Contribution to the systematics and phylogeny of *Prostrepsiceros vallesiensis* Bouvrain, 1982 (Mammalia, Bovidae)

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ABSTRACT

The Vallesian heteronymous spiral-horned antelope *Prostrepsiceros vallesiensis* is revised according to some new specimens from the type locality, Ravin de la Pluie, Northern Greece. The new frontlet and isolated horn-core are larger, display weaker horn-core compression, and looser spiralling than in the holotype specimen of *P. vallesiensis*. These morphological differences are interpreted as representing sexual dimorphism, with the holotype being a female individual of the species. Morphological comparisons and a cladistic analysis of several late Miocene spiral horned antelopes allow for recognizing *P. vallesiensis* as the most likely ancestor of *P. vinayaki*, *P. libycus* and *Dytikodorcas*, while the *P. houtumschindleri* lineage probably originated from a pre- *P. vallesiensis* stock.

KEY WORDS
Mammalia,
Bovidae,
late Miocene,
SE Europe,
systematic,
phylogeny.

RÉSUMÉ

Contribution à la systématique et affinités phylogénétiques de Prostrepsiceros vallesiensis *Bouvrain, 1982 (Mammalia, Bovidae).*

L'antilope vallésienne à cornes spiralées hétéronymes *Prostrepsiceros vallesiensis* est révisée sur la base de nouveaux spécimens trouvés dans la localité type, le Ravin de la Pluie, Grèce septentrionale. Les nouvelles pièces, un massacre et un fragment de cheville, sont de plus grande taille et montrent une plus faible compression de la base des cornes et une spirale plus lâche que le spécimen holotype de *P. vallesiensis*. Ces différences morphologiques sont interprétées comme révélatrices d'un dimorphisme sexuel, l'holotype de l'espèce étant un individu femelle. Des comparaisons morphologiques et une analyse cladistique de quelques antilopes à cornes spiralées du Miocène supérieur permettent d'identifier *P. vallesiensis* comme l'ancêtre le plus probable de *P. vinayaki*, *P. libycus* et *Dytikodorcas*, tandis que la lignée de *P. houtumschindleri* tire probablement son origine d'un stock pré-*P. vallesiensis*.

MOTS CLÉS
Mammalia,
Bovidae,
Miocène supérieur,
Europe du Sud-Est,
systématique,
phylogénie.

INTRODUCTION

Known since the seventies, the primate-bearing late Vallesian (MN10) site Ravin de la Pluie (RPl, Lower Axios valley, N Greece; 40°46'N, 22°45'40"E), has provided a poorly diverse but significant artiodactyl assemblage that includes four bovid species: ?*Palaeoryx* sp., *Mesembriacerus melentisi* Bouvrain, 1975, *Samotragus praecursor* Bouvrain & Bonis, 1985 and *Prostrepsiceros vallesiensis* Bouvrain, 1982. Although scantily documented and hitherto geographically restricted, *P. vallesiensis* is believed to be an important stage in the evolutionary history of spiral-horned antelopes with heteronymous torsion (e.g., Bouvrain 1982; Bouvrain & Thomas 1992; Gentry & Heizmann 1996; Gentry 2003).

Apart from limited dental remains, skull material originally attributed to *P. vallesiensis* comprises an almost complete cranium (RPl-234) and a frontlet (Bouvrain 1982, Bouvrain & Bonis 1985). However, the latter specimen has never been re-described, refigured or even mentioned later. This speciman is not stored in the Laboratory of Geology and Paleontology of the Thessaloniki University.

Recent excavations in Ravin de la Pluie led by Prof. Louis de Bonis (University of Poitiers) and Prof. George Koufos (University of Thessaloniki), resulted in the discovery of an isolated horn-core (RPl-114n) and a frontlet (RPl-115n) of an heteronymous spiral-horned antelope. Both specimens are described here and compared with the type specimen of *P. vallesiensis*, providing new data on the morphological variability of the species and leading to a revision of its relations with other members of the genus.

ABBREVIATIONS

APD	anteroposterior diameter;
AUH	Abu Dhabi (Baynunah Formation), United Arab Emirates;
b	horn-core basis;
GSI	Geological Society of India;
LGPUT	Laboratory of Geology & Paleontology, University of Thessaloniki, Greece;
MNHNP	Muséum national d'Histoire naturelle, Paris;
MOL	Molayan (Afghanistan);
NHML	Natural History Museum, London;
RPl	Ravin de la Pluie, Axios Valley, Greece;
TD	transverse diameter;

SYSTEMATICS

Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Genus *Prostrepsiceros* Major, 1891

Prostrepsiceros vallesiensis Bouvrain, 1982

HOLOTYPE. — Cranium RPl-234 illustrated by Bouvrain (1982: figs 2, 3); Fig. 1.

TYPE LOCALITY. — Ravin de la Pluie, Axios valley, Greece.

NEW REFERRED MATERIAL. — Frontlet, RPl-115n; horn-core, RPl-114n; Fig. 2.

DEPOSIT. — Laboratory of Geology & Paleontology, University of Thessaloniki.

EMENDED DIAGNOSIS. — *Prostrepsiceros* of small size; females horned; basioccipital long and narrow with strong medial groove; nasal bones short, ending anteriorly at a single point; face slightly inclined to the opisthocranium; frontals very weakly inflated between the horn-cores in male individuals; supraorbital foramina small, round to pear-shaped and not sunken into pits; postcornual groove very shallow to almost absent; pedicels very short antero-laterally; horn-cores moderate in size compared to the skull; medio-lateral compression strong, increasing rapidly from the base to the top in females; moderate to strong postero-lateral and antero-medial keels; horn-cores weakly twisted (tighter in females) and very closely spiralled (more openly in females); primitive lower premolars; advanced hypsodonty; long, slender limbs.

OTHER OCCURENCES. — Middle Sinap, locality 40, Turkey.

AGE. — Late Vallesian (MN10).

DESCRIPTION

RPl-114n (Fig. 2C)

Proximal part of a right horn-core with part of the frontal bone. The APD at the base is = 31mm and the TD at the base is 23.3mm. The preserved length is about 120 mm but the cross-section at the top level indicates a longer horn-core, which probably attains 200 mm. The pedicel is very short posteriorly and not distinct from the horn-core at the medial and antero-lateral sides. Thin discontinuous grooves run along the horn-core surface. The basal cross-section is oval to elliptical and becomes

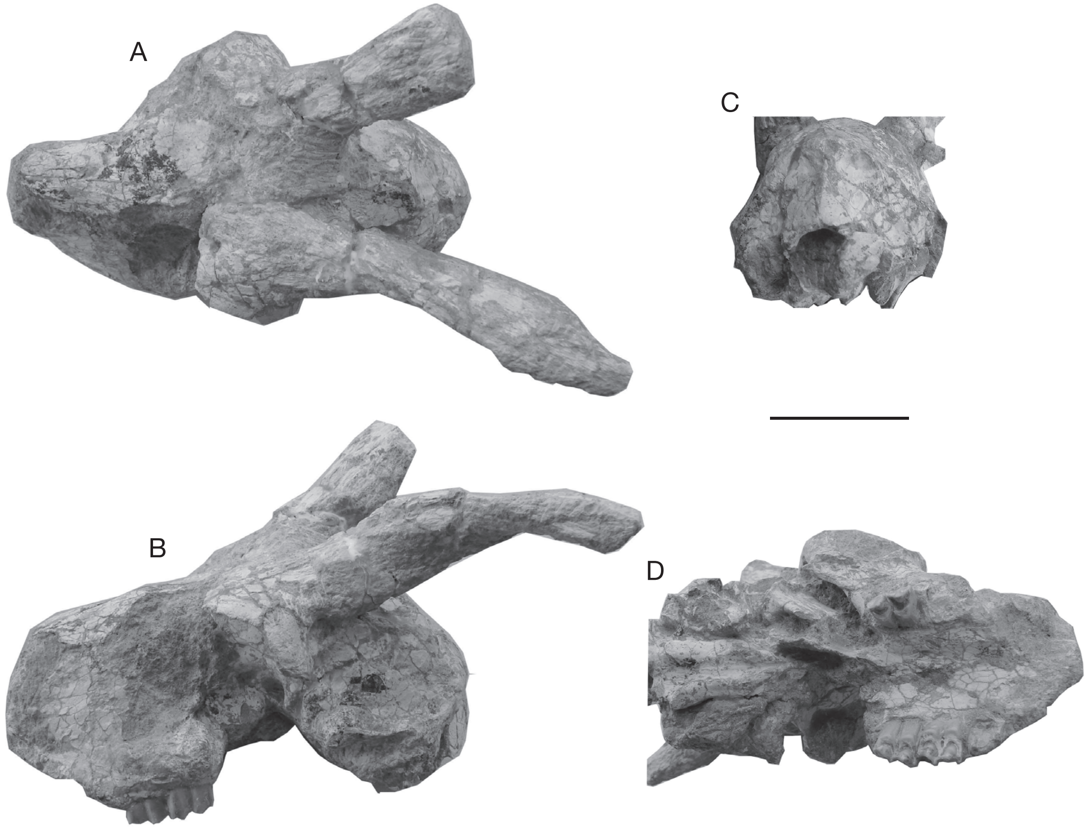

FIG. 1. — *Prostrepsiceros vallesiensis* Bouvrain, 1982, holotype skull RPl234: **A**, dorsal; **B**, lateral; **C**, occipital; **D**, ventral views. Scale bar: 4 cm.

almost semicircular towards the distal tip. The zone of maximum transverse thickness at the base is short and lies anteriorly. Medio-lateral compression is strong (75%) and increases further from the base to the top. The lateral face is slightly convex at the base, becoming flat or even concave upwards. The medial face is strongly convex. Two keels are present; a rather sharp anterior keel descends antero-medially, whereas a blunt posterior keel, probably affected by rolling, descends postero-laterally, giving rise to an almost flat postero-medial basal surface. Spiralling is close with coils weakly deviating from the torsion axis of the horn-core. Torsion is rather loose; at 10 cm from the base the antero-medial keel takes a lateral position, whereas the posterior one is shifted postero-medially (~1/2 of a complete coil).

RPl-115n (Fig. 2A, B, D)

Frontlet with proximal part of horn-cores. The back of the face slopes gently on the cranial roof. The mid-frontal suture is slightly raised in front of the pedicels. The frontals appear slightly thickened between the horn-cores. The supraorbital foramina are small, rounded and not sunken into pits; they are placed rather laterally compared to the descending point of the anterior keel. There are no sinuses in the frontals. The pedicel is observable only in the antero-lateral side of the horn-core base, while a smooth ridge occurs in its antero-medial face. The horn-cores are rather closely set on the cranial roof; the internal distance between the horn-core bases is 17.7 mm and the external one about 70.5 mm. The external distance between the supraorbital foramina is 35.3 mm. The APD at the base of the right horn-core is about 30 mm and the TD is 20.4 mm. The horn-cores are moderately divergent (~40°). The major axis of the horn-core base (APD) forms an angle of about 45° with the sagittal plane of the skull. The horn-cores are strongly tilted backwards; their angle with the preserved part of cranial roof is about 35°. They show a strong posterior keel descending postero-laterally and a blunt anterior keel descending antero-medially; the latter seems however, to be post-mortem weathered. Their torsion and spiralling are similar to those of the specimen RPl-114n.

REMARKS

According to the original diagnosis of *Prostrepsiceros vallesiensis* given by Bouvrain (1982: 118) this species is characterized as: "*Prostrepsiceros* of small size; horn-cores strongly compressed medio-laterally and small relatively to the skull; nasal bones short, ending anteriorly at a single point; face slightly inclined to the braincase; supraorbital foramina small and not sunken into pits" (translated from French). As Gentry (2003) points out, the name of the species was spelled *vallesienis* on the page where it was formally founded (Bouvrain 1982: 118), but it appears almost everywhere else as *vallesiensis,* which should be considered as the valid name (ICZN Art. 32.5).

As noted by Bouvrain (1982), the holotype of *P. vallesiensis* (Fig. 1) belongs to a young adult individual; the M3 is fully erupted but in the first stage of wear. Although the cranium represents a pre-mature stage of ontogenetic development, its horn-core morphology and size should correspond to a final stage. In similar sized extant antilopines (e.g., *Gazella dorcas*) a fully erupted and unworn M3 is usually associated with completely developed horn-cores.

The two new specimens RPl-114n and RPl-115n share in common with the holotype cranium RPl-234 of *P. vallesiensis* the weak inclination of the face on the cranial roof, the small and rounded supraorbital foramina without surrounding pits, and the general pattern of the horn-core morphology with close spiralling and loose torsion, strong medio-lateral compression and two more or less equally developed keels (Fig. 2). There is, therefore, no doubt that both new specimens belong to *P. vallesiensis*. Their absolute dimensions are, however, significantly larger (at about 10-15% in skull measures and 30-40% in horn-core dimensions; Fig. 3) than those of the holotype, indicating important intraspecific variability. Equivalent size differences are quite commonly displayed in sexually-dimorphic living and extinct bovids of open landscapes. Other morphological features come across as sexual dimorphism as well: even partly destroyed, the frontals of the holotype do not show the slight thickening between the horn bases seen in RPl-115n, whereas the horn-cores of RPl-234 are comparatively more widely spaced at their bases than those of RPl-115n (Figs 1, 2). Both features are usually indicative of horned female bovids in contrast to their male counterparts.

Judging from the comparison it is, consequently, suggested that the holotype cranium of *P. vallesiensis* should be ascribed to a female individual. According to this concept, the males of *P. vallesiensis* are larger, with thickened interfrontal region and more closely set horn-cores on the cranial roof, more loosely twisted and less coiled with a more convex medial face, elliptical to semicircular cross-section (instead of elliptical to spindle-shaped in females) and weaker medio-lateral compression towards the distal tips. The TD*100/APD index at the base is 72 in the type specimen (RPl-234) vs. 68 in RPl-115n and 75 in RPl-114n. At 4 cm above the base, however, the same index becomes 49.5 in the type specimen vs. 69.6 and 69.2 for the other two, indicating that the females have more compressed and faster tapering horn-cores than the males. The diagnosis of *P. vallesiensis* is, consequently, modified according to the new data, while the remaining cranial, postcranial and dental features follow Bouvrain (1982) and Bouvrain & Bonis (1985).

Outside the Axios valley, forms referred to *P. vallesiensis* have been recently described from Turkey. The specimen Loc. 40 89.457 from the MN 10 of Middle Sinap is described and figured by Gentry (2003: 350, fig.15.12) as *P.* aff. *vallesiensis* because it is similar to the type of this species but larger, less twisted, with less prominent postero-lateral keel and more convex medial surface. As already

FIG. 2. — *Prostepsiceros vallesiensis* Bouvrain, 1982 from RPl: **A**, **B**, **D**, frontlet RPl115n; **C**, right horn-core RPl114n; **A**, anterior; **B**, **C**, lateral; **D**, posterior views. Scale bar: 4 cm.

mentioned, these differences fall into the observed intraspecific variation seen in the type locality and they are interpreted as sexual dimorphism. The Turkish specimen shows great morphological and dimensional similarity to the male specimen RPl-114n (Fig. 3) and it could therefore be fully attributed to *P. vallesiensis*; the compatible geological age of both forms further supports such a decision.

Gentry (2003) also referred to *Prostrepsiceros* sp. a few additional specimens from the MN 9 of Middle Sinap (Fig. 3), mentioning affinities to *P. vallesiensis*. Although the described specimens are collected from different sites, they show most of the characters credited to *P. vallesiensis* from RPl. As Gentry (2003) points out, the most important differences of the Loc. 91 specimens from *P. vallesiensis* are the weaker spiralling and the narrower dorsal orbital rims.

DISCUSSION

Prostrepsiceros is a quite common late Miocene bovid genus in the Greco-Iranian province. It includes eight fossil species, the taxonomic status of these not always clearly defined nor generally accepted among specialists. Based mostly on differences in the horn-core pattern, Bouvrain (1982) already recognized a basic morphological division into species having horn-cores with closed spiralling, strong posterior keel and medio-lateral compression and species with somewhat lyrated or openly spiralled horn-cores, anteroposteriorly compressed and without keels or with a predominant anterior keel. The first group includes *P. vallesiensis*, *P. houtumschindleri* (Rodler & Weithofer, 1890), *P. vinayaki* (Pilgrim, 1939) and *P. libycus* Lehman & Thomas, 1987, while *P. rotundicornis* (Weithofer, 1888), *P. fraasi* (Andree, 1926), *P. zitteli* (Schlosser, 1904) and *P. axiosi* Kostopoulos, 2004 belong to the second group. Bouvrain (1982) credited subgeneric value to these two species-assemblages, probably implying an early split in the evolution of the genus. Nevertheless, species ascribed to the second group could have arisen from different predecessors. Namely, *P. axiosi* and its possible descendants *P. zitteli* and *P. rotundicornis* might have originated from a stock close to *Majoreas elegans* (Ozansoy, 1965), in which a well-defined anterior keel and an incipient spiralling were already present, whereas the horn-core pattern seen in *P. fraasi* (including the Maragheh variety) could indicate affinity to *Sinapodorcas* Bouvrain, Sen & Thomas, 1994, which shows widely spaced and lyrated horn-cores without keels and uprightly inserted on the cranial roof. Since the revision of the entire genus is beyond the scope of the present article, comparisons will be restricted within the first group of species, from which *P. vallesiensis* belongs to.

Prostrepsiceros houtumschindleri from Maragheh, Iran shares several morphological features with *P. vallesiensis* (e.g., Bouvrain 1982; Gentry 2003): strong medio-lateral compression of the horn-cores, sharp posterior keel that is stronger than the anterior one, similar horn-core insertion and backward inclination, slightly inclined cranial roof, relatively long face, long and narrow basioccipital with central longitudinal groove and strong anterior tuberosities, and a relatively short premolar row. *P. houtumschindleri* is, however, larger with much stronger spiralling/twisting on the horn-cores and more advanced dental and cranial features. *Prostrepsiceros houtumschindleri syridisi* Kostopoulos & Koufos, 1996 from the latest Vallesian locality Nikiti-1 (Greece) shows more primitive craniodental features than the type subspecies, but it is still different from *P. vallesiensis* in its larger size, longer, more divergent, less compressed and more spiralled horn-cores, and a face more flexed on the braincase.

Pilgrim (1939: 42) described from the Dhok Pathan (Siwaliks, Pakistan) a proximal part of a horn-core (specimen GSI B799; studied cast: NHML M42957) as representing a new species (aff. ?*Helicotragus*) *vinayaki* Pilgrim, 1939, later moved to *Prostrepsiceros* by Thomas (1984), who had further clarified its taxonomic status (see also Made & Hussain 1993). Although *P. vinayaki* is scarcely documented in the fossil record, it seems to cover a broad geographic area from Pakistan to Afghanistan and to Abu Dhabi (Thomas 1984; Gentry 1999; Merceron *et al.* 2004). According to the original diagnosis given by Pilgrim (1939), *P. vinayaki* is a small sized bovid with small, deep and pear-shaped supraorbital foramina and flat frontals. Its horn-cores diverge rather strongly and form a loose heteronymous spiral of about a quarter of a revolution, with an oval shaped cross-section and a well-marked anterior keel. Examination of a cast of the holotype confirms the above-mentioned characters in addition to a shallow postcornual groove, a flat medial surface of the horn-core, strong

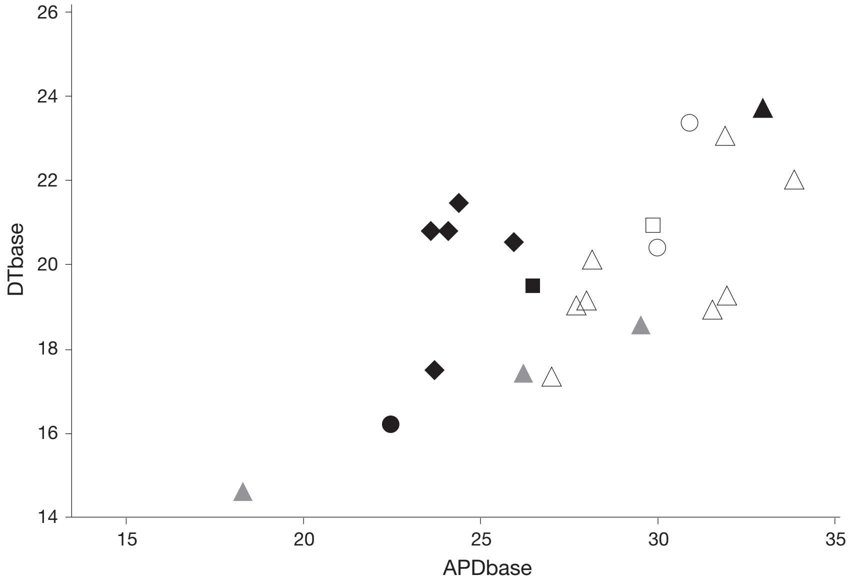

FIG. 3. — Scatter diagram comparing the horn-core basal dimensions of several late Miocene spiral-horned antelopes. *Prostepsiceros libycus* Lehman & Thomas, 1987 is placed outside the present metrical frame; ●, *P. vallesiensis* Bouvrain, 1982 holotype; ○, *P. vallesiensis* RP1 114n, 115n; ◆, *Dytikodorcas longicornis* Bouvrain & Bonis, 2007; ■, *P. vinayaki* (Pilgrim, 1939) holotype; □, *P.* aff. *vinayaki* Baynunah; ▲, *P. vallesiensis* M. Sinap Loc. 40; ▲, *Prostrepsiceros* sp. M. Sinap Loc. 91; △, *P.* aff. *vallesiensis* Middle Sinap. Abbreviations: **APD**, anteroposterior diameter; **DT**, transverse diameter.

medio-lateral compression (73.5%; Fig. 3), and a strongly grooved posterior face.

Based on two more specimens from Dhok Pathan and Malhuwala (Pakistan), Thomas (1984) noted that the horn-cores of *P. vinayaki* show clear posterior curvature, weak torsion, closed spiralling and – in contrast to Pilgrim's statement – an anterior keel that is less marked than the posterior one. On the other hand, Gentry (1999) observed in the Baynunah horn-core specimen (AUH441; Fig. 3) of *P.* aff. *vinayaki* a shallow postcornual groove, small supraorbital foramina without surrounding pits, weak horn-core divergence and backward inclination, flatter lateral than medial surface, an anterior keel that descends antero-medially and an approach to a posterior keel. More complete specimens of *P. vinayaki* have been unearthed from Molayan (Afghanistan; Bouvrain pers. comm. 2005) but the material is still awaiting publication. A brief examination of the best preserved specimen MNHNP MOL3502 confirms, however, most of the species characters.

P. vinayaki and *P. vallesiensis* are very similar in having comparable small size (Fig. 3), similar horn-core pattern (including torsion, spiralling, keel and ornament development, length, divergence, implantation, inclination, medio-lateral compression…), low frontals, weakly inclined face on the cranial roof, shallow to absent postcornual fossae, small pear/round-shaped supraorbital foramina not sunken into depressions and only weakly projected orbital rims. In fact, very few features distinguish *P. vinayaki* from the revised concept of *P. vallesiensis*: relatively larger supraorbital foramina, more medially shifted descending point of the anterior keel (resulting to a more perpendicularly placed long basal axis of the horn-core section comparatively to the sagittal plane) and presence of an anterior furrow along the horn-core or in its upper half at least. Unfortunately, apart from horn-cores and frontal morphology, no other skull characters of *P. vinayaki* are known that would enable a more detailed comparison with *P. vallesiensis*. Dental characters of *P. vinayaki* are not available but the Molayan material suggests advanced hypsodonty similar to that seen in *P. vallesiensis*.

Two more species are worth including in this comparison: *P. libycus* Lehman & Thomas, 1987 from the late Turolian of Sahabi (Libya) and *Dytikodorcas longicornis* Bouvrain & Bonis, 2007 from the late Turolian of Dytiko (Northern Greece). A few horn-core specimens from Baynunah Formation, Abu Dhabi referred by Gentry (1999) to as *P*. aff. *libycus* might in fact belong to *P.* aff. *vinayaki* from the same site. Although *P. libycus* is significantly larger than *Dytikodorcas,* it has similarly long and mediolaterally compressed horn-cores with feeble torsion/spiralling and a well-marked anterior groove. Based on these similarities Bouvrain & Bonis (2007: 16) propose transferring the Sahabi species to *Dytikodorcas*. These features are, however, present to some degree in *P. vinayaki* and *P. vallesiensis* as well. The long-narrow basioccipital with central longitudinal groove, the bi-laterally facing occipital with small condyles, the horn-core insertion above the back of the orbits, the anteroposterior direction of the maximum basal axis of the horn-core, the absence of frontal sinuses, the absence of supraorbital depressions and the presence of central islets on the upper molars are also features shared by *Dytikodorcas longicornis* and *P. vallesiensis*. On the other hand, *D. longicornis* has significantly longer pedicels than *P. vinayaki* and especially *P. libycus* and *P. vallesiensis*, whereas *D. longicornis* and *P. libycus* have more distantly spaced and less mediolaterally compressed horn-cores than the other two species (Fig. 3). The extremely feeble torsion, the large and deep postcornual fossae and the reduced hypsodonty of *D. longicornis* seem to be particular features of this species.

PHYLOGENETIC RELATIONSHIPS

Bouvrain (1982) suggested close relationships between *P. vallesiensis* and the type species of the genus *P. houtumschindleri*, while Gentry & Heizmann (1996) detected in *P. vallesiensis* the possible ancestor of both the small Jebel Hamrin form (referred to as *P. zitelli* by Bouvrain & Thomas 1992) and *P. houtumschindleri*. More recently, Gentry (2003) thought that *P. vallesiensis* and its more primitive allies from Middle Sinap (Turkey) might represent the ancestral stock of most late Miocene *Prostrepsiceros*, as well as, of some other Miocene spiral-horned antelopes.

The phylogenetic relationships of *P. vallesiensis* with the rest of the compared species are traced through a cladistic analysis based on a character matrix of 15 binary and 4 multi-state skull and horn-core features (Appendix). *Prostrepsiceros* from the early middle Turolian site Perivolaki (Greece) is also included in this analysis. This species was originally described as *Prostrepsiceros* cf. *fraasi* (Kostopoulos 2006) but it is now believed to be more closely related to the group incorporating *P. vallesiensis* and *P. houtumschindleri*.

The exhaustive method and the ordered optimization criteria with accelerated transformation of the characters (ACCTRAN) have been followed (PAST version 1.84, Hammer *et al.* 2001). The cladogram is rooted to a hypothetical ancestor (outgroup in Fig. 4), in which all characters are shown to be plesiomorphic. The analysis provided a single most parsimonious tree of 36 steps, ECI: 0.63 (Fig. 4) that supports sister-group relationships between ((*P. houtumschindleri* + Perivolaki *Prostrepsiceros*) + *P. h. syridisi*), and (*P. vinayaki* + (*P. libycus* + *Dytikodorcas*)), even though bootstrapping with 1000 pseudoreplicates shows low statistical credibility. *P. vallesiensis* comes out as the sister-group of both lineages (Fig. 4).

Nevertheless, some objections have to be raised on the topography of the cladogram and the distribution of the character states (Fig. 4) that indicates a high frequency of homoplasies and reversals as it would be probably expected for matrices dealing mainly with horn morphology. The cladogram shows that most of the features characterizing *P. vinayaki* appear to be homoplastic with those of *P. vallesiensis*, probably suggesting a higher degree of relationship than the exposed one. On the other hand, the preference of homoplastic advances over homoplastic reversals in Hc7 (mediolateral compression) and Hc8 (posterolateral keel) does not seem to be the most appropriate choice of character distribution, as it underestimates secondary losses and treats them as truly plesiomorphic. An option supporting the parallel loss of the posterolateral keel and the secondary decrease of the

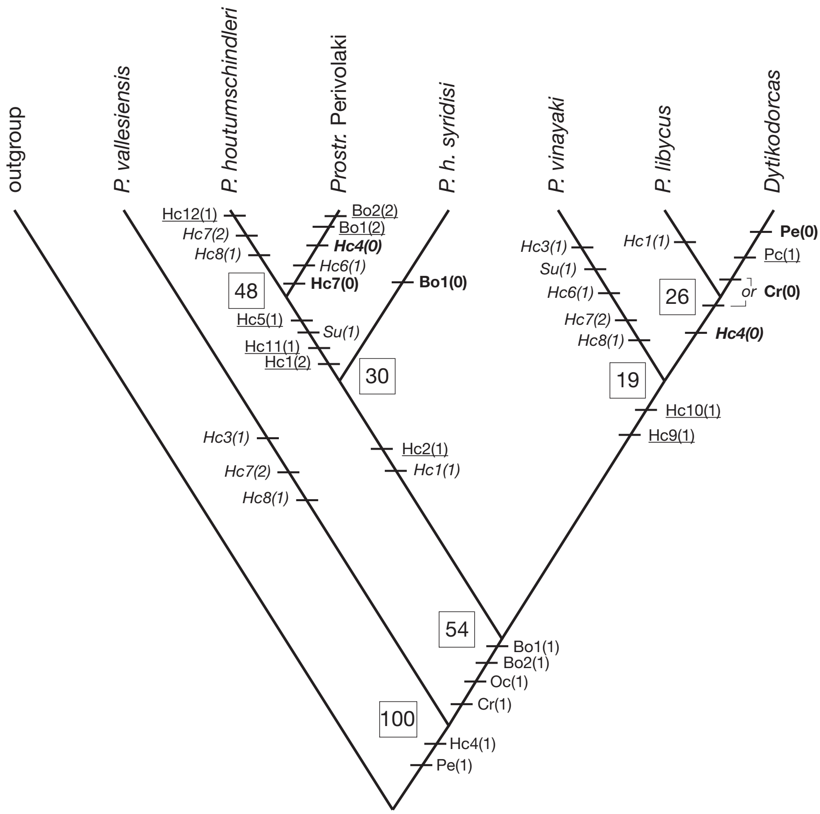

FIG. 4. — One maximally parsimonious cladogram of seven fossil spiral horned antelopes based on the character matrix of Appendix. Characters on the diagram indicated with bold letters represent reversals; characters indicated with italics represent homoplasies; characters marked as bold-italics indicate homoplastic reversals; underlined characters show apomorphies and autapomorphies. Character abbreviations as in the Appendix. Numbers in squares represent % values of bootstrapping support with 1000 pseudo-replicates. Abbreviations: ***P.***, ***Prostr.***, *Prostrepsiceros*; **h.**, *houtumschindleri.*

mediolateral compression in some terminal taxa or clades is suggested. Conversely, morphological turnbacks on basic cranial features like those supposed by the character distribution of Bo1 (basioccipital shape) seem unreasonable; a delayed transformation scenario that precludes such kind of reversals ought to be preferred in such cases.

In an alternative slightly longer tree (length: 38, ECI: 0.60, number of trees 32), which is preferred here, *P. vallesiensis* would be the sister group of "*P. vinayaki-P. libycus- Dytikodorcas*" with the clade of "*P. houtumschindleri*" branching next (Fig. 5). Most of the nodes are much better supported by bootstrapping and the secondary losses are now recognizable. Figure 6 composes these results and the available chronological data into a phylogenetic scenario.

Although *Prostrepsiceros* sp. from Loc. 91 of Middle Sinap is excluded from the parsimony analysis because of inadequate data, its general aspect looks more primitive than that of *P. vallesiensis* from MN 10 in the lower degree of torsion and the weaker development of keels and it should be directly related to the origin of *P. vallesiensis*. "*Prostrepsiceros houtumschindleri*" clade might originate from a somewhat earlier stage, in which mediolateral compression was not yet exaggerated, in contrast to the horn-core lengthening and divergence. In comparison with other species referred to *Prostrepsiceros,* the entire clade is generally distinguished by the presence of a long and narrow

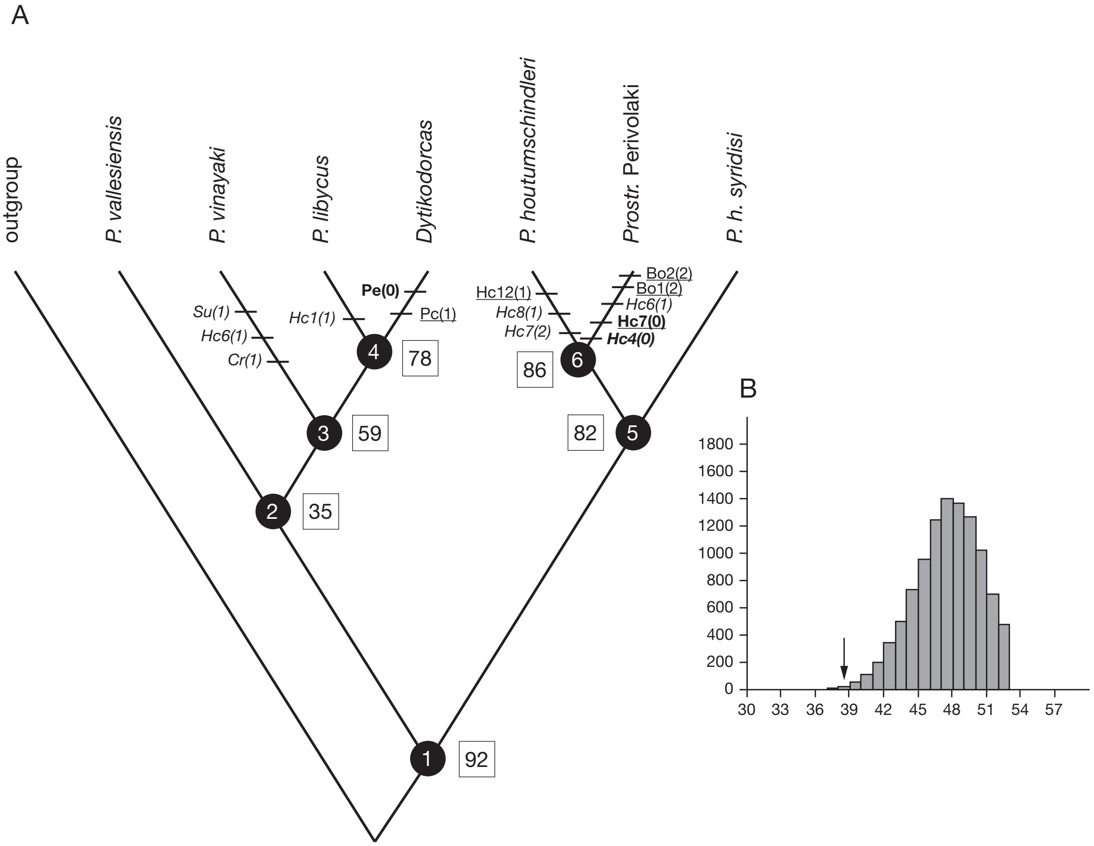

FIG. 5. — **A**, One of the 32 most parsimonious trees with length 38, ECI: 0.60 that is preferred here. A delayed transformation scenario has been chosen for characters Oc and Bo2 (see text). Character changes supporting nodes 1-6 are: Node 1 = *Hc4(1), *Pe(1) and obviously Hc7(1); Node 2 = Hc3(1), *Hc7(2)*, *Hc8(1)*; Node 3 = Hc9(1), Hc10(1), *Oc(1)*, *Bo1(2)*, *Bo2(1)*; Node 4 = **Hc3(0)**, ***Hc4(0)**, *Hc7(1)*, *Hc8(0)*; Node 5 = *Hc2(1), **Hc1(1)*, *Bo2(1)*, *Oc(1)*, *Cr(1)*; Node 6 = *Hc1(2), *Hc5(1), *Hc11(1), *Bo1(1), *Su(1).* Unambiguous character changes supporting the same nodes on both trees are marked with an asterisk. Characters supporting terminal taxa are all the same in the favored and most parsimonious trees except for *Cr(1)*. Character coding as in Figure 4. Numbers in squares represent % values of bootstrapping support with 1000 pseudoreplicates; **B**, Distribution of cladogram lengths. Abbreviations: ***P.***, ***Prostr.***, *Prostrepsiceros*; **h.**, *houtumschindleri.*

basioccipital with a central longitudinal groove, short pedicels, strongly inclined horn-cores that might stand more uprightly in later forms, increased mediolateral compression, presence of a posterior keel that might weaken through time, and presence of an anterior keel that might be lost or replaced by a longitudinal furrow in younger species.

Apart from overall size increase, the "*P. houtumschindleri*" lineage seems to follow a quite different horn-core evolutionary pattern to that of *P. vallesiensis-P. vinayaki-P. libycus-Dytikodorcas*, showing increasing lengthening, massiveness, backward curvature, divergence, and spiralling of the horn-cores, but retaining a less pronounced mediolateral compression that may later be lost. Additionally, the anterior keel fades out, the supraorbital foramina sink into large pits and the basioccipital shortens losing its medial groove. *Prostrepsiceros* from Perivolaki shows several advances, such as the shortening and widening of the basioccipital, the more upright insertion of the horn-cores and the mediolaterally shifted great basal axis of the horn-cores associated with the reduction of the mediolateral compression. Several of these features are certainly homoplastic with those oc-

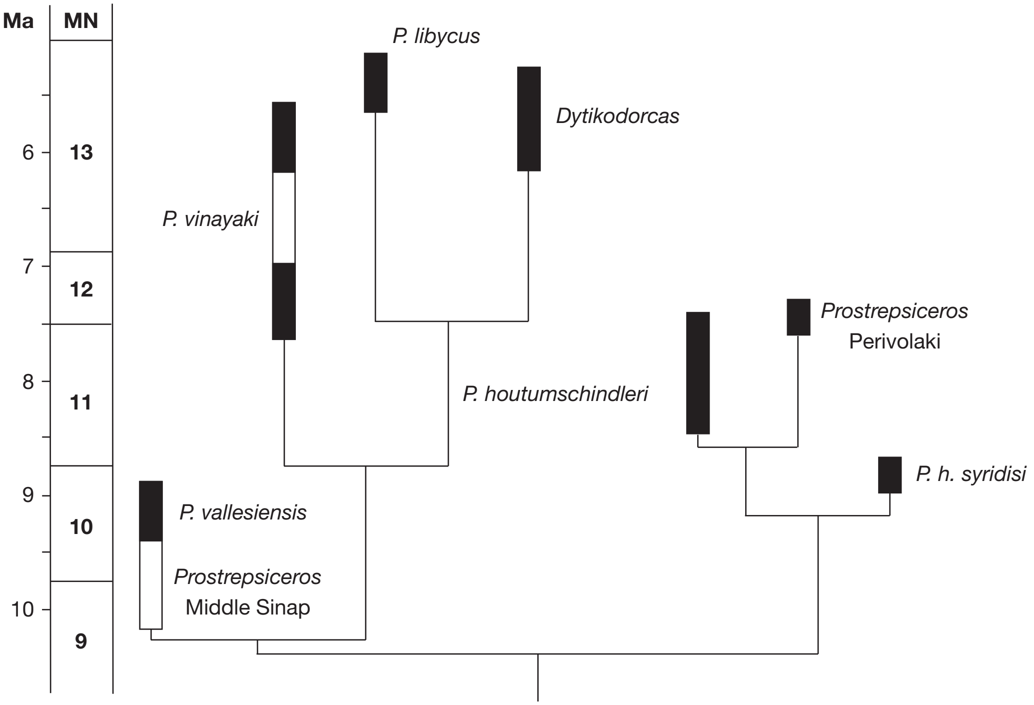

FIG. 6. – Phylogenetic scenario indicating possible relationships among the species discussed. Abbreviations: ***P.***, *Prostrepsiceros*; ***h.***, *houtumschindleri.*

curring in other species referred to the same genus, such as in *P. fraasi*.

The clade starting with *P. vallesiensis* shows supraorbital foramina without surrounding pits, weak horn-core divergence, torsion and spiralling, persistence of an anterior keel associated or replaced later by a furrow, and increased mediolateral compression secondarily reduced in younger species, in which horn-cores might also stand more upright and apart loosing entirely their posterior keel. *Prostrepsiceros vinayaki* retains several primitive cranial features seen in *P. vallesiensis*; these two species seem to comprise a morphological continuum characterized by basic transformations, these being the decrease of the slope of the cranial roof and the mediolateral shift of the great basal axis of the horn-cores.

As suggested by the cladistic analysis, *P. libycus* is probably related to the *Dytikodorcas* clade, but the lack of adequate evidence concerning the cranial anatomy of the Libyan species does not allow more accurate conclusions for the moment. On the other hand, the distant geographic signal of these two forms rather opposes a late common ancestry. *P.* aff. *vinayaki* from Abu Dhabi might be proved to be critical in the resolution of the *P. vinayaki*-*P. libycus* transition. The *D. longicornis* clade is characterized by a basically primitive skull, slightly more advanced than that of *P. vallesiensis,* a few horn-core novelties such as the reduction of the posterior keel and several particularities such as the development of large and deep postcornual grooves, high pedicels and less hypsodont teeth, features apparently primitive that could be, however, associated with the endemic character of the Dytiko fauna (Bouvrain & Bonis 2007).

CONCLUSIONS

New material of *Prostrepsiceros vallesiensis* from its type locality, Ravin de la Pluie, Greece, allows revision of its diagnostic characters and identification of the holotype skull as a female individual of the species. Cladistic analysis and morphological comparisons of *P. vallesiensis* with a set of late Miocene spiral horned antelopes indicate *P. vallesiensis* as a possible ancestor of *P. vinayaki*, *P. libycus* and *Dytikodorcas*, whereas the "*P. houtumschindleri"* lineage and *P. vallesiensis* seem to share an older common ancestry.

The study raises a number of questions concerning the validity of the current systematics of several late Miocene spiral horned antelopes. The regard of *Dytikodorcas* as a distinct genus for *D. longicornis* and *D. libycus*, as Bouvrain and Bonis suggested (2007), implies a paraphyletic nature for *Prostrepsiceros*. From a phylogenetic perspective, however, the obvious resolution would be the absorption of the former by the latter. Alternatively, *Dytikodorcas* could incorporate the species *vinayaki* and *vallesiensis*, leaving *Prostrepsiceros* for the "*P. houtumschindleri"* lineage, a resolution that would trigger new problems for the systematics of species outside the present group but still referred to *Prostrepsiceros*.

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APPENDIX

TABLE 1. — Character-taxon matrix used for phylogenetic analysis. Outgroup = hypothetical ancestor. **Hc1**, horn-cores short and slim (0), long and slim (1) or long and massive (2); **Hc2**, horn-cores weakly (0) or strongly (1) divergent; **Hc3**, horn-cores set apart (0) or close together (1); **Hc4**, horn-cores weakly-moderately (0) or strongly (1) tilted backwards; **Hc5**, horn-cores weakly (0) or strongly (1) curved backwards; **Hc6**, great basal axis of horn-core more (0) or less (1) parallel to the sagittal plane; **Hc7**, mediolateral compression weak (0; > 85%), moderate (1) or strong (2; < 75%); **Hc8**, posterolateral keel absent to rudimentary (0) or moderate to strong (1); **Hc9**, anterior keel weak-absent (0) or moderate-strong (1); **Hc10**, anterior horn-core furrow absent (0) or present (1); **Hc11**, horn-core closely (0) or openly (1) spiralled; **Hc12**, horn-core torsion absent/weak (0) or strong (1); **Pe**, pedicles high (0) or short (1); **Su**, supraorbital foramina small without pits (0) or larger into pits (1); **Pc**, postcornual groove weak/absent (0) or large-deep (1); **Bo1**, basioccipital long and narrow posteriorly (0), long and moderately wide posteriorly (1), shorter and wide posteriorly (2); **Bo2**, basioccipital with strong medial longitudinal groove (0), with anteriorly localized groove (1) or without groove (2); **Oc**, occipital facing bi-laterally (0) or posteriorly (1); **Cr**, cranial roof curved down posteriorly (0) or slightly inclined-horizontal (1). Hc1, Hc2, Hc3, Hc4, Su, Pc, Bo, Oc, Cr polarization follows Gentry (1992); Hc5, Hc6, Hc8, Hc9, Hc10, Hc11, Hc12 polarization is traced by outgroup comparison with other members of Antilopini (gazelles and neotrages). Although outgroup comparison with other members of Antilopini indicate state (0) as the primitive condition of character Hc7, is assumed that state (1) might better reflect the primitive condition in the ingroup node. Abbreviations: ***P.***, *Prostrepsiceros*; ***h.***, *houtumschindleri*; **PER***,* Perivolaki, Greece*.*

	Hc1	**Hc2**	**Hc3**	**Hc4**	**Hc5**	**Hc6**	**Hc7**	**Hc8**	**Hc9**	**Hc10**	**Hc11**	**Hc12**	**Pe**	**Su**	**Pc**	**Bo1**	**Bo2**	**Oc**	**Cr**
outgroup	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
P. vallesiensis	0	0	1	1	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0
P. houtumschindleri	2	1	0	1	1	0	2	1	0	0	1	1	1	1	0	1	1	1	1
P. vinayaki	0	0	1	1	0	1	2	1	1	1	0	0	1	0	0	1	1	1	1
P. libycus	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	?	?	?	?
Dytikodorcas	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0
P. h. syridisi	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1
Prostrepsiceros PER	2	1	0	0	1	1	0	0	0	0	1	0	1	1	0	2	2	1	1