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Parastrepsiceros koufosi n. sp. (Mammalia: Bovidae); note on the possible presence of a *Prostrepsiceros* descendant in the latest Pliocene of northern Greece

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Abstract. The present paper deals with some bovid remains from the latest Pliocene locality of Gerakarou (Mygdonia basin, Greece). The material belongs to the new species of a small, spiral – horned antelope *Parastrepsiceros koufosi* n.sp. A short description and comparison of the material as well as discussion of the generic position and phylogenetic relationships of the Greek form are also given.

Key words: systematics, Bovidae, latest Pliocene, Greece.

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I. INTRODUCTION

In 1978, after the great earthquake in the Thessaloniki region, a geological team discovered some fossil remains in the Dervouna ravine (Mygdonia basin) (ZAMANIS et al. 1980). A geologist R. DIMITRAKOPOULOS showed the fossiliferous site to Prof. G. KOUFOS of Thessaloniki University, who undertook excavations in the area. The first data were published by KOUFOS & MELENTIS in 1983 and the locality was named "Gerakarou" (GER). Continuous paleontological investigations brought to light an important collection of fossil mammals. Part of the material as well as the stratigraphy of the basin, were studied by KOUFOS (1986a; 1986b; 1987; 1992), KOUFOS *et al.* (1989; 1995), and KOLIADIMOU (1996). The Artiodactyls of Gerakarou make a part of the subject of the author's PhD Thesis (KOSTOPOULOS 1996). The locality is considered to be of latest Pliocene age (end of Senèze Faunal Unit); most of the typical "Villafranchian" faunal elements are present, while more recent and/or evolved forms also appear (KOSTOPOULOS 1996; KOSTOPOULOS & KOUFOS in press).

Amidst the bovid materials from Gerakarou are some spiral horn-cores and few dental and postcranial remains, corresponding to those of a small- sized "antelope". The description of this material as well as its comparison with the known spiralled antelopes of Eurasia, together with an extensive discussion of their generic determination will be given in this paper.

A c k n o w l e d g m e n t s. Thanks are due to Prof. G. KOUFOS, Prof. A. GENTRY and Dr. G. BOUVRAIN for fruitful advice and discussion. I would also like to thank the State Scholarship Foundation and the Naval Administration of Northern Greece for their assistance. Thanks are also due to Dr. E. CREGUT for his critical review of the manuscript. Linguistic amelioration by G. KOSTOPOULOU; drawings by I. SYLVESTROU.

II. SYSTEMATICS

Genus *Parastrepsiceros* VEKUA, 1968

Parastrepsiceros koufosi n. sp.

Fig. 1-4, Tab. 1

S y n o n y m s: 1996 – "*Prostrepsiceros*" *koufosi*. KOSTOPOULOS, p. 226

T y p e s p e c i m e n: Right horn-core, GER-273.

T y p e l o c a l i t y: Gerakarou, Mygdonia basin, Macedonia, Greece.

A g e: Latest Pliocene (end of Seneze Faunal Unit).

N a m e d e r i v a t i o n: In honour of my teacher Prof. G. KOUFOS who found the material.

S t u d y m a t e r i a l: Right horn-core, GER-270; right and left horn-core, GER-274/275.

P o s s i b l y c o n s p e c i f i c: Maxilla, GER-48; P^2-P^4 *in situ*, GER-349; P^4-M^1 *in situ*, GER-348; part of mandible with P_3-M_3, GER-148, Mc_{III+IV}, GER-276.

D i a g n o s i s: Small-sized antelope with normal, open spiralled horn-cores. The horn-cores are long, with very loose torsion and an insert above the orbit. They are strongly curved backwards in their middle and fairly recurved upwards in their distal part. The divergence of the horn-

Table 1

Comparative table of horn-core and dental measurements (in mm) of different Miocene / Pliocene antelopes (measurements from VEKUA 1970 and LEHMANN & THOMAS 1987); *=length along the external surface of the horn-core

Horn-cores	Length*	Height	DAP base	DT base
Parastrepsiceros koufosi GER-274	280	190	–	–
GER-275	200	190	32.0	27.0
GER-270	230	190	30.0	24.0
GER-273	220	180	34.7	28.5
Parastrepsiceros sokolovi Georgia	302-335	–	48.3	58.8
Prostrepsiceros libycus Sahabi, Liby	350	–	32.1	26.8
Maxilla	P^2-M^3 (1)	P^2-P^4 (2)	M^1-M^3 (3)	(2) × 100/(1)
P. koufosi mean	64.3	24.6	42.7	38.3
P. sokolovi N596	102.0	32.0	68.0	31.6
P. sokolovi N602	90.0	32.0	58.0	35.5

cores is great. The medio-lateral compression is smooth; the cross-section elliptical to round. A vestigial posterior keel is present, originating on the postero-lateral side. The pedicle and postcornual fossae are absent. Fine longitudinal grooves run along the surface of the horn-cores. The subtriangular, supraorbital pits are large and deep. Short premolar row relatively to the molars. Upper molars with strong styles. P_3 with clear parastylid separated from the elongate elliptical paraconid. P_4 with free metaconid, vertical to the longitudinal axis of the tooth. Pli-caprin and ectostylid present on the lower molars. Third lobe of M_3 subrounded. Elongated and slender metacarpal.

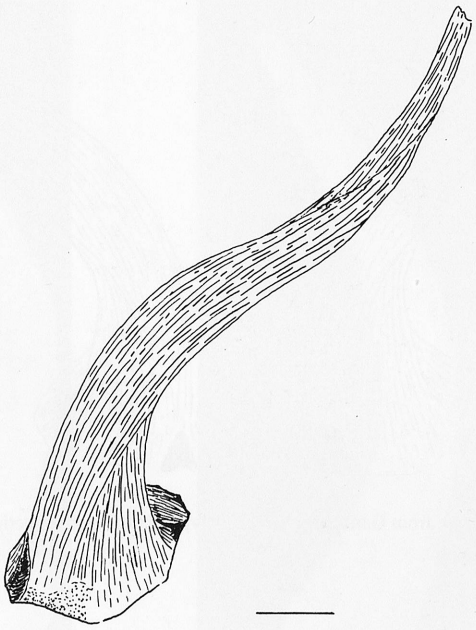

Fig. 1. *Parastrepsiceros koufosi* n. sp. from Gerakarou, Greece. Horn-core specimen GER-270, lateral view. Scale: 2cm.

II. DESCRIPTION

Horn-cores. In the specimen GER-274/275, where a part of the frontal is preserved, there is no vestige of the pedicle and the horn-cores are in direct contact with the cranial roof. The supraorbital pits are subtriangular, large and deep (Fig. 2,4). There are no sinuses in the frontals or in the horn-core base. The postcornual fossa is absent. Although all the specimens of horn-cores are equally massive, indicating adult individuals, their length varies: the specimens GER-274/275 are longer than GER-273 and GER-270. This is probably due to sexual dimorphism but the material is not large enough to allow certain conclusions. In lateral view, the horn-cores are inserted above the orbits, almost perpendicular to the cranial roof. In frontal view, they are well separated from each other at the base and slightly in lateral position (Fig. 1, 2). The basal distance between the horn-cores (internal) is above 27 mm. In their proximal part the horn-cores slightly incline backwards and laterally, while in their distal part are strongly diverged (Fig. 1, 2, 4). They are normally spiralled (the right horn-core is anticlockwise spiralled from base to top) and a very loose torsion is present. The horn-core torsion forms – on average – a complete helix (Fig. 2,4). In the middle of their height

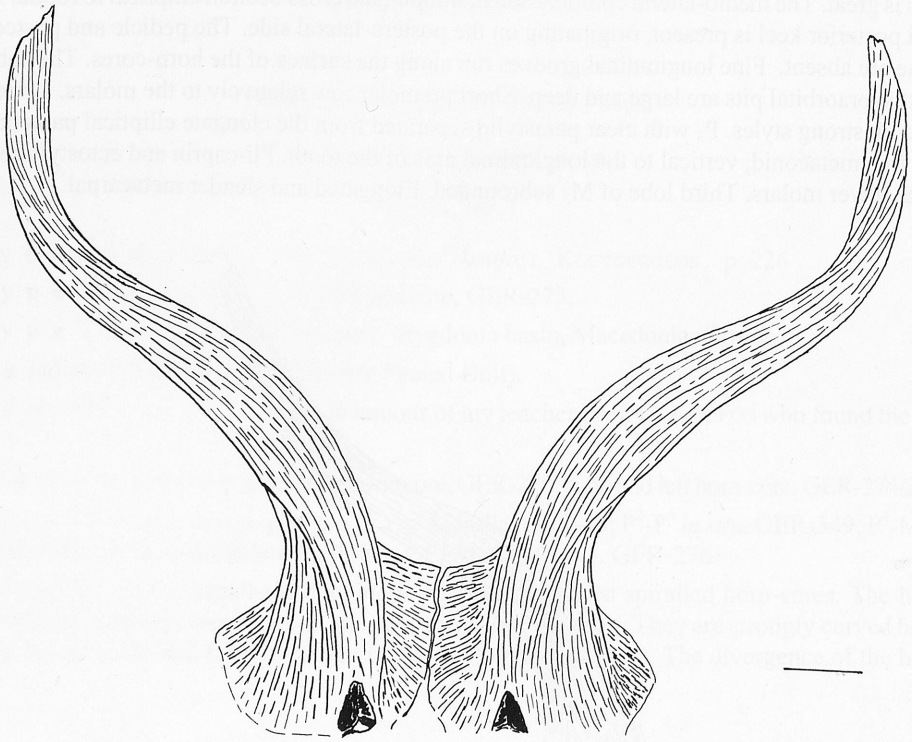

Fig. 2. *Parastrepsiceros koufosi* n. sp. from Gerakarou, Greece. Hypothetical reconstruction of the frontlet GER-274/275, frontal view. Scale: 2cm

the horn-cores are strongly curved backwards and laterally, and they are recurved upwards in their uppermost part (Fig. 1, 4). In their distal part the horn-cores present a slightly lateral depression. In the two better-preserved specimens (GER-273, 270) a vestigial posterior keel is present. This keel descents in a postero-lateral insertion and becomes invisible to the top. Fine longitudinal grooves run along the surface of the horn-cores.

Upper toothrow. The P^2-M^3 length is 63.5 mm, with the index "LP^2-P^4 $100/L \times M^1$-M^3" 38.3, indicating a short premolar row. P^2 presents a lingual bilobation with a strong hypocone. P^3 is similar to P^2 with a strong parastyle and paracone. The protocone and the hypocone are equally developed. In the occlusal face there are two fossettes. P^4 is not bilobate; it appears smaller and more rounded than P^3, while its hypocone is under-developed. The molar styles are well developed. The strong metastyle of M^3 is directed posteriorly and forms a smooth wing.

Lower toothrow. The known length of P_3-M_3 is 62.5 mm, while the length of the molar row is 44 mm. P_3 has a clear parastylid and an elongate elliptical paraconid. Both are situated anteriorly (Fig. 3). The first valley is open in the upper half of the tooth. The metaconid is situated laterally to the anteroposterior axis of the tooth. The second valley is V-shaped, while the third one is narrow and opens only in the upper third of the crown. The entoconid is elliptical, vertical to the anteroposterior axis of the tooth and connected with the entostylid since the first stage of wear (Fig. 3). P_4 has a strong parastylid separated from the paraconid. The latter is sub-squarish, directed backwards

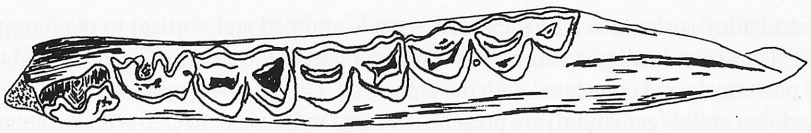

Fig. 3. *Parastrepsiceros koufosi* n. sp. from Gerakarou, Greece. Left mandibular ramus, GER-148, occlusal view. Scale: 2cm.

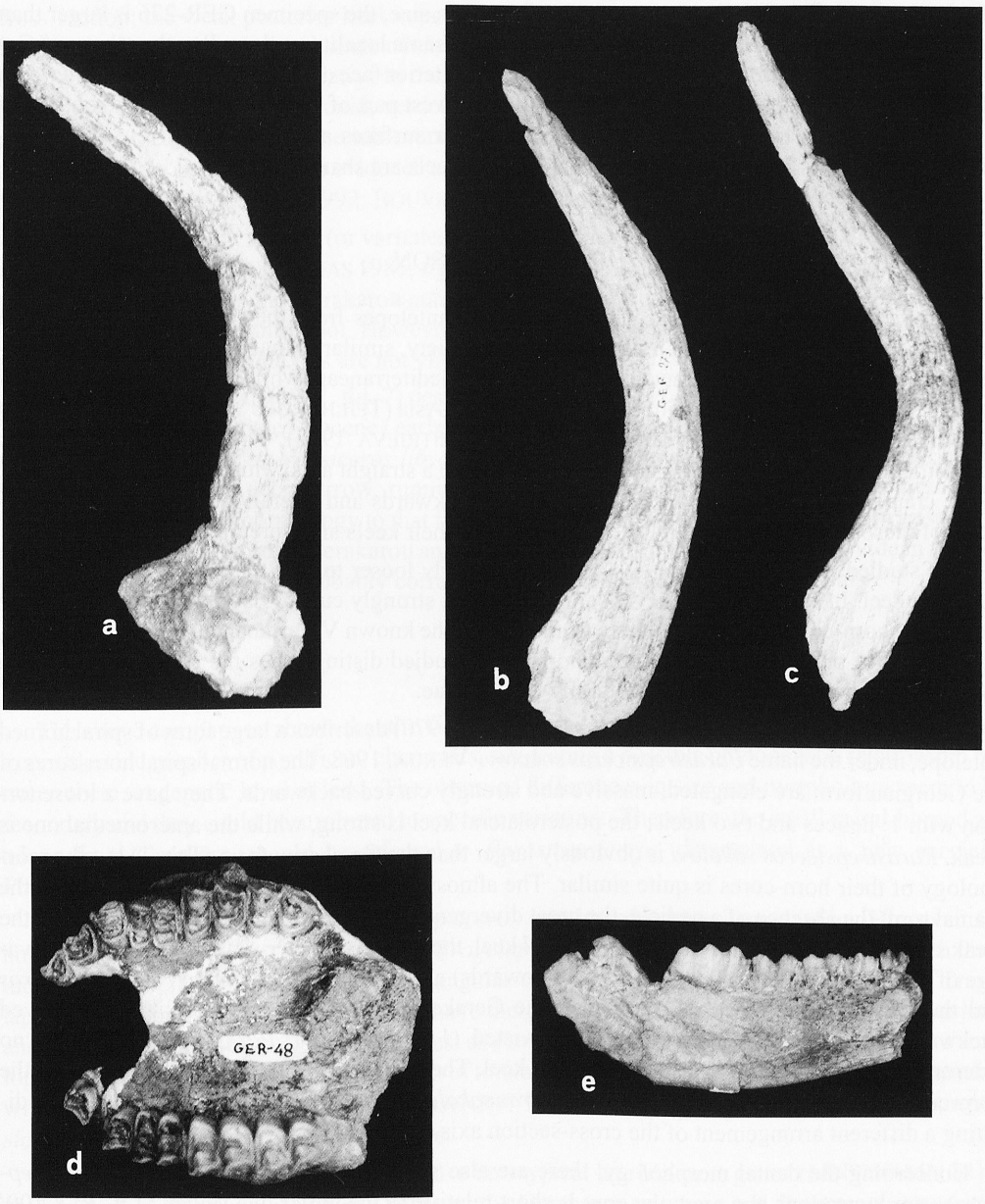

Fig. 4. *Parastrepsiceros koufosi* n. sp. from Gerakarou, Greece. a – left horn-core, GER-275, internal view; b – left horn-core, GER-273, internal view; c – left horn-core, GER-270, internal view; d – maxilla, GER-48, occlusal view. ca 1/2 natural size; e – left semi-mandible, GER-148, lingual view. ca 1/2 natural size.

(Fig. 3). The first valley is shallow. The metaconid is sub-rounded and vertical to the longitudinal axis of the tooth. The second valley opens only in the upper part of the crown. The entoconid is elongated, directed posteriorly and connected with the entostylid. On the lower molars a weak pli-caprin and a small interlobar stylid (ectostylid) are present. The ectostylid is connected with the anterior rib of the hypoconid. The third lobe of M_3 is sub-rounded in shape (Fig. 3).

Postcranials. The metacarpal is elongated and slender (Length=195 mm; DT_{prox}=23.5 mm; DAP_{prox}=16.3 mm; DT_{diaph}=14.7mm; DAP_{diaph}=13.2 mm; $DT_{dist\text{-}art}$=22.5 mm; $DAP_{dist\text{-}art}$=18 mm). The robustness index ("$DT_{diaphysis}$ x 100 / L") is 7.5. In size, the specimen GER-276 is larger than the metacarpals of *Gazella* and *Croizetoceros* from the same locality and smaller than those of *Gazellospira*. The furrow for the Lateral Extensor in the anterior face of the proximal part is very weak. The groove of co-ossification is present only in the lowest part of the anterior face. The outline of the distal epiphysis looks squarish: the distal articular surfaces are high and narrow. The intertrochlear incision is very narrow and V-shaped. The keels are sharp.

III. COMPARISON

Despite their great importance, the spiral horned antelopes from the so called Villafranchian faunas of Eurasia do not present a significant form variety, similar to that of the late Miocene. *Gazellospira* is the sole known genus from the western Mediterranean, while *Antilospira*, *Spiroceros* and *Gazellospira* are reported from eastern Europe and Asia (TEILHARD & YOUNG 1931; TEILHARD & TRASSAERT 1938; PILGRIM & SCHAUB 1939; DMITRIEVA 1977). The horn-cores of all the above-mentioned genera have torsion superimposed on a straight axis, which can be perpendicular to the cranial roof or variably inclined (normally backwards and laterally). Moreover, the horn-cores of these genera are more tightly twisted, while their keels are more or less well developed.

The studied horn-cores from Gerakarou have clearly looser torsion and only traces of a weak posterior keel. In addition, their axis is not straight but strongly curved backwards. Therefore, the Gerakarou horn-cores differ completely from those of the known Villafranchian genera. Moreover, the absence of pneumatization from the horn-cores studied distinguishes the Gerakarou antelope from the members of the younger subfamily of Caprinae.

From the Upper Pliocene of East Georgia VEKUA (1970) describes a large form of spiral horned antelope, under the name *Parastrepsiceros sokolovi* VEKUA, 1968. The normal spiral horn-cores of the Georgian form are elongated, massive and strongly curved backwards. They have a loose torsion with $1\frac{1}{2}$ helices and two keels; the posterolateral keel is strong, while the anteromedial one is weak. *Parastrepsiceros sokolovi* is obviously larger than the Gerakarou form (Tab. 1) but the morphology of their horn-cores is quite similar. The almost vertical insertion of the horn-cores in the cranial roof, the absence of a pedicle, the great divergence of the horn-cores in their upper half, the weak spiralling, the presence of a posterolateral keel, the oval to round cross-section and the curvature of the torsion axis (backwards and then upwards) are characters common to *Parastrepsiceros* and the Gerakarou antelope. Nevertheless, the Gerakarou horn-cores are more strongly curved backwards, more diverged at their base, less twisted (1 helix versus $1\frac{1}{2}$ *Parastrepsiceros*), have no anteromedial keel and a weaker posterolateral keel. The index "DT x 100/DAP" at the base of the horn-cores is greater than 100 in *Parastrepsiceros sokolovi* and smaller in the Gerararou form, indicating a different arrangement of the cross-section axis.

Concerning the dental morphology, there are also some similarities. The teeth of *Parastrepsiceros* are hypsodont, the premolar row is short relative to the molar one (index "LP^2-P^4 x 100/ LP^2-M^3"= 31.6-35.5) (Tab. 1), the upper molars have not entostyles, M^3 has a strongly developed metastyle and the lower molars have pli caprin. Nevertheless, the premolar row is larger in

Gerakarou (index "LP^2-P^4 x 100/ LP^2-M^3 = 38.3), the ectostylid is missing from the lower molars of *Parastrepsiceros*, (present in Gerakarou) and the P_4 of *Parastrepsiceros* has a separated anterior valley (open in Gerakarou).

The members of the late Miocene genus *Prostrepsiceros* MAJOR, 1891 also seem to resemble the Gerakarou antelope in the morphology of the horn-cores and in some dental characters. The large supraorbital pits, situated near the base of the horn-cores; the elongated, normally spiralled and loosely torsioned horn-cores; the strongly curved backwards horn-cores; the elliptical to round cross-section; the weak posterior keel in posterolateral insertion; the absence of anterior keel; the fine longitudinal grooves; the absence of sinus; a short to absent pedicle; the absence of postcornual fossa; the short premolar row relative to the molars; the strong styles of the upper molars; the morphology of P_4 with a free metaconid, vertical to the longitudinal axis of the tooth; the presence of pli-caprin on the lower molars; the sub-rounded third lobe of M_3; the absence of entostyle / presence of ectostylid, are features which evidence a great similarity between the GER antelope and *Prostrepsiceros* (BOUVRAIN 1982, 1992; BOUVRAIN & THOMAS 1992).

Among the different species (or varieties) of *Prostrepsiceros, P. fraasi* ANDREE, 1926 from Samos and Maraghe (e.g. SOLOUNIAS 1981, fig. 43; ANDREE 1926, pl 11, fig 4 and pl. 15, fig. 1) seems to be the most similar to the Gerakarou antelope, as regards the general structure of the horn-core and its insertion in the cranial roof. However, *P. fraasi* is much larger, has only a trace of the anterior keel and its supraorbital pits are not visible.

LEHMANN & THOMAS (1987, fig. 7) describe new species, *Prostrepsiceros libycus* LEHMAN & THOMAS, 1987 from the late Miocene / early Pliocene of Sahabi which may be the youngest known member of the genus. *Prostrepsiceros libycus* is a large-sized form (Tab. 1), characterized by the presence of an anterior deep furrow, running along the surface of the horn-core. The Gerakarou form is quite similar in morphology to that from Sahabi but the anterior furrow is totally missing. It is also interesting that in both, Gerakarou and Sahabi specimens the horn-cores are divide in view of dimensions into two groups, probably corresponding to male and female individuals.

IV. DISCUSSION

The above comparison shows that the Gerakarou antelope and *Parastrepsiceros sokolovi* share a considerable number of significant characters, suggesting a possible phylogenetic relationship between them, at generic level at least. The observed differences in size and morphology seem to be secondary and they could be attributed to specific variation. Therefore, the small spiral-horned antelope from Gerakarou could be referred to *Parastrepsiceros,* determined as a new species, *Parastrepsiceros koufosi* n.sp.

According to VEKUA (1970), *Parastrepsiceros* can be referred to Tragelaphini. However, the horn-cores of the extant tragelaphine (e.g. *Tragelaphus*, *Taurotragus*) are more twisted, with three more or less well developed keels and triangular cross-section. On the other hand unlike Tragelaphini, Antilopini are of smaller size and have their horn-cores often above the orbits, less twisted and less often keeled (SOLOUNIAS 1981), just as *Parastrepsiceros sokolovi* and the Gerakarou antelope. In any case, the keels and the direction of torsion of the tragelaphine horn-cores are compatible with those of Boselaphini and Antilopini (GENTRY 1990) and thus, a certain situation of *Parastrepsiceros* to Tragelaphini seems questionable.

Although *Prostrepsiceros* is considered to be a typical late Miocene genus (MN9/10-MN 13), it is also evident that the resemblance between the Gerakarou antelope and *Prostrepsiceros* (especially *Prostrepsiceros fraasi* and *P. libycus*) cannot be ignored. VEKUA (1970) separates *Parastrepsiceros sokolovi* from *Prostrepsiceros*-like forms mainly on the basis of different number and

development of keels, different shape of cross-sections and a lower degree of the horn-core curvature. Nevertheless, all these characters seem to vary even within the genus *Prostrepsiceros* (see also ANDREE 1926; SOLOUNIAS 1981; BOUVRAIN 1992 and GENTRY pers. com. 1993).

One of the reasons why the relations between the late Miocene and recent faunas are still obscure is the inadequate fossil record of Pliocene faunas. The question "to what extent the late Miocene faunas are an evolutionary stage in the development of modern faunas" has already been put forward by GENTRY & HEIZMANN (1996).

The Gerakarou antelope and *Parastrepsiceros sokolovi* compose a late Pliocene group, different from the isochronous group of *Gazellospira- Antilospira-Spiroceros*. But, if the latter group could be related to *Protragelaphus* (GENTRY 1971; GENTRY & HEIZMANN 1966; SOLOUNIAS 1981), the *Parastrepsiceros koufosi* / P. *sokolovi* group seems to be closely related to the oldest *Prostrepsiceros*.

According to GENTRY & HEIZMANN (1996), "a *Prostrepsiceros* species somewhere in Eurasia must have been ancestral to the extant Indian *Antilope cervicapra*". The horn-cores of the fossil forms of this genus (e.g. *Antilope* from Shungura C, Omo Depositis, Africa; GENTRY 1976) show less torsion than in the living species, as well as a vestigial posterolateral keel, features which approach to *Parastrepsiceros koufosi*.

On the other hand, the African *Aepyceros*, whose systematic position is still uncertain (GENTRY 1992), could be a descendant of a late Miocene group of antelopes, which includes *Prostrepsiceros fraasi* and *P. libycus* (GENTRY & HEIZMANN 1996; SOLOUNIAS 1981 and GENTRY pers. com 1995). As has been shown, both *P. fraasi* and *P. libycus* seem to bear great affinities with the Gerakarou antelope and thus, a possible relation between *P. koufosi* and the recent impala cannot be dismissed from consideration.

In view of the foregoing, is it still utopian to consider *Parastrepsiceros koufosi* as one of the missing links between the Miocene *Prostrepsiceros* and the extant antilopine?

REFERENCES

ANDREE J. 1926. Neue Cavicornier aus dem Pliocaen von Samos. Palaeontographica, **67**:135-175.

BOUVRAIN G. 1982. Revision du genre *Prostrepsiceros* Major 1891. Palaeontologische Zeitschrift, **56**:113-124.

BOUVRAIN G. 1992. Antilope a chevilles spiralees du Miocene superieur de la province Greco-Iranienne: nouvelles diagnoses. Annales de Paleontologie, **78**: 49-65.

BOUVRAIN G., THOMAS H. 1992. Une antilope a chevilles spirales: *Prostrepsiceros zitteli* (Bovidae). Miocene superieur du Jebel Hamrin en Irak. Geobios, **25**: 525-533.

DMITRIEVA E.-L. 1977. Neogene antelopes of Mongolia and adjacent territories. The Joint Soviet-Mongolian Paleontological Expedition, Transactions vol. **6**, Hayka Ed. Moskow, 116 pp. (In Russian).

GENTRY A. W. 1971. The earliest goats and other antelopes from the Samos Hipparion fauna. Bulletin British Museum (natural History), Geology, **20**: 229-296.

GENTRY A. W. 1976. Bovidae of the Omo Group deposits. [In:] Y. COPPENS et al. (Eds) – Earliest man and Environment in the Lake Rudolf basin. University Chicago Press Pp. 275- 292.

GENTRY A. W. 1990. Evolution and dispersal of African Bovidae. [In:] G. A. BUBENIK, A. B. BUBENIK – (Eds). Horns, Pronghorns and Antlers, New York. Springer Verlag, Pp. 195-227.

GENTRY A. W. 1992. Subfamilies and Tribes of Bovidae. Mammal Review, **22**: 1-32

GENTRY A. W., HEIZMANN P. J. 1996. Miocene ruminants of the central and eastern Tethys and Paratethys. [In:] RAYMONT L. et al. (Eds) – Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press. New York. Pp. 378-391.

KOLIADIMOU K. 1996. Palaeontological Biostratigraphical and study of the Neogene/Quaternary micromammals from Mygdonia Basin. Doct. Thesis, University of Thessaloniki, Pp. 360 "unpublished". (In Greek with English summary)

KOSTOPOULOS D. 1996. The Plio-Pleistocene artiodactyls of Macedonia (N. Greece); Systematics, Biochronology, Biostratigraphy, Palaeoecology. Doct. Thesis, University of Thessaloniki, Pp. 612 unpublished. (In Greek with English summary).

KOSTOPOULOS D., KOUFOS G. 1995. A new consideration for the division of Villafranchian. Proccesus X Congress C.M.N.R.S., Journal of Palaeontology-Geological Survey of Romania. (in press).

KOUFOS G. 1986a. The presence of *Gazella borbonica* (Mammalia, Bovidae) in the Villafranchian (Villanyan) of Macedonia (Greece) and its significance to the stratigraphic disrtibution of the species. Neues Jahrbuch fuer Geologie und Palaeontologie Monatsheft, **9**: 541-554.

KOUFOS G. 1986b. The presence of *Sus strozzii* (Mammalia, Bovidae) in the Villafranchian (Villanyan) of Macedonia (Greece). Palaeontologiche Zeitschrift, **60**(3/4): 341-351.

KOUFOS G. 1987. *Canis arnensis* DEL CAMPANA, 1913 from the Villafranchian (Villanyan) of Macedonia (Greece). Paleontologia i Evolucio, **21**:3-10.

KOUFOS G. 1992. Early Pleistocene equids from Mygdonia basin (Macedonia, Greece). Palaeontografia Italica, **79**: 167-199.

KOUFOS G., MELENTIS J. 1983. New data from the Villafranchian mammal locality of Gerakarou (Macedonia, Greece) Proccesus Academy of Athens, **58**:181-185.

KOUFOS G., SYRIDES G., KOLIADIMOU K. 1989. A new Pleistocene mammal locality from Macedonia (Greece). Contribution to the study of Villafranchian (Villaniyan) in central Macedonia. Bulletin Geological Society Greece, **23**(2): 113-124.

KOUFOS G., SYRIDES G., KOSTOPOULOS D., KOLIADIMOU K. 1995. Preliminary results about the stratigraphy and the palaeoenvironment of Mygdonia basin, Macedonia, Greece. Geobios Memoire Special, **18**: 243-249.

LEHMANN U., THOMAS H. 1987. Fossil Bovidae from the Mio-Pliocene of Sahabi (Libya). [In:] N. T. BOAZ et al. (Eds) – Neogene Paleontology and Geology of Sahabi. New York: Liss. Pp. 323-335.

PILGRIM G. E., SCHAUB S. 1939. Die schraubenhoernige Antilope des europaeischen Oberpliocaens und ihre systematische Stellung. Abhandlung. schweize palaeontologische. Gesselschaft, Basel, **62**: 1-30.

SOLOUNIAS N. 1981. The Turolian fauna from the island of Samos, Greece. Contribution to Vertebrate Evolution, **6**: 1-232.

TEILHARD DE CHARDIN P., YOUNG C. C. 1931. Fossil mammals from the late Cenozoic of Northern China. Palaeontologia Sinica, C **9**(1): 1-66.

TEILHARD DE CHARDIN P., TRASSAERT M. 1938. Cavicornia of South-Eastern Shansi. Palaeontologia Sinica, C **6**(115): 1-106.

VEKUA A. 1970. New representative of Tragelaphini from the Pliocene of Georgia. [In:] Metsniereba Tbilisi (Ed.) – The Mesozoic and Cenozoic fauna of Georgia and its geohistoric significance:120-136. (In Russian).

ZAMANIS A., FAUGERES L., BONIS L., FOUNTOULIS D., SIMEAKIS C., PANAYOTIS I., DIMITRAKOPOULOS R., MERCIER J. 1980. Decouverte d' une faune de mammiferes du Quaternaire ancien dans les formations du lac Langhada (Macedoine centrale, Grece). Implications neotectoniques . Compte Rendus de l' Academie des Sciences, Paris, **291**(D): 813-816.