral surface (Bouvrain and Bonis 1988: figs. 1, 2; Fig. 2A). The upper third of the posterior surface of the horncore of *H. orientalis* shows a rather deep, longitudinal furrow with sharp, keel-like edges, similar to the condition seen in *H. torrubiae* (Thomas et al. 1982: 214).

Geographic and stratigraphic range.—Late Turolian (Late Miocene) of Greece.

Hispanodorcas cf. *orientalis* Bouvrain and Bonis, 1988

Fig. 3.

1996 *Oioceros* cf. *atropatenes* (partim); Kostopoulos and Koufos 1996: 279, pl. 4.

1996 ?*Gazella* sp.; Kostopoulos and Koufos1996: 278, pl. 3: e, f.

Material.—Partial braincase with left horncore, LGPUT NKT-227; frontlet, LGPUT NKT-118, 228; proximal part of right horncore, LGPUT NKT-231; distal part of left horncore, LGPUT NKT-232; part of left mandibular ramus with p3–m3, LGPUT NKT-250. All specimens are from the primate-bearing locality of Nikiti-1, located in the upper part of the Nikiti Formation (Vallesian, MN10; Koufos 2006) exposed on the Chalkidiki Peninsula, northern Greece (Koufos et al. 1991).

Description.—The width of the braincase (LGPUT NKT-227; Fig. 3B) behind the horncores is 57.6 mm, very similar to that of the holotype of *H. orientalis* (56.9 mm). The frontals are strongly flexed between the horncores (Fig. 3B), indicating either that the face was significantly inclined compared to the braincase (but less so than in *H. orientalis*; Bouvrain and Bonis 1988: 101), or that the area between the nasals and the pedicles was strongly depressed, as also seen in *Oioceros* (e.g., Roussiakis 2003). The postcornual fossa of the Nikiti-1 taxon varies in size and is positioned laterally, as in *H. orientalis*. The homonymously twisted horncores are inserted above

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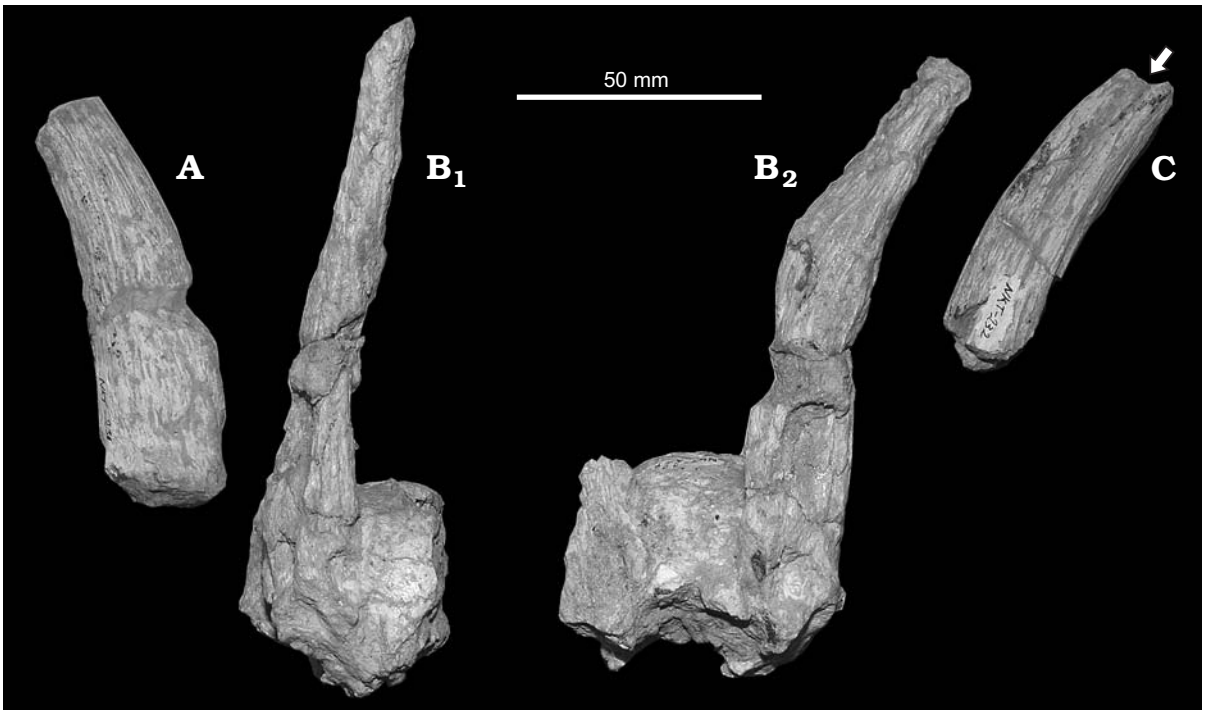


Fig. 3. Oiocerin antelope *Hispanodorcas* cf. *orientalis* Bouvrain and Bonis, 1988 from Nikiti-1 (NKT), Chalkidiki Peninsula, Northern Greece, latest Vallesian. **A**. LGPUT NKT-231, lateral view of the right basal horncore. **B**. LGPUT NKT-227, left lateral (B_1) and anterior (B_2) views of the frontlet. **C**. LGPUT NKT-232, lateral view of the left distal horncore. The arrow indicates the distal end of the lateral depression and marks the distal "bilobation" of the lateral side of the horncore.

the orbits, located far apart from each other, weakly inclined, and curved backwards (Fig. 3B). While being almost parallel at the base, they are strongly divergent distally. In cross section, the horncore is elliptical to semicircular in outline, and strongly compressed transversely (Fig. 1), with the greater basal axis forming a moderately large angle with the sagittal plane. The medial surface of the proximal horncore is strongly convex, whereas the lateral surface is flattened, but barely depressed (Fig. 3A). However, towards the tip, the flattened lateral surface gives rise to a deep furrow dividing the horncore into a thin and long anterior and a wide and short posterior part (LGPUT NKT-232; Fig. 3C). A narrow groove opening towards (but not extending on to) the pedicle is present on the proximal lateral surface of some specimens (LGPUT NKT-118, 228). A moderately developed, anteromedially descending anterior keel occurs in LGPUT NKT-231 and 227, while a deep posterior furrow appears in LGPUT NKT-232, thus resembling both *H. torrubiae* and *H. orientalis*.

The length of the lower molar row is 34.3 mm. The lower molars lack goat folds, and a strong parastylid and well-defined metastylid occur on m2 and m3. The ribs of the metaconid and the entoconid are well developed lingually. A basal pillar is present only on m1. On p4, the parastylid is weakly separated from the paraconid, while the metaconid curves distally and fuses with the posterior stylid (entoconid + entostylid). On p3, the metaconid is directed posteriorly, but otherwise p3 is similar to p4.

Remarks.—Kostopoulos and Koufos (1996) mistakenly referred the material from Nikiti-1 to ?*Gazella* sp. or *Oioceros* cf. *atropatenes*. It is now evident that the specimens from Nikiti-1 represent *Hispanodorcas*, even though some additional dental material from the same site (LGPUT NKT229, 230, 102; Kostopoulos and Koufos 1996: 29) belongs to another, slightly larger, as yet unidentified bovid. Apart from some minor morphological differences, which may be attributed to its older age, the Nikiti-1 specimen of *Hispanodorcas* is strikingly similar to *H. orientalis* from Dytiko-3.

Hispanodorcas heintzi Alcalá and Morales, 2006

Holotype: Frontlet, CSIC LCA-81-234 (Alcalá and Morales 2006: fig. 1, pl. 1: 1).

Type locality: La Calera, Teruel Basin, Spain.

Type horizon: Early Pliocene (MN14).

Diagnosis.—As in Alcalá and Morales (2006).

Differential diagnosis.—*H. heintzi* differs from other members of the genus in having horncores which are strongly divergent from the base, bear an anterior, and occasionally a posterior, keel, and are characterized by a reduced lateral depression in form of a weak, longitudinal groove.

Geographic and stratigraphic range.—Early Ruscinian (Early Pliocene) of Spain.

?*Hispanodorcas pilgrimi* (Azanza, Nieto, and Morales, 1998)

1998 *Samotragus pilgrimi*; Azanza et al. 1998: 378, fig. 1.

Holotype: Partial skull with frontals, CSIC MNCN/TO3-1000 (Azanza et al. 1998: fig. 1).

Type locality: Toril 3, Catalayud-Teruel Basin, Spain.

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Type horizon: Late Middle Miocene (MN7/8).

Emended diagnosis.—Medium-sized species with rather thick, homonymously twisted horncores; horncores moderately compressed transversely (Fig. 1), weakly torsioned, gently curved and inclined posteriorly, elliptical in cross section, and bearing a wide lateral depression; frontals low; braincase long and deep; basioccipital narrow, and bearing a medial groove.

Remarks.—Azanza et al. (1998) assigned the Toril 3 taxon to *Samotragus* based on (i) the open helical spiraling of the horncores, with an abrupt narrowing of the cross section in their upper half, (ii) the backward curvature of the horncore axes, and (iii) the V-shaped anterior extension of the horncores over the pedicles. Roussiakis (2003) already noted that characters (i) and (ii) were misinterpreted in the Toril 3 species, whereas character (iii) is occasionally present in species of other genera (e.g., *Oioceros* and *Hispanodorcas*) and therefore not uniquely indicative of *Samotragus*.

Although the braincase of the holotype is strongly deformed, several features mentioned by Azanza et al. (1998), or observed directly on the illustrated material and some pictures kindly provided by the authors, clearly separate the Toril 3 species from *Samotragus*. The latter include a rather simple and barely pinched interfrontal suture; moderately protruding orbital margins; frontals not raised above the orbital level; a narrow basioccipital with a medial groove; weakly torsioned horncores spaced far apart on the frontals, inserted above the orbits, weakly inclined posteriorly, and faintly curved laterally in their preserved distal part; the absence of a well-delimited lateral furrow on the horncores, but presence of a depression on their lateral surface; an elliptical cross section throughout the length of the horncore, with the greater axis oriented anteroposteriorly at the base and transversely along the preserved distal portion; an almost straight posterior edge of the horncores in lateral profile; and horncores with strong posterior and lateral basal relief.

This set of characters, and especially the wide, shallow and gently concave depression deepening upwards on the lateral surface of the horncores, clearly resembles *Hispanodorcas*. However, the Toril 3 taxon differs from other species included in this genus in its probably shorter and thicker horncores (about 40% larger in absolute basal dimensions than the largest known specimen of *Hispanodorcas*), a less inclined face compared to the braincase, a rather deep braincase (instead of shallow as in *H. orientalis*) and a groove running all along the basioccipital (instead of being restricted to its anterior portion as in *H. orientalis*). Nevertheless, it seems that, out of the Late Miocene genera with homonymously twisted horncores, *Hispanodorcas* provides a better fit for the Toril 3 species than *Samotragus*. At the same time, similarities of the Toril 3 species with earlier bovids showing homonymous twisting are much less evident.

Geographic and stratigraphic range.—Astaracian (Middle Miocene) of Spain.

Genus *Samodorcas* Bouvrain and Bonis, 1985

Type species: *Samodorcas kuhlmanni* (Andrée, 1926); see below.

Diagnosis.—As for the type and only species.

Remarks.—The debatable generic affiliations of *Ovis kuhlmanni* Andrée, 1926 (e.g., Pilgrim 1934; Solounias 1981) were thoroughly discussed by Bouvrain and Bonis (1985: 287), who proposed a new genus for this taxon.

Samodorcas kuhlmanni (Andrée, 1926)

Holotype: Partial skull, PIM 142 (Andrée 1926: pls. 13: 5, 15: 11).

Type locality: Samos, Greece (unknown level).

Type horizon: Most likely Turolian, Late Miocene.

Emended diagnosis.—Plesiomorphic traits: face short and shallow; lacrimal fossa large, round and moderately deep; ethmoidal fissure present; infraorbital foramina located above the level of P2; postcornual fossae present. Apomorphic traits: medium size; face rather strongly inclined compared to the braincase; frontals moderately elevated between the horncores; opisthocranium short; postcornual fossae large and shallow, and situated laterally; supraorbital foramina located in deep, large, and closely spaced depressions; horncores long, homonymously twisted, closely spaced, strongly posteriorly inclined, and inserted at the posterior part of the dorsal margins of the orbits; horncores anteroporteriorly compressed at the base and bearing a strong anteromedial keel proximally, as well as a strong posterolateral keel on their distal portion; anterior surface of distal part of horncores bearing a wide and shallow depression that continues proximally as a moderately deep furrow with sharp edges; premolars short compared to molars; upper molars with central islets; lower molars with basal pillars.

Remarks.—This extremely rare bovid species, known only from its holotype and some uncertainly assigned dental material (Solounias 1981: 167), shows a combination of advanced and primitive features. The position of the postcornual fossae, the degree of homonymous torsion, and the strong horncore compression (here, however, anteroposterior), as well as the presence of a medial keel developed along the proximal portion of the horncores and the wide and shallow depression along their anterior surfaces (Andrée 1926: pl. 13: 5) resemble *Hispanodorcas*.

Geographic and stratigraphic range.—Turolian (Late Miocene) of Greece.

Genus *Samotragus* Sickenberg, 1936

Type species: *Samotragus crassicornis* Sickenberg, 1936; see below.

Emended diagnosis (modified from Bouvrain and Bonis 1985).—Plesiomorphic traits: Small to medium-sized bovids with short horncores inserted above the orbits; horncores with a convex lateral surface, elliptical to sub-rounded in cross section (compression index: 79–97%; Fig. 1); braincase moderately long, with parallel sides. Apomorphic traits: horncores robust, homonymously twisted (1 coil), closely spiraled, abruptly tapering, and situated relatively close to each other on the frontals; horncores moderately to strongly curved posteri-

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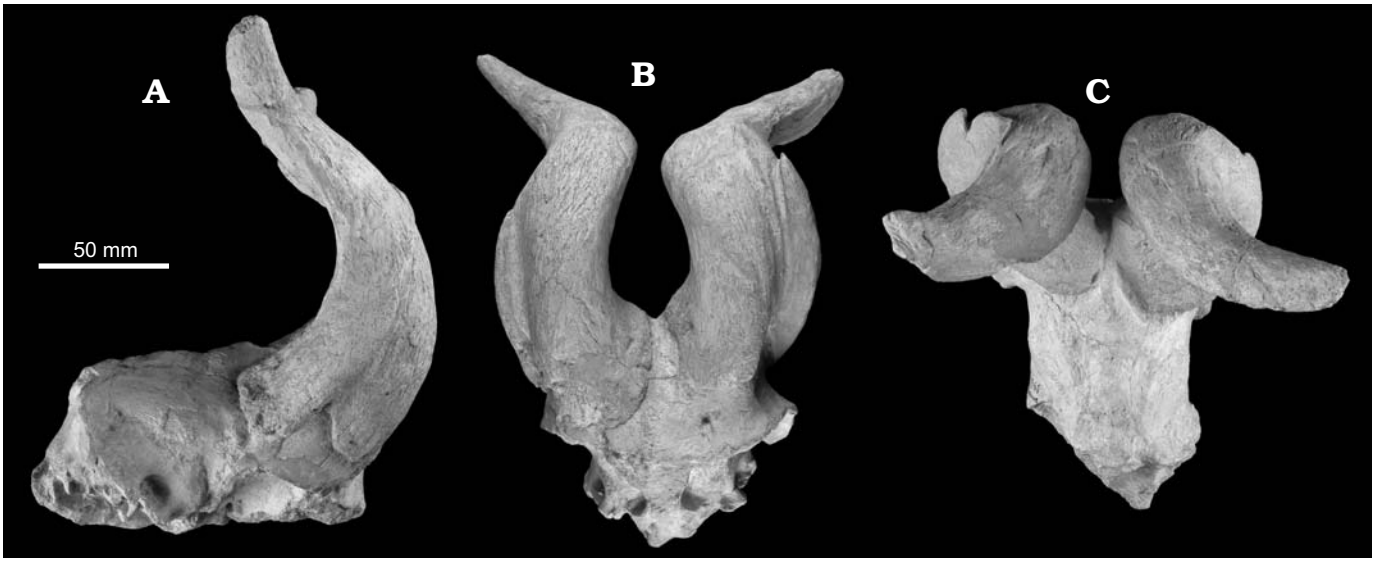


Fig. 4. Oiocerin antelope *Samotragus crassicornis* Sickenberg, 1936, partial skull SMF M1965 from Samos, Greece (Turolian, Late Miocene), in lateral (**A**), anterior (**B**), and dorsal (**C**) views. Photo courtesy of Senckenberg Museum Frankfurt.

orly at halfway point, with the tips trending posterolaterally or laterally; lateral sulcus on the proximal part of the horncores developed as a deep and narrow furrow; frontals moderately elevated between the horncores; orbits protruding laterally; face moderately to strongly inclined compared to braincase (≥90°); lacrimal fossae shallow or absent; supraorbital foramina small and situated within wide pits; short basioccipital, widened anteriorly, and bearing a medial longitudinal crest; auditory bullae small and compressed.

Remarks.—*Samotragus* was originally described from the Late Miocene of Samos Island, Greece (Sickenberg 1936), and later reported to occur in the Vallesian faunas of the Axios Valley, Greece (Bouvrain and Bonis 1985). Solounias (1981) suggested synonymizing *Samotragus* with *Sinotragus* Bohlin, 1935, but Bouvrain and Bonis (1985: 285) challenged this option, thoroughly revising and re-validating the genus. The present generic concept largely follows Bouvrain and Bonis (1985) in excluding later referrals, such as *Samotragus pilgrimi* Azanza, Nieto, and Morales, 1998 (see previous section) and *Samotragus occidentalis* Masini and Thomas, 1989 (see following section).

Samotragus crassicornis Sickenberg, 1936

Fig. 4.

Holotype: Frontlet, NHMW A4787 (Sickenberg 1936: pl. 3: 1, 2).

Type locality: Samos, Greece (unknown level).

Type horizon: Judging from the quality and color of fossilization of the holotype in Vienna, it seems likely that it came from the Main Bone Beds Member of the Mytilinii Formation, Samos, indicating a middle Turolian (Late Miocene) age (Kostopoulos et al. 2003).

Material.—Frontlets, NHMW A4787, AMNH 22639 (cast); partial skulls SMF M1965, AMNH 104791.

Emended diagnosis.—*Samotragus* of medium size; braincase moderately long and narrow, with weak temporal lines; frontals moderately elevated between the horncores and hollowed out anteriorly; occipital facing bilaterally; horncores uprightly inserted above the orbits, strongly curved posteriorly at halfway point, and abruptly tapering; horncores very close together at the base, closely converging at mid-height, and strongly diverging laterally in their distal part; horncore cross section squared at the base (Fig. 1) with a proximally flattened posterior surface, changing to roughly triangular at mid-height; proximal part of horncores bearing a deep lateral furrow and showing pronounced "exostosis".

Remarks.—Apart from the holotype, two additional specimens from Samos have been referred to this species (Solounias 1981): a frontlet from the Korff Collection, Hanaw, Germany (cast AMNH 22639); and a partial skull (SMF M1965; Fig. 4), on which the revised diagnosis of the species is mainly based. Gentry and Heizmann (1996) and Gentry et al. (1999) suggested that *Samotragus crassicornis* from Samos may represent males of *Oioceros rothii* from Pikermi (allowing synonymy at the generic level), without providing strong evidence. However, horncore size variation within *Oioceros rothii* supports the presence of horned females like in *O. atropatenes* at Maragheh, Iran, whereas some hornless specimens from Samos (e.g., AMNH 104791) may represent females of *S. crassicornis*, given their morphological compatibility with both male skulls of *S. crassicornis* and females of *S. praecursor* Bouvrain and Bonis, 1985 from the Axios Valley, Greece.

Geographic and stratigraphic range.—?Middle Turolian (Late Miocene) of Greece.

Samotragus praecursor Bouvrain and Bonis, 1985

Fig. 5A, B, E.

Holotype: Skull, LGPUT RPl-480 (Bouvrain and Bonis 1985: figs. 1, 3; Fig. 5B).

Type locality: Ravin de la Pluie, Axios Valley, Greece (RP1).

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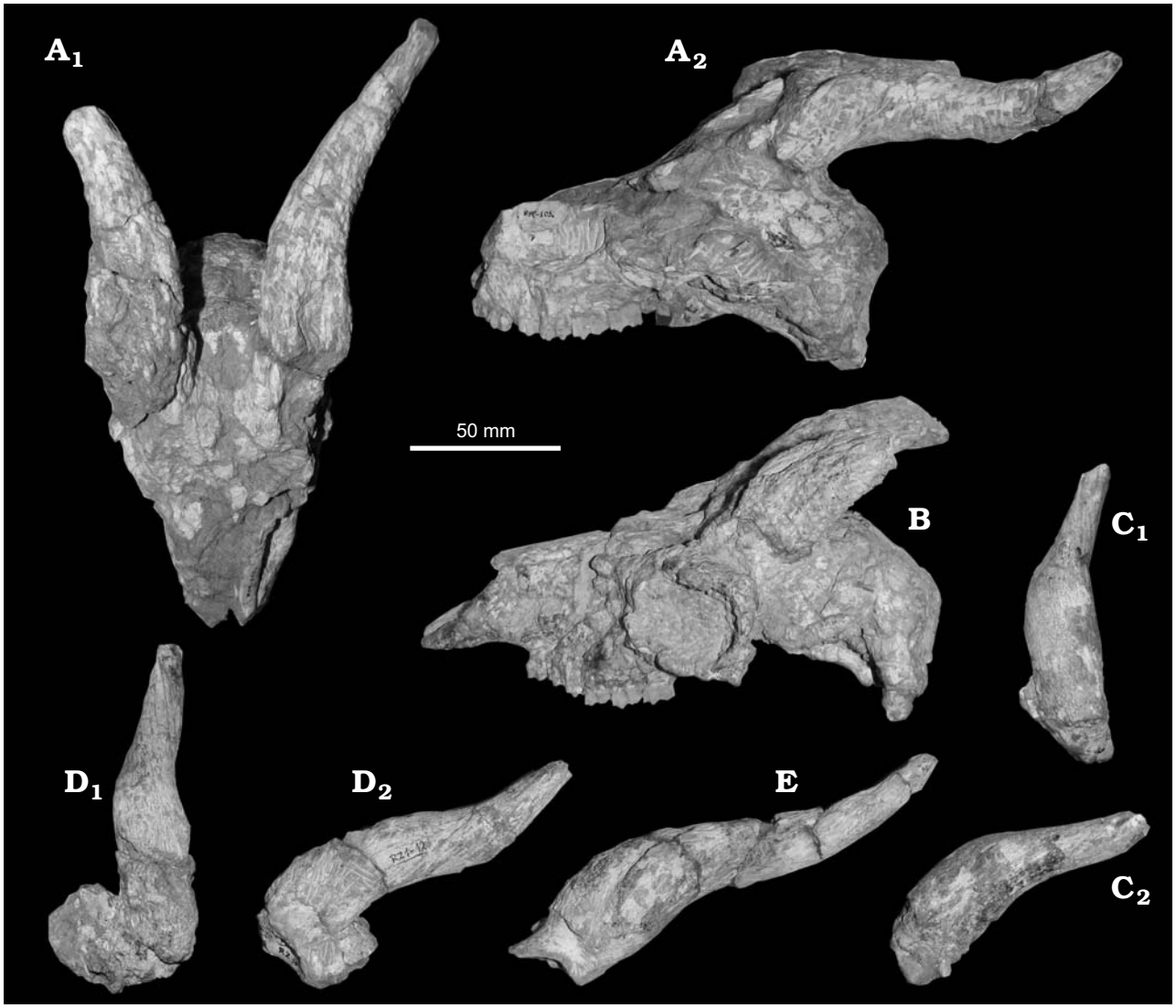


Fig. 5. Oiocerin antelope *Samotragus* from Northern Greece. **A**, **B**, **E**. *Samotragus praecursor* Bouvrain and Bonis, 1985 from Ravin de la Pluie (RPl), Axios Valley, late Vallesian (Late Miocene). **A**. LGPUT RPl-105n, cranium in dorsal (A_1) and lateral (A_2) views. **B**. LGPUT RPl-480, holotype cranium in lateral view. **E**. LGPUT RPl-37, left horncore in lateral view. **C**, **D**. *Samotragus* cf. *praecursor* Bouvrain and Bonis, 1985 from Ravin des Zouaves 1 (RZ1), Axios Valley, late Vallesian (Late Miocene). **C**. LGPUT RZ1-11, left horncore in anterior (C_1) and lateral (C_2) views. **D**. LGPUT RZ1-17 left horncore in anterior (D_1) and lateral (D_2) views.

Type horizon: Late Vallesian (magnetostratigraphically calibrated at 9.3 Ma; Sen et al. 2000), Late Miocene.

Material.—Horned skulls and frontlets, LGPUT RPl-480, RPl-38, RPl-263, RPl-264, RPl-280, RPl-394, RPl-349, RPl-481, RPl-105n, RPl-109n, RPl-111n, RPl-112n; isolated horncores, LGPUT RPl-37; RPl-350, RPl-385, RPl-108n, RPl-110n; hornless skulls, LGPUT RPl-211, RPl-479, RPl-482; dental and postcranial material as in Bouvrain and Bonis (1985).

Emended diagnosis (modified from Bouvrain and Bonis 1985).—Small-sized *Samotragus*; females hornless; opithocranium relatively short and box-like, with a rough dorsal surface around the fronto-parietal suture; supraorbital pits located close to the bases of the pedicles; face shallow and rather short, and moderately inclined compared to the braincase; nasals flat and rather short, roofing a shallow narial opening; contact between praemaxillae and nasals short; ethmoidal fissure very narrow or closed; choanae opening posterior to M3 and the lateral indendations of the palate; occiput moderately high and square-shaped, facing posteriorly; paroccipital processes strong and bearing posterior keels; foramen ovale large; horncores inclined more posteriorly than in *S. crassicornis*; premolars moderately short compared to the molars; postcranials slender.

Remarks.—Several unpublished specimens of *S. praecursor* have been unearthed from its type locality during the past decade. Most of them fall well within the limits of the size and morphological variation defined by Bouvrain and Bonis (1985). One almost complete skull (LGPUT RP1-105n; Fig. 5A) helps, however, to clarify some previously unknown or badly defined cranial details, as included in the species diagnosis provided here.

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Geographic and stratigraphic range.—Late Vallesian (Late Miocene) of Greece.

Samotragus cf. *praecursor* Bouvrain and Bonis, 1985

Fig. 5C, D.

Material.—Frontlet (LGPUT RZ1-10), left horncore (LGPUT RZ1-12), left juvenile horncore (LGPUT RZ1-11), distal part of tibia, calcaneum, and astragalus (LGPUT RZ1-68), distal part of humerus, radius, and metacarpal III+IV (LGPUT RZ1-69), proximal part of humerus (LGPUT RZ1-70), distal part of humerus, metacarpal III+IV, and proximal phalanges (LGPUT RZ1-71), metacarpal III+IV and phalanges (LGPUT RZ1-72), femur, tibia, metatarsal III+IV, and phalanges (LGPUT RZ1-73). All specimens come from the locality of Ravin de Zouaves 1 (RZ1) in the Axios Valley of northern Greece, which provided a limited number of fossils. The locality is usually considered to be isochronous with Ravin de la Pluie (RPl; late Vallesian, MN10), the type locality of *Samotragus praecursor*. Nevertheless, the presence of *Ouzocerus* Bouvrain and Bonis, 1986 and the absence of *Prostrepsiceros* Major, 1891 from this site may be indicative of a slightly older age, probably closer to the age of the locality of Xirochori (Axios Valley, Greece), dated to 9.6 Ma (Sen et al. 2000).

Description.—The *Samotragus* from RZ1 is known from a frontlet, two isolated horncores and several postcranials, all of them so far undescribed (Bouvrain and Bonis 1985, 1986). The RZ1 horncores closely resemble those of *S. praecursor* from RPl (similar position above the orbits, similar degree of torsion; compare Fig. 5C, D with Fig. 5E). However, the taxon from RZ1 differs from *S. praecursor* in its smaller (about a quarter shorter and 15% thinner in absolute basal dimensions) and more gradually tapering horncores (Fig. 5C, D), as well as the presence of a less well-defined lateral furrow restricted to the laterobasal part of the horncores, the presence of a moderately developed anterior keel descending anteromedially and becoming stronger towards the apices (Fig. $5C_1$, D_1), the weaker posterior curvature of the horncores in lateral profile, the dorsal (instead of lateral) deflection of the distal portions of the horncores, the presence of wide and moderately deep postcornual fossae, less elevated frontals between the horncores, smaller supraorbital foramina located closer to the horncore bases, and an anteriorly notched fronto-parietal suture (Y-shaped as in *S. crassicornis*, and unlike the T-shape of *S. praecursor*). The available postcranials from RZ1 do not, however, differ from those of *S. praecursor*.

Remarks.—Although poorly documented, the RZ1 *Samotragus* differs from *S. praecursor* in terms of both its horncore size and morphology, casting doubt on its previous taxonomic assignment (Bouvrain and Bonis 1985, 1986). Several features of the RZ1 taxon seem less derived than in the material from RPl, whereas others, such as the anterior keel and the straight axis of the horncore, show a residual occurance within the RPl polulation (e.g., a blunt anterior keel is present in the young male individual LGPUT RPl-109n, whereas LGPUT RPl-37 exhibits a straight horncore axis; Fig. 5E). This may suggest a transition from the RZ1 to the RPl morphotype.

Genus *Paraoioceros* Meladze, 1985

Type species: *Paraoioceros wegneri* (Andrée, 1926); see below.

Emended diagnosis.—Plesiomorphic traits: Small to medium-sized bovids with gradually tapering horncores; horncores oval or rounded in basal cross section (Fig. 1); postcornual fossae present. Apomorphic traits: horncores moderately thick, long, homonymously twisted, distally divergent, closely spiraled, and bearing multiple deep, longitudinal furrows with keel-like edges; premolars short compared to the molars; goat folds present on the lower molars.

Remarks.—Kostopoulos and Koufos (1996) suggested *Oioceros wegneri* Andrée, 1926 and *Samotragus occidentalis* Masini and Thomas, 1989 to be related. At the same time, Gentry and Heizmann (1996) were the first to comment on the possible synonymy between *Paraoioceros improvisus* Meladze, 1985 and *O. wegneri*. Later, the original referral of *P. wegneri* to *Oioceros* was further challenged by Roussiakis (2003).

Paraoioceros wegneri (Andrée, 1926)

1985 *Paraoioceros improvisus* Meladze, 1985; Meladze 1985: 28, pl. 2.

Holotype: Skull, PIM 141 (Andrée 1926: pl. 15: 3, 6).

Type locality: Samos, Greece (unknown level).

Type horizon: Turolian, Late Miocene.

Material.—Skull, PIM 141; frontlet, PIM-140; frontlets GNMT R-555, NHMI no number.

Emended diagnosis (modified from Bouvrain and Bonis 1985).—Medium size; face long and deep, with the anterior rim of the orbit located posterior to M3; opisthocranium short and slightly widening anteriorly; orbits strongly protruding laterally; strong basicranial flexion; frontals thick, pneumatized, and strongly elevated between the horncores; interfrontal suture constricted and forming a sharp crest anterior to the horncores; supraorbital foramina large and located in deep and wide depressions far from the horncore bases; infraorbital foramina located dorsal to P2; ethmoidal fissure long and narrow; temporal lines weak and rapidly converging posteriorly; auditory bullae moderately large and compressed, extending ventrally below the level of the basioccipital; basioccipital short and bearing a medial longitudinal groove; pedicles very short anteriorly and absent posteriorly; horncore long, slightly compressed anteroposteriorly, inserted above the posterior border of the orbit, and gradually tapering; horncores closely spaced, moderately to strongly diverging distally, and showing double flexion in lateral view, curving posterolaterally at mid-height and upwards distally; basal horncore surface bearing between one and four wide and deep, anterolaterally to anteriorly descending furrows with sharp edges, with the lateral edge of the posteriormost furrow usually developed into a keel; premolars short compared to molars; weakly molarized P2 and P3; presence of central islets on the upper molars, and goat folds on the lower ones.

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Remarks.—Although the skull features of this species are mainly known from the holotype, the horncore structure and variation are better documented by five additional frontlets from Samos, Turkey, and Georgia. The horncores of the illustrated frontlet from Rustavi (Meladze 1985: pl. 2; GNMT R-555) and that of the Kavakdere specimen (NHMI PV-186) are strongly divergent from the base, and bear a single, wide, and rather deep anterolaterally descending furrow with sharp edges, with the lateral edge being shaped like a keel. By contrast, in the holotype, and probably the poorly preserved specimen from Eski Bayirkoy (NHMI no number), the horncores are less divergent and become sub-parallel along their distal parts. In addition to a main furrow resembling that of the specimens from Rustavi and Kavakdere, there are two additional, smaller furrows descending more anteriorly. Meladze (1985) reports a similar condition in other specimens from Rustavi. In PIM 140 from Samos and in the specimen from Duzyayla (NHMI PV-348), the divergence is similar to that of the holotype, but the horncores bear four similarly sized and equally spaced furrows, with the lateral keel being poorly developed or absent. However, all specimens preserving enough of the horncores (PIM 140, PIM 141, NHMI PV-186, GNMT R-555) display double horncore flexion in lateral view.

Roussiakis (2003) concluded that *P. wegneri* differed from both *Oioceros* and *Samotragus*, but avoided a final systematic decision. The cranial, dental and horncore features of the specimens described here clearly distinguish them from *Oioceros*, supporting a distinction at the generic level as proposed by Meladze (1985) for the material from Rustavi. By contrast, the differences between the horncores of the individual specimens still seem to fall within the limits of intraspecific variation.

Geographic and stratigraphic range.—The holotype of this species and an additional frontlet (PIM 140) were found in an unknown fossiliferous level of Samos, Greece. The species is further represented by cranial remains occurring at the early to middle Turolian localities of Mahmutgazi (MN11), Garkin (MN11) (Köhler 1987), Eski Bayirkoy (MN11), Kavakdere (MN11), and Duzyayla (MN12?) of Turkey, as well as at the latest Vallesian/earliest Turolian site of Rustavi, Georgia (Meladze 1985).

?*Paraoioceros occidentalis* (Masini and Thomas, 1989)

1989 *Samotragus occidentalis* Masin and Thomas; Masini and Thomas 1989: 309; pl. 1.

Holotype: Frontlet, MCSNF BRS5-29 (Masini and Thomas 1989: pl. 1: 1).

Type locality: Monticino quarry site BRS5, Brisighella, Italy.

Type horizon: Latest Turolian (MN13), Late Miocene.

Emended diagnosis (modified from Masini and Thomas 1989).—Small-sized species characterized by protruding orbital rims, a pinched interfrontal suture, the presence of well-developed postcornual fossae, and moderately grooved, distally diverging horncores.

Remarks.—Although the material from Brisighella is currently insufficient for a definitive generic assignment, most of the dental and horncore features seem to indicate an association with *Paraoioceros* (e.g., Kostopoulos and Koufos 1996), rather than *Samotragus*, as originally proposed by Masini and Thomas (1989). The strongly and distinctly grooved lateral horncore surfaces of the Brisighella frontlet, combined with its long and gradually tapering horncores, the presence of well-developed and posteriorly located postcornual fossae, the pinched interfrontal suture, the thickened frontals (Masini and Thomas 1989: 310), the relatively long lacrimal fossae (Masini and Thomas 1989: pl. 1: 2), the hypsodont dentition, the length of the lower premolar tooth rows, the hint of a goat fold on the lower molars, the strong paracone rib in a central position on the upper molars, and the presence of a strong mesostyle (Masini and Thomas 1989: pl. 1: 2, 7) all resemble *Paraoiocerus wegneri*. Although the posterior curvature of the Brisighella horncores is comparable to that of *Samotragus crassicornis*, the overall spiraling is closer, resembling *S. praecursor* and *P. wegneri*. By contrast, the presence of a main lateral furrow linked to the postcornual fossa is a feature also seen in some *Hispanodorcas*, whereas the two structures are separate in both *Samotragus* and *P. wegneri*.

Geographic and stratigraphic range.—Latest Turolian (Late Miocene) of Italy.

Genus *Oioceros* Gaillard, 1902

Type species: *Oioceros rothii* (Wagner, 1857); see below.

Emended diagnosis.—Plesiomorphic traits: small-sized bovids with moderately thin and gradually tapering horncores; horncores inserted above the orbits, moderately spaced on the frontals, weakly divergent at mid-height, and running parallel distally; lacrimal fossa deep; ethmoidal fissure open; postcornual fossae present; premolars long compared to the molars. Apomorphic traits: horncores homonymously twisted (≥1 coil), relatively long, and weakly or moderately compressed mediolaterally (Fig. 1), with a flattened anterolateral surface; anterior keel blunt or absent; lateral keel well developed and associated with an anterior longitudinal furrow dividing the horncore into a larger anterior and a smaller posterior portion; orbits protruding laterally; frontals depressed anterior to the pedicles; supraorbital foramina small and located within deep pits.

Oioceros rothii (Wagner, 1857)

Holotype: Frontlet, BSPM AS II 601 (Wagner 1857: pl. 8: 20).

Type locality: Pikermi, Greece.

Type horizon: Middle Turolian (MN12), Late Miocene.

Diagnosis (modified from Roussiakis 2003).—Medium size; horncores homonymously torsioned (1 coil), lyrate in anterior view, and moderately compressed throughout their length (Fig. 1); anterior keel blunt; posterolateral keel strong and running along most of the horncore; interfrontal and frontoparietal sutures open and complex in outline; interfrontal suture only slightly elevated between the horncore bases; ethmoidal fissure present; occipital and roof of the braincase forming an obtuse angle in lateral view; basioccipital relatively long, slightly wider posteriorly than anteriorly, and bearing a weak medial groove anteriorly.

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Remarks.—Until recently, only the horncores and dentition of *O. rothii* were known, but Roussiakis (2003) described an almost complete skull together with other dental and cranial material from the type locality of Pikermi, and provided an emended diagnosis. More recently, Kostopoulos and Bernor (2011) reviewed occurrences from a range of other localities (see below).

Geographic and stratigraphic range.—Apart from the type locality, this species has also been recorded from the early–middle Turolian (MN11, MN12) localities of the Axios Valley (Arambourg and Piveteau 1929), the early Turolian (MN11) locality of Çorak Yerler, Turkey (Köhler 1987), the Lower, Middle, and Upper Maragheh, Iran (Mecquenem 1925; Kostopoulos and Bernor 2011), the middle Turolian locality of Bazaleti, Georgia (Meladze 1967) and the localities of Khirgis-Nur III (Turolian) and Dzagso-Khairkhar-4 (Early Pliocene) of Mongolia (Dmitrieva 2007: pl. 12: 1, 2, misintentified as *O. atropatenes*). Other reports of *O. rothii* have not been adequately documented.

Oioceros atropatenes (Rodler and Weithofer, 1890)

Lectotype (designated by Bouvrain and Bonis 1985): Right horncore, NHMW 1886/0028/0004 (Rodler and Weithofer 1890: pl. 6: 5).

Type locality: Maragheh, Iran (unknown level).

Type horizon: Presumably Turolian, Late Miocene.

Emended diagnosis.—Small size; homonymosusly torsioned horncores weakly compressed mediolaterally (Fig. 1); anterior keel absent; supraorbital pits large, triangular, and located close to the horncore bases; nasals widening posteriorly, and long compared to the frontals; ethmoidal fissure almost closed; basioccipital relatively broad and grooved; braincase relatively shorter than in *O. rothii*, with a less convex dorsal profile.

Remarks.—*O. atropatenes* was revised by Heintz (1963), with later additions and modifications by Bouvrain and Bonis (1985), Watabe (1990), and Kostopoulos and Bernor (2011).

Geographic and stratigraphic range.—Kostopoulos and Bernor (2011) reported this species from the MMTT9 Maragheh fossil site upwards, suggesting a late early to middle Turolian age. The species furthermore occurs in the middle Turolian locality of Ivand-1, Iran (Sen and Purabrishemi 2010). Additional occurrences at Kayadibi, Turkey and Rustavi, Georgia, are doubtful.

Genus *Urmiatherium* Rodler, 1889 (= *Parurmiatherium* Sickenberg, 1932)

Type species: *Urmiatherium polaki* Rodler, 1889; see below.

Emended diagnosis.—Apomorphic traits: Medium to large-sized bovids with strong cranio-facial flexion, strongly elevated, thick and pneumatized frontals, and an extremely short opisthocranium; parietals strongly reduced on the skull roof; face deep; occipital large and thick, with occiput facing mostly dorsally; basioccipital thick; posterior tuberosities of basioccipital well-developed and partly or completely fused, forming an additional oval-shaped posterior facet for the atlas; horncores thick, short, homonymously twisted, anteroposteriorly expanded over the frontals, very close to each other or merging at the base, and bearing a wide and well-defined lateral depression; mandibular corpus shallow; hypsodont dentition; premolars short compared to the molars; tight articulation between occipital and atlas; metapodials moderately long and robust, with relatively wide epiphyses.

Urmiatherium polaki Rodler, 1889

Holotype: Partial skull (Rodler 1889: pls. 1–4; cast NHMUK M4114); according to Rodler (1889) the holotype skull was part of a private collection by J.E. Polak. Unfortunately, I was unable to locate it in any of the mentioned institutions.

Type locality: Maragheh, Iran (unknown level).

Type horizon: Turolian, Late Miocene.

Emended diagnosis (modified from Jafarzadeh et al. 2012).—Medium to large-sized species of *Urmiatherium* with an almost flat occipito-parietal angle; parietals almost absent from skull roof; face deep and long, with a moderately broad rostrum; nasals relatively long and not in contact with the premaxillae; lacrimal fossae moderately deep; ethmoidal fissure absent; orbits relatively small and round, and located posterior to the level of M3; horncores short and distinctly grooved, showing weak homonymous torsion, fused at the base, and with a slightly posteriorly curved distal portion; lower molars with strong parastylids and weak goat folds, but without basal pillars; upper molars with strong paracone ribs and central islets.

Remarks.—Until recently, this species was known only from its opisthocranium (Rodler 1889; Mequenem 1925), but a newly discovered specimen from the type area provides details of most of its cranial morphology (Jafarzadeh et al. 2012). Some metapodials from Maragheh provide additional information about the postcranial anatomy of this species, as well as its ecological adaptations (Kostopoulos and Bernor 2011).

Geographic and stratigraphic range.—*Urmiatherium polaki* has so far only been reporeted from the middle and upper intervals of the Maragheh sequence, Iran, with its oldest possible record dated to 7.7– 8.6 Ma (Jafarzadeh et al. 2012).

Urmiatherium intermedium Bohlin, 1935

Type material: Bohlin (1935) did not indicate any holotype specimen for *U. intermedium*. EMUU Ex. 1 (Bohlin 1935: fig. 2, pl. 2: 1–3), an almost complete male skull from Locality 30 of Shaanxi Province, China, is therefore here designated as the lectotype of this species.

Type locality: Locality 30, Shaanxi Province, China.

Type horizon: Most likely middle or late Turolian, Late Miocene.

Emended diagnosis (modified from Bohlin 1935).—Slightly smaller than the type species; horncores short and wide at the base; rostrum relatively long and narrow; maxillae short; lacrimal fossae shallow; frontals abruptly stepped in lateral view; molars relatively small; females horned.

Geographic and stratigraphic range.—The species is known from Loc. 30, 43, 44, 49, and 108 of Shaanxi and Loc. 115, 116 of Kansu Province in N. China, all of them of Late Mio-

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cene, and most probably of middle–late Turolian, age (Chen and Zhang 2009).

Urmiatherium rugosifrons (Sickenberg, 1932)

Lectotype: Partially preserved skull, NHMW A4758 (illustrated by Sickenberg 1933: pl. 5)

Type locality: Samos, Greece (unknown level).

Type horizon: Middle–late Turolian, Late Miocene.

Emended diagnosis (modified from Kostopoulos 2009).—Small-sized species od *Urmiatherium* with very short, robust, medially unfused, strongly homonymously twisted, and grooved horncores, prolonged anteriorly along the frontals by low buttresses; exposure of parietal on skull roof small and forming a large angle with the occipital plane; premolars relatively longer than in other species of *Urmiatherium*; p4 with an open anterior valley and anteroposteriorly expanded metaconid; lower molars without goat folds or basal pillars; oval shaped talonid on m3.

Remarks.—The morphology of the species is poorly known, with available material currently restricted to some opisthocrania, mandibles and metapodials. Gentry et al. (1999) and Kostopoulos (2009) suggested synomymizing *Parurmiatherium* Sickenberg, 1932 with *Urmiatherium*. Until recently, *U. rugosifrons* was exclusively known from Samos, Greece (see discussions in Kostopoulos 2009; Bernor and Kostopoulos 2011), but recent discoveries at the neighboring middle Turolian localities of Serefkoy-2 and Sahalipasalar, Turkey (Kaya et al. 2012; Tanju Kaya personal communication 2010, and DSK unpublished data) provide additional evidence of its geographic distribution and ontogenetic development.

Geographic and stratigraphic range.—Middle to late Turolian (Late Miocene) of Greece and western Turkey.

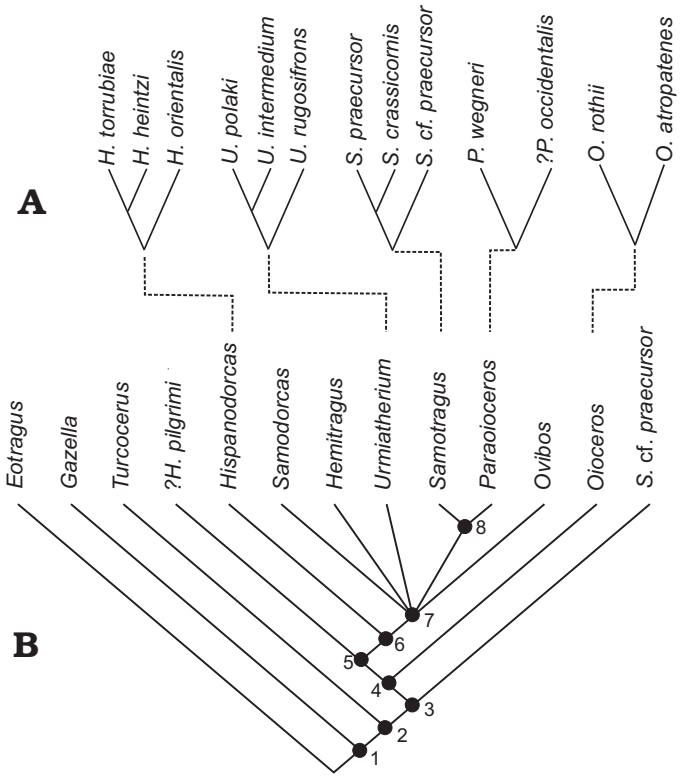


Fig. 6. Cladograms showing the evolutionary relationships within Oiocerina. **A**. Intrageneric relationships (rooted to *Eotragus* Pilgrim, 1939), based on available morphological and zoogeographic evidence (see text). **B**. 75% majority-rule consensus of the four most parsimonious trees (length: 172; CI: 0.46; RI: 0.65) showing the relationships of eight fossil genera of Oiocerina, *Gazella* Blainville, 1816, *Ovibos* Blainville, 1816, *Hemitragus* Smith, 1826, and *Turcocerus* Köhler, 1987, based on the character matrix of Appendix 1. Outgroup: *Eotragus* Pilgrim, 1939. Synapomorphies supporting nodes (marked with bold letters) are discussed in the text.

Phylogenetic relationships

The limited number of species per genus, combined with a wealth of morphological and chronological evidence, allows a relatively easy assessment of the intrageneric relationships of the species discussed in this paper (Fig. 6A). Thus *O. atropatenes* and *O. rothii* are de facto sister taxa, with the same being most likely true for *Paraoioceros wegneri* and ?*P. occidentalis* as well. Within *Samotragus*, *S. praecursor* + *S. crassicornis*, share several synapomorphies to the exclusion of *S.* cf. *praecursor* from RZ1, including a narrower craniofacial angle, raised frontals between the horncores, the lack of postcornual fossae, and longer, curved, and abruptly tapering horncores, strongly divergent distally and lacking keels (Figs. 6A, 7D, G_2). Similarly, *Urmiatherium rugosifrons* is considered to be the sister group of *U. polaki* + *U. intermedium*, which are united by proximally merged horncores, a much more reduced dorsal sector of the parietal, a flat fronto-parieto-occipital surface, and short premolars (Fig. 6A). Within *Hispanodorcas*, the available data, mostly related to horncore morphology, are insufficient to corroborate any of the three possible phylogenetic solutions. However, taking zoogeographic criteria into account, *H. orientalis* (including *H.* cf. *orientalis* from Nikiti-1) might be considered the sister group of *H. torrubiae* + *H. heintzi*, with the latter most likely representing a southwestern branch of the genus (Fig. 6A).

Analysis of the intergeneric relationships resulted in four most parsimonious trees of 172 steps (CI = 0.46, RI = 0.65; Fig. 6B), showing *Gazella* to be the sister group of a clade including *Turcocerus* and all other taxa (node 2 in Fig. 6B). The latter is supported by the presence of moderately to strongly homonymously twisted horcores [02(1), 03(1, 2)]; the presence of an anterior keel [16(1)], secondarily lost in later forms; and the regular presence of central islets on the upper molars [59(1)]. "Oiocerines", as defined here (node 3 in Fig. 6B), are diagnosed by the presence of a moderately to strongly developed lateral sulcus [18(1), 19 (1, 2), 20(1,2)] variously dividing the lateral horncore surface [21(1, 2, 3)]; the presence of a strong lateral notch on the crown of the cornual process [24(1)]; the near absence of pedicles [26(1), 27(1)]; reduced or absent temporal ridges [32(2)]; and a grooved basioccipital [45 (1)] with closely placed anterior

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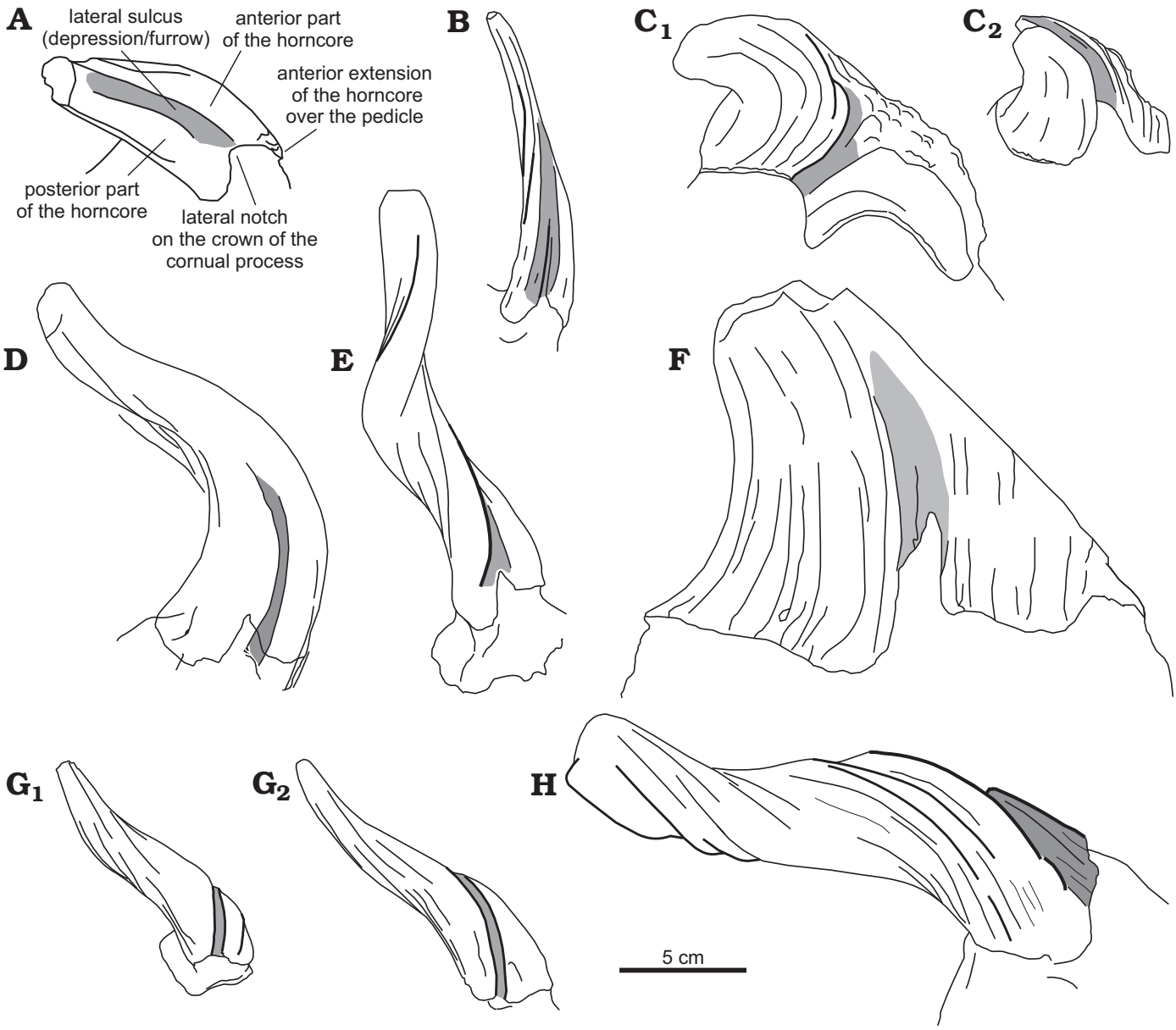


Fig. 7. Drawings of the horncores of several Oiocerina in right lateral view, showing the main shared characters. **A**. ?*Hispanodorcas pilgrimi* from Toril-3, Spain. **B**. *Hispanodorcas orientalis* from Dytiko-3, Greece. **C**. *Urmiatherium rugosifrons* from Samos (Greece) and Turkey, adult (C_1) and juvenile (C_2) individual. **D**. *Samotragus crassicornis* from Samos, Greece. **E**. *Oioceros rothii* (combination of Pikermi, Greece and Maragheh, Iran specimens). **F**. *Urmiatherium polaki* from Maragheh, Iran. **G**. *Samotragus* cf. *praecursor* from Ravin des Zouaves 1 (G_1) and *Samotragus praecursor* from Ravin de la Pluie, Greece (G_2). **H**. *Paraoioceros wegneri* from Samos, Greece.

tuberosities [48(0), interpreted as an apomorphic reversal]. Despite its poor fossil record and incomplete dataset (Appendix 1), *Samotragus* from RZ1 appears as the sister group of all other discussed "oiocerines" (Fig. 6B). Within the latter, *Oioceros* was found to be the sister group of a clade including all remaining taxa (node 5 in Fig. 6B), which share a variable degree of lateral deflection of the horncore tips [11(1)], laterally situated or absent postcornual fossae [34(1, 2)], strong anterior tuberosities of the basioccipital [47(1)], and laterally expanded or fused posterior tuberosities of the basioccipital [49(2, 3)]. ?*Hispanodorcas pilgrimi* appears as the sister group of a clade including *Hispanodorcas* and all remaining taxa (node 6 in Fig. 6B), which is supported by a strongly curved frontal profile [29(1)] and proximally diverging horncores [9(1)]. In light of these results, the clear distal "bilobation" of the horncores of *Hispanodorcas* cf. *orientalis* from Nikiti-1 (Fig. 3C; resulting from the combination of characters 19, 20, and 21), which is barely visible on the apices of the Dytiko-3 holotype specimen (Figs. 2, 7B) might represent a vestige of the condition seen in ?*H. pilgrimi* (Fig. 7A).

The analysis failed to resolve the phylogenetic relationships of *Samodorcas*, *Urmiatherium*, *Samotragus*, and *Paraoioceros* (node 7 in Fig. 6B), which form a clade supported

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by anteroporsteriorly compressed horncores with large basal diameters [12(1), 13(1)] placed close to each other on the elevated and pneumatized frontals [8(1), 28(1,2), 31(1)], anteriorly shifted supraorbital foramina or pits [36(1)], a narrow craniofacial angle [39(1,2)], a short braincase with a posteriorly curved roof [40(1), 41(1)], short premolars [56(1)], and small, compressed auditory bullae [54(0), 55(0), interpreted as reversals]. Crown Caprini with homonymously twisted horncores (i.e., *Hemitragus*, *Ovibos*; from hereon referred to as HCC) are diagnosed by the same set of morphological traits, and are shown to be deeply nested within "oiocerines", thus rendering the latter paraphyletic. Although terminal "oiocerines" may share some true apomorphies with HCC, this result looks spurious, as HCC lack most of the original features diagnosing "oiocerines" [i.e., 19(1,2), 20(1,2), 21(1,2,3), 24(1), 48(0), as well as 27(1) and 45(1) for *Ovibos*]. Instead, most of the features uniting HCC with advanced "oiocerines" are likely related to the evolution of a fighting style involving ramming [25(1,2)], and may hence have arisen convergently several times. This hypothesis needs to be tested further using a more comprehensive analysis, which is beyond the scope of this study.

Three of the four most parsimonious trees showed *Paraoioceros* + *Samotragus* to form a clade to the exclusion of all other taxa (node 8 in Fig. 6B), diagnosed by spiraled [04(1)], posteriorly curved [7(1)], and strongly distally divergent horncores [10(2)] bearing a deep lateral furrow [19(2)], as well as weak or absent lacrimal fossae [52(1)]. The inclusion of this clade in the above mentioned polytomy (node 7 in Fig. 6B) may be questionable, and the result of inadequate data for *Samotragus* from RZ1, as well as potentially convergent morphological traits related to ramming. By contrast, *Paraoioceros* + *Samotragus* share at least one potentially genuine synapomorphy with *Samotragus* from RZ1 [19(2): presence of a lateral horncore furrow]. The presence of a similar feature on the horncores of *Oioceros* is likely homoplastic: while the correspondent lateral furrow of *Oioceros* represents the remnant of a wide and shallow lateral depression [19(1)] secondarily eliminated by advanced torsion, the furrow in *Samotragus* and *Paraoioceros* is not initially related to the degree of twisting (compare Fig. 7E with B and G).

Zoogeographic and ecological settings

Occuring from Spain to Greece, and from Vallesian to Ruscinian times (MN10–MN14), *Hispanodorcas* is a wide-ranging genus from both a geographic and a chronological point of view (Fig. 8). To date, the Western European record of *Hispanodorcas* is restricted to the Mediterranean part of the Iberoccitanian region (Catalayud-Teruel Basin and Elche-Alicante graben), thus possibly implying some degree of endemicity. Based on the apparent absence of a likely ancestor of *Hispanodorcas* from Western Europe, Made et al. (2006) suggested a dispersal of *Hispandorcas* into Spain around 6.9 Ma. On the other hand, the morphological continuum between the latest Vallesian Nikiti-1 and the late Turolian Dytiko-3 *Hispanodorcas* indicates a single dispersal event of the genus into the southern Balkans. Given the newly-referred Toril-3 (MN7/8; ?*H. pilgrimi*) and Nikiti-1 (end of MN10; *Hispanodorcas* cf. *orientalis*) taxa from Spain and Greece, respectively, two equally parsimonious zoogeographic scenarios can therefore be formulated:

(i) Vallesian–Turolian *Hispanodorcas* originated from a close Iberian relative of ?*H. pilgrimi* that dispersed into the Balkans probably during the mid-Vallesian (contra Made et al. 2006). In this case, the Astaracian–early Vallesian ?*Hispanodorcas* would be interpreted as endemic to the Iberian Peninsula.

(ii) Turolian–Pliocene Iberian *Hispanodorcas* originated from an eastern ancestor that spread towards Iberia probably during the middle Turolian (in agreement with Made et al. 2006); in this case, ?*H. pilgrimi* and its early Vallesian relatives would have had a much wider geographic distribution than presently known, covering the whole of southern Europe.

The remarkable interspecific stability of the horncore shape of *Hispanodorcas* is indicative of a conservative taxon. Although the ecology of the genus is barely known, the sharp, weakly twisted, and slightly curved male horncores lacking a catching arch (e.g., Lundrigan 1996: fig. 1) imply stabbing as the predominant fighting behavior (Lundrigan 1996; Caro et al. 2003). Additionally, some vertebral and postcranial characters of *H. orientalis* discussed by Bouvrain and Bonis (1988) show caprine-like adaptations, whereas its dentition shares strong affinities with extant browsers and mixed feeders (Merceron et al. 2005). The particular atlanto-occipital joint of *H. orientalis* (see Bouvrain and Bonis 1988: 103, fig. 5) suggests a backward movement of the head to obtain food items from higher sources. This combination of features implies solitary or small herd habitation of uneven forested areas (Jarman 1974; Janis 1982), an ecological profile that might apply to the entire genus (Fig. 8).

Little is known about the ecology of *Samodorcas kuhlmani*, recorded only from the Turolian of Samos Island, Greece. Solounias et al. (2010) indicated *S. kuhlmani* was a mixed feeder, which, together with the caprine-like skull features, may suggest an open bushland habitat. All available evidence indicates that *Urmiatherium* is endemic to Asia, and emerged no earlier than the Turolian. Although the genus appears to have a vast spatial distribution from Asia Minor to China, its species show a high degree of localism, probably indicating particular ecological niches also reflected in their extremely specialized cranial anatomy. Limited dental micro- and mesowear data of *U. rugosifrons* from Samos and *U. polaki* from Maragheh indicate grazing habits (Fig. 8; Koufos et al. 2009; Jafarzadeh et al. 2012), whereas the metapodial anatomy of all known species suggest moderate running and climbing abilities (Kostopoulos and Bernor 2011; Jafarzadeh et al. 2012). In addition, the skull structure and horncore shape

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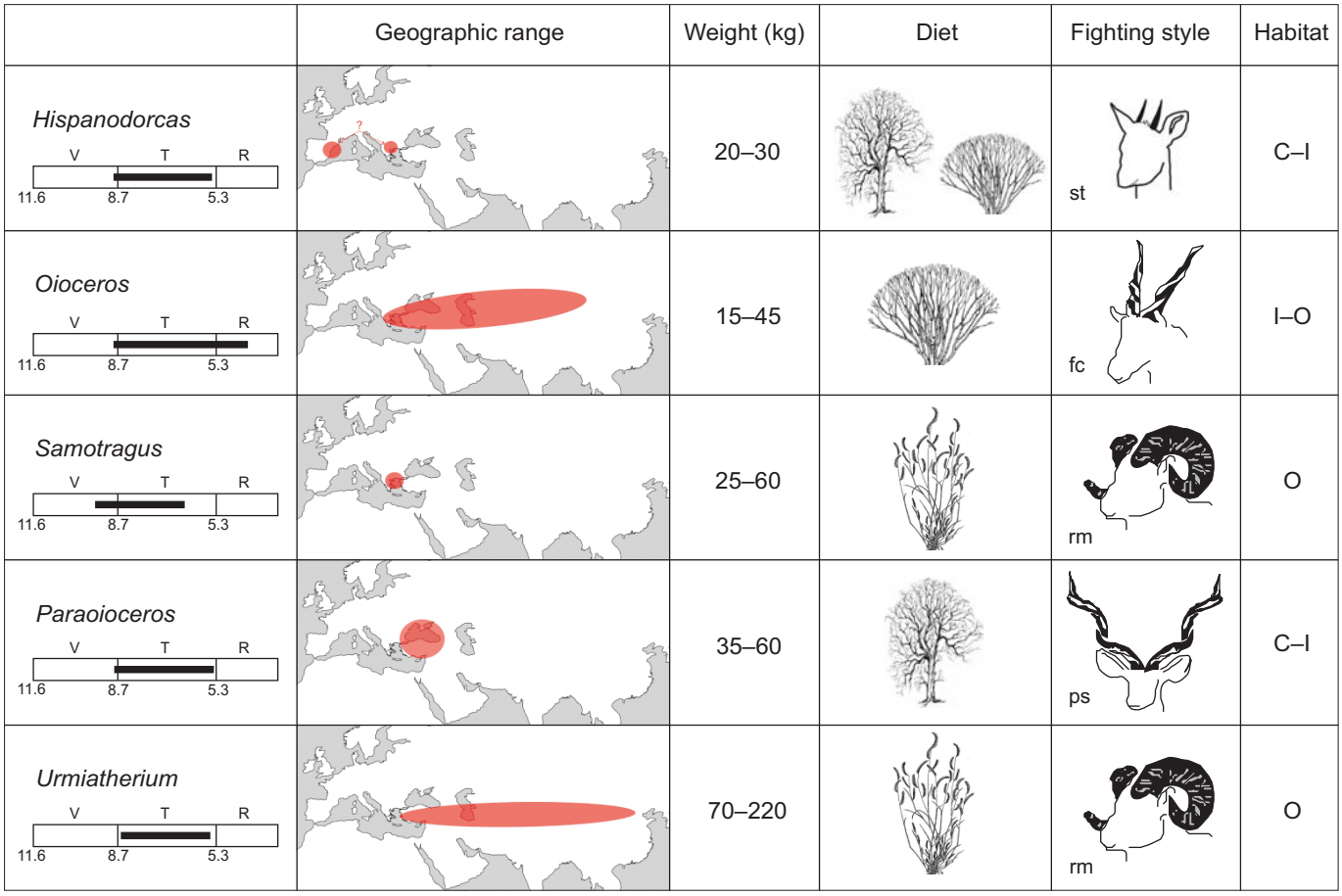


Fig. 8. Time range, geographic distribution, ecological features, and paleoenvironment of several members of the Oiocerina. Abbreviations: V, Vallesian; T, Turolian; R, Ruscinian; O, open, I, intermediate, and C, closed environment; grass for grazing, scrub for mixed, and tree for browsing diets; sheep for ramming (rm), kudu for wrestling/pushing (ps), eland for wrestling/fencing (fc), and dik-dik for stabbing (st) fighting style (some drawings adopted from Lundrigan 1996).

suggest a pushing (probably in *U. rugosifrons*) to ramming (in *U. polaki* and *U. intermedium*) fighting style (Kostopoulos and Bernor 2011; Jafarzadeh et al. 2012).

During the early Turolian, *Oioceros* was already established in the eastern part of the sub-Paratethyan province. So far, *O. atropatenes* is known only from the surroundings of Lake Urmia in Iran, suggesting a high degree of endemicity. By contrast, *O. rothii* is the most widespread species of all of the taxa studied here, and occurs from Greece to Mongolia (Fig. 8). The oldest specimens of *O. rothii* come probably from the eastern part of the sub-Paratethyan Province (e.g., Kostopoulos and Bernor 2011, and literature therein), although some latest Vallesian to earliest Turolian material of *O. rothii* has been reported from Georgia (e.g., Meladze 1967, 1985). The youngest record of *O. rothii* comes from the Early Pliocene (4.0–4.6 Ma) of Dzago-Khairkhar, Mongolia (Dmitrieva 2007; Fortelius 2012), and possibly marks the geographic restriction and final extinction of this species. Almost nothing is known about the ecology of *O. rothii* and *O. atropatenes*. The incipient spiraling and the higher degree of torsion compared to *Hispanodorcas* might indicate that wrestling formed part of the fighting behavior of these species—in particular in *O. rothii,* in which the horncores show a rather well-developed catching arch (Lundrigan 1996). Both species exhibit round-wearing cusps incompatible with browsing habits, and Solounias et al. (2010) classified *O. rothii* among mixed feeders, based on the dental microwear scores of the Pikermi population (Fig. 8). Among extant bovids, small-sized species (< 25 kg) with equally sized horncores in both male and female individuals, resembling *O. atropatenes* and probably *O. rothii* (e.g., Kostopoulos and Bernor 2011), are found in forested or bushland habitats (Jarman 1974; Janis 1982).

Samotragus is a rare genus, geographically restricted to the area around the Aegean Sea (Fig. 8). Ecomorphological and dental microwear studies indicate mixed feeding or grazing habits in rather open landscapes (Bouvrain and Bonis 1985; Köhler 1993; Kostopoulos 2000; Merceron et al. 2005) (Fig. 8). Changes in the horncore shape from the RZ1 *Samotragus* cf. *praecursor* to *S. crassicornis* from Samos also imply a clear shift from a primarily stabbing to a mainly ramming fighting behavior. This change is indicated by an overall size increase (up to 100% in absolute horncore basal dimensions); lengthening and basal widening of the horn-

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cores; a decrease in the distance between the horncores along the mid-frontal suture; increased spiraling with the horn tips facing progressively more laterally; flattening of the posterior horncore surface; elimination of the postcornual fossae; and an increase in the degree of cranio-facial flexion.

The oldest known occurrence of *Paraoioceros wegneri* most likely comes from the easternmost coasts of the Paratethys (Meladze 1985), from where the species spread southwestwards during the early Turolian, without crossing into the southern Balkans (Fig. 8). The ecology of *Paraoioceros* is not fully understood, but Solounias and Saunders (1988) and Solounias et al. (2010) classified *P. wegneri* from Samos among browsers, whereas the horncore morphology of this species indicates a pusher/wrestler (Köhler 1993; Lundrigan 1996; Fig. 8). The ecology of the latest Miocene (~5.8–5.3 Ma) Brisighella species remains unknown.

Discussion and concluding remarks

Following Bouvrain and Bonis (1985), the cladistic analysis of Azanza et al. (1998) supports the monophyly of "oiocerines" on the basis of (i) homonymous twisting and (ii) grooved and keeled horncores. Both features are, however, simultaneously present in many other Eurasian Neogene genera, especially of the phylogenetically unresolved *Urmiatherium*-group (Sickenberg 1933; Gentry 1996; Gentry et al. 1999; Chen and Zhang 2004, 2009), thus raising doubts regarding the status and composition of both bovid taxonomic assemblages. Gentry et al. (1999) already proposed that the homonymous torsion of *Urmiatherium*, as well as the deep longitudinal grooving and the tendency towards proximal thickening of the horncores shown by this taxon, may be shared with *Oioceros*. In a recent classification of Bovidae, Gentry (2010: table 38.1) transfered *Urmiatherium* to the fossil tribe Oiocerini, Subfamily Oiocerinae, without providing a discussion. On the other hand, several authors (e.g., Gentry and Heizmann 1996; Chen and Zhang 2004, 2009) have interpreted "urmiatheriines" as the potential descendants of Hypsodontini Köhler, 1987, a group of widely distributed, small, hypselodont, antilopine-like bovids from Eurasia that disappeared arround 14 Ma (Köhler 1987; Gentry et al. 1999; Dmitrieva 2007). The relationships of both "hypsodontines" and "oiocerines" with extant bovid tribes remain unclear. "Hypsodontines" have been interpreted as either the sister group of all other bovids (Gentry et al. 1999; Bibi et al. 2009; Gentry 2010) or as basal members of Caprini sensu lato (Dmitrieva 2007). By contrast, "oiocerines" have been allied with either Caprini (e.g., Gaillard 1902; Pilgrim 1934; Gentry 1970; Dmitrieva 2007) or Antilopini (e.g., Solounias 1981; Thomas et al. 1982; Bouvrain and Bonis 1985, 1988; Gentry and Heizmann 1996; Roussiakis 2003).

The present taxonomic re-appraisal and phylogenetic analysis (Fig. 6) indicate that ?*H. pilgrimi* from Torril 3, as well as *Hispanodorcas* and *Urmiatherium*, belong to "oiocerines", and, along with *Oioceros*, *Samodorcas*, *Samotragus*, and *Paraoioceros*, comprise a bovid clade of likely subtribal rank (Oiocerina Pilgrim, 1934; type genus *Oioceros* Gaillard, 1902), the monophyly of which still needs to be demonstrated. Although most of the diagnostic features of Oiocerina also occur in other groups of bovids (e.g., in *Tethytragus* Azanza and Morales, 1994 and its allies, or in some tragocerines), the combination of traits defining Oiocerina is unique. A comparison of the horncore structure of the oldest members of the subtribe (i.e., *Samotragus* from RZ1, Greece and ?*Hispanodorcas* from Torril 3, Spain; Fig. 7) indicates that the origin of Oiocerina likely predates the late Astaracian, since the almost conical and rather straight, slightly mediolaterally compressed, distinctly homonymously twisted, keeled and grooved horncores of the late Vallesian *Samotragus* from RZ1 retain more primitive features than those of the late Astaracian ?*H. pilgrimi* (Fig. 6). The RZ1 horncore morphotype is still unknown from the late Astaracian–early Vallesian Eurasian mammal faunas, and, while being quite unlike that of *Tethytragus* and its relatives, broadly resembles that of some "hypsodontines", such as *Turcocerus* (e.g., Köhler 1987; Dmitrieva 2007).

Though somewhat preliminary, the present phylogenetic analysis supports *Turcocerus* as the sister group of Oiocerina, with the *Turcocerus* + Oiocerina clade branching next to *Gazella* (Fig. 6). These results imply that the closest ancestry of Oiocerina lies within, or close to, the Middle Miocene "hypsodontines", and inside Antilopinae. It must be stressed, however, that the monophyly of "hypsodontines" is debatable, and that the phylogenetic relationships of tribes within Antilopinae are difficult to detect owing to their rapid late Neogene radiation, with molecular data frequently contradicting morphological and paleontological evidence (e.g., Gentry 1992, 2010; Hassannin and Douzery 1999; Vrba and Schaller 2000; Marcot 2007; Bibi et al. 2009; Hassanin et al. 2012). Oiocerina and crown Caprini with homonymously twisted horncores appear to share some important evolutionary trends, and likely some genuine synapomorphies, but their interrelationships need to be tested further.

The main radiation of Oiocerina took place during the late Vallesian (Fig. 9), roughly along the present day 40°N parallel, resulting in the widespread *Hispanodorcas* and *Oioceros*, and the southeastern European *Samotragus* and *Paraoioceros*. Slightly later, the Asian *Urmiatherium* and the apparently endemic *Samodorcas* from Samos emerged. Each of these genera developed a unique combination of ecomorphological features (i.e., body mass, dietary preferences, and intraspecific behaviors; Fig. 8), depending on their particular niche within the complex Neogene habitat spectra southwards of the western and in between the eastern branches of the Tethyan Mountain System. Although the unrooted cladogram of Azanza et al. (1998: fig. 3) provides possible evidence for a basal dichotomy within Oiocerina, the present analysis failed to confirm this (Fig. 6), owing to either inadequate data or multiple convergences towards a common ram-

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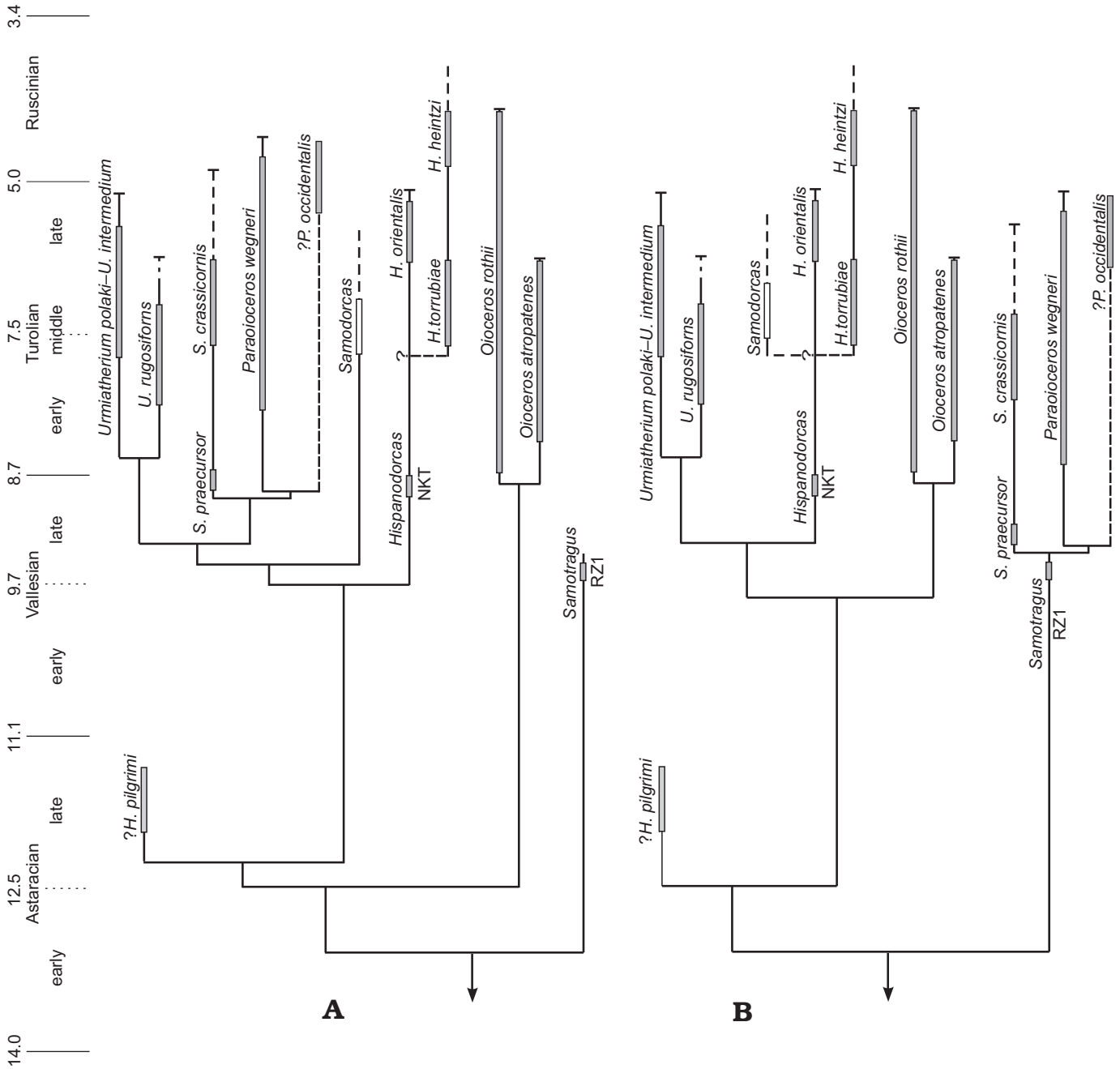


Fig. 9. Phylogenetic history of the subtribe Oiocerina at the species level (**A**) according to the results of the cladistic analysis (Fig. 6) and (**B**) assuming a morpho-chronological and regional continuum for *Samotragus*. Grey and white boxes indicate reliably known and questionable chrono-stratigraphic occurrences, respectively. Dashed lines indicate presumed ranges (vertical) or relationships (horizontal). Abbreviations: NKT, Nikiti-1; RZ1, Ravin de Zouaves 1.

ming fighting style among terminal "oiocerines". The cladistic results support *Samotragus* + *Paraoioceros* as part of an unresolved clade branching next to *Hispanodorcas*, and lead to a phylogenetic scenario (Fig. 8A) different from the one I propose, in which the clade comprising *Samotragus* + *Paraoioceros* is more closely related to *Samotragus* from RZ1 (Fig. 8B). Though less parsimonious, this phylogenetic scenario is supported by at least one synapomorphy (19[2]: presence of a lateral horncore furrow), is more consistent with chronological and geographic criteria, and further strengthened by the occasional occurrence of some primitive features characterizing the horncores of the RZ1 *Samotragus* in the RPl population of *S. praecursor*.

The geographic distribution of both *Paraoioceros* and *Samotragus* points to the northern Paratethys territory as the source area of their most recent common ancestor. The horncore and skull features of the two species of *Samotragus* (Figs. 4, 5, 7) suggest *S. crassicornis* from Samos to be a direct descendant of *S. praecursor* from RP1, which in my opinion originated from the RZ1 population (Fig. 9B). The origins of *Paraoioceros* likely also lie close to the RZ1 *Samotragus*, which may possibly be reflected in the primi-

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tive features of the Brisighella taxon (Fig. 9B). The presence of ?*P. occidentalis* in Italy is problematic, but a southwestward dispersal via the Balkano-Carpathian region, chronologically linked to the timing of the Paratethyan invasion (Kujumdgieva 1987) and the Messinian Salinity Crisis, may be possible.

The differences in the skull and horncore morphology between the ecologically similar and roughly contemporaneous *Oioceros rothii* and *Samotragus praecursor* suggest that the clades including those taxa likely diverged prior to the Vallesian. Gentry and Heizmann (1996: 383) noted in passing that "*Hispanodorcas* could represent a likely horncore morphology for an *Oioceros* ancestor". The present analysis supports a sister group relationship between *Oioceros* and the clade incorporating ?*H. pilgrimi*, suggesting a common origin (Figs. 6, 9) predating the late Vallesian, and possibly as old as the Astaracian. Compared to *Hispanodorcas*, the part of the *Oioceros* horncore located anterior to the lateral depression is more developed than the posterior one (Fig. 7B, E). Furthermore, twisting resulted in the lateral depression turning into a deep longitudinal furrow, with the posterior edge developing distally into a sharp keel (Fig. 7B, E), whereas the anterior keel remains a blunt crest (Fig. 7B, E). By contrast, the horncore and cranial features of ?*H. pilgrimi* look much closer to the expected ancestral morphology of *Oioceros rothii*, suggesting that *Oioceros* may have diverged from an eastern ?*H. pilgrimi*-like forerunner during the early–mid Vallesian (Fig. 9B)—although, according to the results of the cladistic analysis, a much earlier divergence would be expected (Fig. 9A). The emergence of *Oioceros* implies increasing territoriality (wrestling fighting behavior, mixed feeding habits, and horned females), which might be correlated with an expansion of open landscapes resulting from Late Miocene aridification (Janis 1982; Fortelius et al. 2006). The same environmental drivers might have allowed a branch of Southeastern European *Hispanodorcas*-like stock to develop a mixed diet and caprine-like skull features, giving rise to the East Aegean *Samodorcas kuhlmanni* of Turolian age (Fig. 9).

The present study provides no evidence to support Urmiatheriini Sickenberg, 1933, with all known species of *Urmiatherium* showing the main horncore apomorphies of *Hispanodorcas* (Figs. 6, 7), except homonymous torsion. It also seems reasonable to assume that the atlanto-occipital joint seen in *Hispanodorcas orientalis* could represent a forerunner condition to the extremely specialized joint of *Urmiatherium*. Thus, *Urmiatherium* may have diverged from a Western Asian branch of *Hispanodorcas*-like animals during the Vallesian, well after *?H. pilgrimi* (MN7/8) (Fig. 9). However, important questions regarding the phylogenetic relationships of the remaing members of the "urmiatheriines" remain unanswered, and call for a thorough review. The East Asian *Hezhengia* Qiu, Wang, and Xie, 2000—*Plesiaddax* Schlosser, 1903 lineage (Zhang 2003) may also have originated from "hypsodontine" stock via a *Lantiantragus* Chen and Zhang, 2004 stage, as proposed by Chen and Zhang (2004). The early Turolian *Shaanxispira* Liu, Li, and Zhai, 1978 is probably distinct from this lineage and nearer to *Samotragus*, judging from the strong anterior keel developed on the horncore and the overall skull morphology. On the other hand, based on their horncore and opisthocranial morphology, the Turolian *Sinotragus* Bohlin, 1935 and *Sivacapra* Pilgrim, 1939 from the Pliocene of India might be more closely related to the *Urmiatherium– Hispanodorcas* ancestry than to the other genera mentioned here. However, these taxa, as well as several other genera, including *Tsaidamotherium* Bohlin, 1935 and *Mesembriacerus* Bouvrain and Bonis, 1984, cannot yet be safely placed within the present framework.

Oiocerina emerged, radiated, and declined within Eurasia. Nevertheless, a marginal distribution in Africa cannot be excluded. Initially proposed to be related to the springbok lineage, the affinities of *Parantidorcas latifrons* Arambourg, 1979 remain unclear. Geraads (2010: 164) and Gentry (2010: 766) suggested the species to resemble the Eurasian Late Miocene *Oioceros.* There is no doubt that its thin, widely-spaced, almost straight, homonymously torsioned, keeled, and striated horn-cores implanted upon very short pedicles, as well as the presence of large supraorbital pits and the absence of sinuses within the low frontals clearly differentiate *Parantidorcas latifrons* from the springbok *Antidorcas* Sundevall, 1847. Most of these features, as well as the presence of a weak anterior keel, the degree of horncore torsion, the distal divergence of the horncores, and the strong labial relief of the upper molars, might indicate a relationship with the Spanish late Turolian–Ruscinian *Hispanodorcas,* which could have spread southwards during the Messinian.

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Appendix 1

Character-taxon matrix used for the phylogenetic analysis of Fig. 6. Outgroup: *Eotragus* Pilgrim, 1939 (data from Solounias and Moelleken 1992 and DSK personal observation). Data for *Turcocerus* Köhler, 1987, *Ovibos* Blainville, 1816, and *Hemitragus* Smith, 1826 are from Pilgrim (1934), Köhler (1987), Gentry (1992), Dmitrieva (2007), and DSK personal observation; data for *Gazella* Blainville, 1816 represent most frequent features and are based on personal observations on Miocene to living gazelles. Characters adopted from Gentry (1992: 4–6) are mentioned in brackets with the letter "G" and the relevant character number used by this author; modified characters are marked "~".

01 (G1): horncores short (0) or medium to long (1); 02 (~G13, 14): horncores without (0) or with homonymous twisting (1); 03: horncores non-twisted (0), weakly to moderately (1) or strongly twisted (2); 04: horncores non-spiraled (0) or spiraled (1); 05 (G7): horncores inserted above (0) or above the back (1) of the orbits; 06 (~G8, 9): horncores weakly to moderately (0) or strongly (1) inclined backwards in lateral view; 07: horncores without or weak (0) or with moderate to strong (1) backward curvature; 08 (G10): horncores inserted widely apart (0) or closely settled/in touch (1); 09 (~G12): horncores parallel to little divergent (0) or moderately to strongly diverent (1) in their proximal part; 10 (~G12): horncores weakly (0) or moderately to strongly (1) diverging distally; 11: horncore tips facing posteriorly or dorsally (0) or variably outwards (1); 12 (G5): horncore basal diameter small to intermediate (0) or large (1); 13 (~G2, 3): horncores uncompressed to mediolaterally compressed (0) or uncompressed to anteroposteriorly compressed (1); 14: horncore compression weak (0) or strong (1); 15: horncores taper gradually (0) or abruptly (1); 16 (~G4): horncores without (0) or with (1) anterior/ anteromedial keel; 17 (~G4): horncores without (0) or with posterior/posterolateral keel; 18: horncores without (0) or with lateral sulcus; 19: horncore lateral sulcus absent (0), forming a wide depression (1) or a furrow (2); 20: horncore lateral sulcus shallow (0) or deep (1); 21: horncore lateral surface undivided (0), equally divided (posterior part = anterior; 1), with posterior part larger than anterior one (2) or with posterior part smaller than anterior one (3); 22: horncore basal lateral surface convex (0) or flattened (1); 23 (~G11): horncore surface smoothly to irregularly grooved (0) or deeply grooved (1); 24: corneal process without (0) or with strong (1) lateral notch; 25: horncore overall pattern for stabbing (0), fencing/wrestling (1) or ramming (2); 26: pedicles strongly to moderately long anteriorly (0) or short to absent (1); 27: pedicles present (0) or absent (1) posteriorly; 28: frontals not raised (0), moderately (1) or strongly elevated (2) between the horncores; 29: frontal profile smooth (0) or strongly curved (1); 30: frontals not depressed (0) or depressed (1) in front of the pedicles; 31 (~G18): frontals without (0), or with moderate to extensive internal sinuses (1); 32 (~G25): temporal ridges rapidly converging posteriorly (0), wide apart (1) or almost absent (2); 33 (~G16): postcornual fossae present (0) or absent (1); 34: postcornual fossae placed posteriorly (0), laterally (1) or absent (2); 35 (~G22): supraorbital foramina/pits without (0), with moderately large (1) or with large (2) surrounding pits; 36 (~G24): supraorbital pits placed close to (0) or far anterior to (2) the pedicles; 37: face long (0) or short (1); 38: face shallow (0) or deep (1); 39: craniofacial angle weak (0), moderate (1) or strong (2); 40 (~G19, 20): cranial roof horizontal to slightly inclined (0) or distinctly angled/ curved posteriorly; 41: braincase long and deep (0), long and shallow (1) or shortened (2); 42 (G23): braincase sides parallel or widening posteriorly (0) or widening anteriorly (1); 43 (~G45): basioccipital elongate-triangular (0) or shortened-rectangular (1); 44: basioccipital normally developed (0) or extremely thickened (1); 45: basioccipital without (0) or with (1) medial longitudinal groove; 46: basioccipital with (0) or without (1) medial longitudinal keel; 47 (~G46): anterior tuberosities of basioccipital weak (0) or strong (1); 48: anterior tuberosities of basioccipital closely spaced (0) or far apart (1); 49: posterior tuberosities of basioccipital weak (0), strong (1), expanded laterally (2) or fused together (3); 50: basioccipital without (0) or with (1) additional facets for atlas; 51 (~G51): occipital surface faces bilaterally (0), posteriorly (1) or dorsally (2); 52 (G34): lacrimal fossa present (0) or weak to absent (1); 53 (G33): ethmoidal fissure present (0) or weak to absent (1); 54 (G44): auditory bullae small (0) or large (1); 55: auditory bullae compressed (0) or bulbous (1); 56 (G57): premolar row long (0; >60% or molars) or short (1); 57 (G75): lower molars without (0) or with (1) goat folds; 58 (~G65, 66, 73): molars without (0) or with (1) basal pillars; 59 (G71): upper molars without (0) or with (1) central islets; 60 (~G56): hypsodonty weak (0), moderate (1) or strong (2).

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