IN THE SHADOW OF BOVIDS: SUIDS, CERVIDS AND GIRAFFIDS FROM THE PLIO-PLEISTOCENE OF GREECE

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"…but the moment the last words of this paper were typed
–a grey day in Athens– you abandoned us for eternity…
We are still looking for the true value of time Kosta"

ABSTRACT

Among ungulates, Artiodactyls constitute the major part of the collected Greek Plio-Pleistocene (MNQ17–MNQ18) faunas, represented by numerous genera and species. Apart from bovids, the Plio-Pleistocene Greek record includes several suid, cervid and giraffid species, which are reviewed and discussed in the present work.

Key words: Plio-Pleistocene, Artiodactyla, Suidae, Cervidae, Giraffidae, Greece.

RÉSUMÉ

À L'OMBRE DES BOVIDÉS : SUIDÉS, CERVIDÉS ET GIRAFFIDÉS DU PLIO-PLÉISTOCÈNE DE GRÈCE

Parmi les Ongulés, les Artiodactyles sont les éléments les plus fréquents dans les faunes plio-pléistocènes (MNQ17–MNQ18) grecques. Ils sont représentés par de nombreux genres et espèces. A l'exception des Bovidés, les faunes plio-pléistocènes grecques comprennent aussi des Suidés, Cervidés et Giraffidés, qui sont revisés et discutés dans l'article présent.

Mots-clés : Plio-Pléistocène, Artiodactyla, Suidae, Cervidae, Giraffidae, Grèce

INTRODUCTION

Several new fossil mammalian faunas from Greece have been found and studied during the last years; many of them are of Plio-Pleistocene age (Koufos & Kostopoulos 1997). Although bovids predominate in the Greek Plio-Pleistocene faunas, both in number of species and individuals, cervids also constitute a great part of the faunal association, while suids and giraffids are sub-represented but equally important. Although several bovid forms are already described in a series of papers (Kostopoulos, 1998a,b; Kostopoulos & Athanassiou, 1997; Athanassiou, 2002 and literature listed), Greek Plio-Pleistocene Suidae, Cervidae and Giraffidae still remain in the shadow, known only by faunal lists and preliminary reports. The basic aim of the present article is to review most of these forms, originally described by Athanassiou (1996) and Kostopoulos (1996), as well as to present the new data about the distribution of these families in the Plio-Pleistocene of Greece. Short descriptions and comparisons will be given.

METHODOLOGY

The description of taxa follows a chronological concept presented by locality, from the older to the younger ones, according to the local scale of Koufos & Kostopoulos (1997) and in reference to the European MN Zones. The studied material comes from the localities of Volakas (also referred to as Wolax, Wolaks or Volax – MNQ17), Sesklo (MNQ17), Dafnero (MNQ17), Gerakarou (MNQ18), Vassiloudi (MNQ18) and Krimni (?MNQ19) (fig. 1). Determinations are mainly based on cranial, dental and antler morphology, while postcranials are occasionally used (e.g. in giraffids) because of their strong relation to the ecological

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Figure 1: Skech-map of the area with the fossiliferous localities included in this study.
Figure 1 : Carte schématique des localités fossilifères concernées par l'article.

factors. Comparative material used for determination comes from the Muséum national d'Histoire naturelle de Paris, Museum of Geology and Paleontology of Florence, Naturhistorisches Museum Basel and Natural History Museum of London. Terminology and measurement techniques generally follow Heintz (1970). Indicative measures for each described taxon are given after list of material. All measures are in mm.

Abbreviations. L=length; W=width; DT=transverse diameter; DAP=anteroposterior diameter; prox=proximal; dia=at the middle of diaphysis; dist=distal; dex=right; sin=left.

Systematics

Order: Artiodactyla OWEN, 1848
Family: Suidae GRAY, 1821
Genus: ***Sus*** LINNAEUS, 1758

Sus strozzii FORSYTH MAJOR, 1881

The European Plio-Pleistocene suids are relatively rare, while their systematics is still under discussion. The small *Sus minor* (?=*arvernensis*) is exclusively known from the early "Villafranchian" of SE and Central Europe, while the younger and larger *Sus strozzii* is a widespread form, occurred in the entire south European region from Spain to the North-Eastern part of the Azov Sea (Faure & Guérin, 1984; Titov, 2000). One part of a suid skull and a quite complete mandible are only known from the latest Pliocene (MNQ 18) faunas of Gerakarou and Vassiloudi (Mygdonia basin) respectively.

GERAKAROU

Material: part of skull with both toothrows, GER-51

Meassurements & Description: *in* Koufos (1986).

VASSILOUDI

Material: M^3 *in situ*, VSL-24; $M^{1/2}$, VSL-13; ?M^1–M^2, VSL-25; part of lower canine, VSL-16; mandible with P_2–M_3 sin and P_3–M_3 dex, VSL-23.

Measurements: LI_1-M_3 alveolar=220; Diastema C-P_2~29.5; LP_2–M_3 =142.5; LP_2–P_4 = 46.0; LM_1–M_3 = 97.0; LM_{3dex} = 49.5, WM_{3dex} = 21.3; LM_{3sin} = 49.8, WM_{3sin} = 21.7.

Description: All the available specimens are obviously belong to a single male individual. The upper molars are badly preserved and in advanced stage of wear. M^3 has well-developed talon. The lower tusk preserves only its anterior part. The tooth is rather massive with sub-triangular cross-section. Strong furrows run along its anterior and external face. The anterior part of the mandible VSL-23 is partly destroyed. The large and massive mandibular branches are well diverged. The index "height of the vertical ramus × 100 / length of the mandible" is about 40. The horizontal ramus is shallow. Two well-developed mandibular tuberosities are present below the lower tusks. The symphysis is elongated and strong; its posterior border is placed at the level of P_2. The mandibular angle is almost vertical. The teeth are much worn to allow detailed morphological observations. The enamel is thick and moderately rippled. The second premolar is small, with strong antero-central cuspid. The anterior and posterior cingula are shallow. P_3 is similar with P_2, and has strong anterior cuspid. P_4 is more complex, with two central cuspids; the external one is situated more anteriorly in comparison with the internal. The anterior cingulum of P_4 is shallow, while the posterior one is more developed but not significantly raised. The third lower molar is strongly elongated with well-developed talonid. The "protoconid" and the "hypoconid" are strong. The first one is labially convex. The "metaconid' and the "entoconid" are more developed, situated posteriorly in comparison with the labial cuspids. The enamel of the labial cuspids is thicker than that of the lingual ones. Between the "metaconid" and the "entoconid" there is a basic pillar. The talonid is formed by two strong sub-squarish tubercles and a sub-rounded posterior cuspid.

Discussion: Both the Gerakarou and Vassiloudi forms are referred to *Sus strozzii* (Koufos, 1986; Kostopoulos, 1996). The morphology and the shape of the transverse section of the studied tusk are similar to those of the "*veruccosus*" type. The large dimensions of the Vassiloudi mandible, the presence of mandibular tuberosities, the elongated M_3 with strong talonid and the moderately wrinkled enamel are features similar to those referred to *Sus strozzii* (Azzaroli, 1954; Geraads *et al.*, 1986; van der Made & Moyà-Solà, 1989). Nevertheless, the length P_2–M_3 is larger than that of the lectotype (IGF-424, Florence; LP_2–M_3 = 134 mm) and Senèze-1275 (LP_2–M_3 = 129 mm) and closer to the larger known specimens of the species IGF-414 (LP_2–M_3 =147 mm) from Upper Valdarno and *Sus* cf. *strozzii* from Khapry (LP_2–M_3~140mm) (pers. data and Titov, 2000). Moreover, M_3 from Vassiloudi is longer and wider than that of the Italian sample and more similar to the large form from Valdegagna II (Spain), Tegelen (The Netherlands) and Palan-Tyukan (Azerbaijan) (van der Made & Moya-Sola, 1989; Titov, 2000) (fig. 2). The morphological characters of P_4 from Vassiloudi seem to be more archaic and closer to those of *Sus palaeochoerus*. Azzaroli (1954) also reports a P_4 of "*palaeochoerus*" type in the mandible of *Sus strozzii* from Senèze (France) and in one specimen from Olivola (Italy). *Sus strozzii* from Gerakarou (Koufos, 1986) is similar to the Senèze suid, while both the Gerakarou and the Vassiloudi forms differ from the typical *Sus strozzii* from the Upper Valdarno by the larger dimensions of their teeth. Symeonidis (1992) also mentions the presence of *Sus* cf. *strozzii* in the fauna of Sesklo (Thessaly) based on a mandibular part. However, this specimen derives from a lower stratigraphic level, and its small dimensions show that it possibly belongs to *Sus minor*. The new material

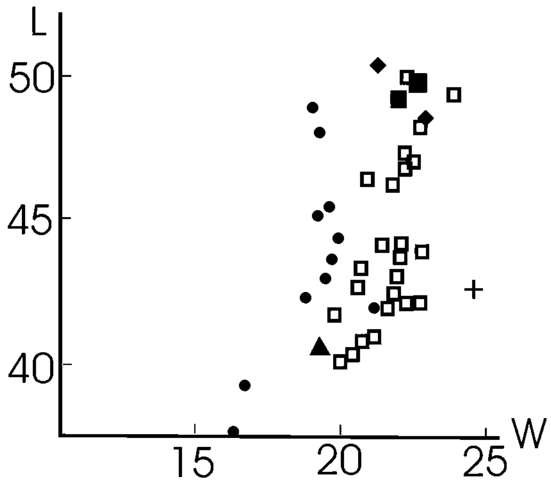

Figure 2: Scatter diagram of suid M_3 dimensions. Closed squares: *Sus strozzii* from Vassiloudi, open squares: Western European *Sus strozzii*, triangle: *Sus strozzii* from Oubeidiyeh, diamond: *S. strozzii* from Palan Tyukan, cross: *S. strozzii* from Khapry, closed circle: *Sus scrofa* (recent). After van der Made & Moyà-Solà (1989), modified with data from Geraads *et al*. (1986) and Titov (2002)

Figure 2 : Diagramme de dispersion de M_3 des suidés. Rectangle noir: *Sus strozzii* de Vassiloudi, rectangle blanc: *Sus strozzii* de l'Europe occidentale, triangle: *Sus strozzii* d'Oubeidiyeh, losange : *S. strozzii* de Palan Tyukan, croix : *S. strozzii* de Khapry, cercle noir: *Sus scrofa* (récent). D'après van der Made & Moyà-Solà (1989), modifié avec les données de Geraads *et al*. (1986) et Titov (2002).

from Sesklo, described by Athanassiou (1996), does not confirm the presence of the species in this locality. Differences in size of *Sus strozzii* local populations are most probably influenced by ecological factors and could regard as mutations, a phenomenon already observed in earlier suines like *Microstonyx*. The idea of an intra-specific taxonomic differentiation mentioned by Azzaroli (1954) and van der Made & Moyà-Solà (1989), cannot be fully supported by the available data.

Family: Cervidae GOLDFUSS, 1820

Genus: ***Eucladoceros*** FALCONER, 1868

Eucladoceros ctenoides (Nesti, 1841)

There are several systematic and nomenclature problems concerning the large sized cervids of Plio-Pleistocene age. The synonymy status and the priority of the described species (*E. falconeri, E. tetraceros, E. tegulensis, E. senezensis, E. sedgwickii, E. boulei, E. ctenoides, E. dicranios, E. giulii* etc.) are still under discussion. According to Azzaroli *et al.* (1988), Azzaroli & Mazza (1992), Spaan (1992) and de Vos *et al.* (1995) *Eucladoceros senezensis* is a junior synonym of *E. tegulensis*. Although the holotype of *E. ctenoides* is not very informative, de Vos *et al.* (1995) and Croitor & Bonifay (2001) also include *E. tegulensis* into the prior *E. ctenoides* (NESTI, 1841); we shall follow them.

VOLAKAS

Synonymy: *Eucladoceros senezensis*, Kostopoulos (1996, 1998a).

Material: Part of skull, VOL-3; part of maxilla with P^3-P^4, VOL-38; prox. part of Radius, VOL-71; dist. part of Radius, VOL-72, 88; dist. part of Tibia, VOL-118; Calcaneum, VOL-127; prox. part of Metacarpal III-IV, VOL-62,64; dist. part of Metatarsal III-IV, VOL-73.

Description: *in* Kostopoulos (1998a)

Measurements: LP^2-M^3=120.0; LP^2-P^4~50.0; LM^1-M^3=70.0; VOL-71 Radius DTprox=57.1, DAPprox=34.6; VOL-88 Radius DTdist=48.2, DAPdist=27.3; VOL-73 Metatarsal III-IV DTdist=48.7, DAPdist=32.2; VOL-127 Calcaneum L=128.

SESKLO

Synonymy: ?*Eucladoceros*, Athanassiou (1996).

Material: Posterior part of skull, Σ-355; trapezoid, hamatum, Metacarpal III-IV, Σ-935; Astragalus, Σ-320; Calcaneum, Σ-1117; proximal part of Tibia, Σ-1122.

Measurements: Metacarpal III-IV L = 253.0, DTprox = 40.9, DAPprox = 28.0, DTdist = 46.0, DAPdist = 28.4; Tibia DTprox = 47.5, DAPprox = 38.5.

Description: Only the occipital and the parietal regions of the skull are preserved. The maximal width of the neurocranium is 130 mm, the width between the mastoid processes is 127.5 mm and the height of the occiput 78 mm. The postcranials have the typical morphology of the genus (Heintz, 1970; Pfeiffer, 1999).

DAFNERO

Synonymy: *Eucladoceros senezensis*, Kostopoulos (1996)

Material: Part of maxilla with P^3–M^3, DFN-76; P^3–P^4 *in situ*, DFN-80; M^2–M^3 *in situ*, DFN-24; M^1, DFN-118; part of maxilla with dP^3–M^2, DFN-168; left M_3, DFN-187; proximal part of Metacarpal III-IV, DFN-61, DFN-186; Scaphocuboid, DFN-55; Astragalus, DFN-39.

Measurements: LP^3–M^3=95.0, LM^1-M^3=68.2; Metacarpal III-IV DTprox=46.6/46.2, DAPprox=31.1/30.3; Astragalus Lexternal=65.2, DTdist=40.3.

Description: The P^3 is elongated and bilobed. The P^4 is less molarized with well-formed hypoconal fold ("éperon hypoconal", Heintz 1970). The molars have wider hypocone that protocone. There is a cingulum mainly mesially, distally and lingually, where it forms a mesostyle. From the lower dentition only a badly preserved M_3 is known. It is about 32–33 mm long and it has a strong ectostylid and a rather weak cingulum. The postcranials show typical morphology of *Eucladoceros* (Heintz, 1970; Pfeiffer, 1999).

GERAKAROU

Synonymy: *Eucladoceros senezensis* cf. *senezensis*, Kostopoulos (1996)

Figure 3: *Eucladoceros ctenoides* lower toothrow (GER-345) from Gerakarou. Occlusal view. Scale: 25mm.
Figure 3 : Denture inférieure d'*Eucladoceros ctenoides* (GER-345) de Gerakarou. Vue occlusale. Échelle: 25mm.

Material: Part of maxilla with dP^2–dP^4, GER-134, GER-186, GER-191, GER-214; part of maxilla with P^2–M^3, GER-187; part of maxilla with P^3–M^3, GER-132; part of mandible with dP_2–M_1 dex and dP_3–M_1 sin, GER-5; part of mandible with P_2–M_2, GER-345; part of mandible with M_1–M_3, GER-136; proximal part of Metacarpal III-IV, GER-331, GER-332, GER-336, GER-338; distal part of Tibia, GER-330; proximal part of Metatarsal III-IV, GER-333; distal part of Metatarsal III-IV, GER-335.

Measurements: LP^2-M^3~122, LP^2-P^4~49.1, LM^1-M^3= 77.3; LP_2-P_4=56.4; LM_1-M_3=85.4; Metacarpal III-IV DTprox=36.6-38.9, DAPprox=25.2-25.8; Tibia DTdist= 51.4, DAPdist=39.9; Metatarsal III-IV DTprox=39.0, DAPprox=40.0, DTdist=43.7, DAPdist=39.0.

Description: P^2 is molarized; the degree of molarization decreases rapidly towards P^4, which is simple. The buccal wall of premolars is slightly convex with weak styles. There is a cingulum in P^2 and P^3, but not in P^4. The hypoconal fold is well developed in P^4, which also has a small accessory cuspid between the parastyle and the metastyle. The molars have prominent styles at the upper part of the crown. The cingulum is strong. A protoconal and a hypoconal fold are usually present. A small cuspid is observed between the parastyle and the mesostyle of M^3. The upper deciduous molars have two asymmetrical lobes and very prominent styles. The entostyle is weak in dP^3 but moderately developed in dP^4. The proximal lower premolars show low degree of molarisation. There is no paraconid in P_2. The parastylid and the paraconid, as well as the metaconid and the entoconid of P_3 are also fused each other (fig. 3). The second valley is V-shaped in P_3 but very narrow in P_4, closing rapidly with the tooth wear. The third valley is also narrow in P_4, but it extends till the base of the crown. The lower molars have well-developed cingulum that forms an ectostylid in M_1 and M_2. The deciduous teeth show typical morphology; dP_2 has no paraconid and a slightly developed entostylid. Postcranials cannot offer clear morphological structures because of bad preservation.

KRIMNI

Synomymy: *Eucladoceros senezensis*, Kostopoulos (1996)

Material: P^2–M^3, KRI-30.

Measurements & Description: The length P^2–M^3 is 137.4 mm (LP^2–P^4 = 58.5, LM^1–M^3 = 80.7). The tooth morphology is similar to that of *Eucladoceros* from Gerakarou, but the P^3 is less molarized, the P^4 is stronger and the paracone of M^3 is larger.

Discussion: The Volakas, Dafnero, Sesklo, Gerakarou and Krimni large cervids appear to be closer to *Eucladoceros* than to other genera of the same age. They differ from the similar sized *Arvernoceros* by the less developed cingulum and the less wide molars and from "*Cervus" perrieri* by the presence of hypoconal fold, cingulum and the larger molar dimensions. In comparison to the West European species of *Eucladoceros*, the dimensions of the skull fragment from Sesklo and Volakas, as well as the proportions of metacarpals, tibias and tarsals from Dafnero, Sesklo and Volakas approach those of *Eucladoceros ctenoides (=tegulensis =senezensis)* from Senèze, St.Vallier (France) and La Puebla de Valverde (Spain) (Heintz, 1970), being, however, somewhat smaller than the latter two populations.

The tooth morphology of the Gerakarou form and especially the reduced protoconal fold, the wide parastyle, the development of the cingulum on the molars and P^3, the presence of protoconal and hypoconal folds, the unmolarized P_4 with closed trigonid and the absence of "*palaeomeryx*" fold on the molars and paraconid in P_2, suggest the attribution of the studied form to *Eucladoceros ctenoides* (Heintz, 1970; Azzaroli 1947; Azzaroli & Mazza, 1992; de Vos *et al*., 1995). In comparison to the West European forms, the premolar row of Gerakarou appears slightly shorter, and the second molar predominates in the molar row. The Gerakarou form shows clear morphological and metrical similarities with the Senèze one and more advanced characters than the Sesklo, Dafnero and Volakas forms. The data for *Eucladoceros* from Krimni are too few and it is therefore revised to *Eucladoceros* aff. *ctenoides*.

Genus: ***Metacervoceros*** DIETRICH, 1938

Metacervoceros rhenanus (DUBOIS, 1904)

The "fallow deer-like" cervids from the European "Villafranchian" faunas take part of a long discussion with many controversies (e.g. Heintz, 1970; Azzaroli, 1947, 1992, 2001; Boeuf *et al*., 1992; Spaan, 1992; de Vos *et al.*, 1995; Kahlke, 1997; Di Stefano & Petronio, 1998; Pfeiffer, 1999; van der Made, 1999; Croitor & Bonifay, 2001). Judging by the arguments of de Vos *et al*. (1995), Kahlke (1997) and Croitor & Bonifay (2001), we also think *pardinensis* and *rhenanus* (*=philisi =perolensis =ischnoceros =Pseudodama lyra)* to be distinct generically from *Pseudodama nestii* and *P. farnatensis* and we adopt the proposal of Croitor & Bonifay (2001) recalling *Metacervoceros* DIETRICH, 1938 as a valid genus with type species *M. pardinensis* (CROIZET & JOBERT, 1828).

VOLAKAS

Synonymy: *«Cervus» philisi*, Kostopoulos (1996, 1998a)

Material: P^3-M^3, VOL-37; P^2-P^4, VOL-41; P^4-M^1, VOL-46; M^3, VOL-95; P_2-M_3, VOL-16; P_3-M_3, VOL-13; P_2-M_2, VOL-11, P_4-M_3, VOL-17; M_3, VOL-12; prox. part of Metacarpal III-IV, VOL-87; dist. part of Metacarpal III-IV, VOL-101; Cubovavicular, VOL-134; Astragalus, VOL-131, 132; prox. part of Metatarsal III-IV, VOL-67, 76, 83, 99, 100, 102, 103; dist. part of Metatarsal III-IV, VOL-74, 75.

Description: *in* Kostopoulos (1998a).

Measurements: LP^2-P^4=38.7; LM^1-M^3=55.0-56.2; LP_2-M_3=110.0/105.0, LP_2-P_4=43.0/44.0, LM_1-M_3= 67.0/62.7; Metacarpal III-IV DTprox=36.3, DAPprox= 24.5; Astragalus Lexternal=41.9/43.8, DTdist=24.6/25.5; Metatarsal III-IV DTdist=34.9/33.4, DAPdist=22.8/22.9

DAFNERO

Synonymy: «*Cervus*» *philisi* cf. *valliensis*, Kostopoulos (1996).

Material: Part of maxilla with P^2–M^3, DFN-185; P^4, DFN-191; P^{2-3}, DFN-177; right mandibular part with P_2–M_3, DFN-158; left mandibular part with P_2–M_3, DFN-159; P_3–M_3 *in situ*, DFN-85; P_2–M_1 *in situ*, DFN-137.

Measurements: LP^2–M^3 =86.4, LP^2-P^4=39.6, LM^1-M^3= 48.5; LP_2–M_3 =89/90/89, LP_2-P_4=-/38.7/35.3, LM_1-M_3= 53.5/54.0/53.9; Metatarsal III+IV DTprox=36.3, DAPprox=37.5.

Description: The species is represented by a limited number of toothrows, as well as by some isolated teeth and a few postcranials. The premolar/molar ratio of the single available upper toothrow is 76%. P^2 is long (L=13.9mm). The premolars are molarized. The protocone is smaller than the hypocone in P^2, while both cusps are more or less equally developed in P^3. The paracone is separated from the parastyle by a deep V-shaped valley. A hypoconal fold is present in P^4 (DFN-185), while an isolated specimen (DFN-191) also shows a hypoconal islet. A weak cingulum is formed in all premolars. The upper molars have rather triangular lingual cusps. The parastyle is always prominent but the metastyle is weak. The cingulum occurs mainly lingually. The lower premolar/molar ratio is 65.5–71.5%. P_2 has a prominent parastylid, separated from the metaconid by a wide valley. There is no paraconid in the three available specimens. The entoconid and the entostylid are well developed, fused together well above the base of the crown. The parastylid and the paraconid of P_3 are close together, separated only at the first stage of wear. A wide second valley separates the paraconid from the metaconid. The metaconid, the entoconid and the entostylid are elongated, separated by narrow valleys, which disappear in advance stage of wear. The parastylid and the paraconid are also fused in P_4, forming a single elongated cuspid. In one specimen there is a small enamel islet in the occlusal surface, corresponding to a vestigial first valley. Generally the fourth premolar is not molarized, as the other three valleys are open. The lower molars have triangular labial cuspids. The main cuspids are well separated almost till the base of the crown. There is a short ectostylid between the lobes. No hypoconal neither protoconal fold are present.

SESKLO

Synonymy: Cervidae indet. (ex gr. « *Cervus* » *philisi*), Athanassiou (1996).

Material: part of pedicel, Σ-1175; M^3 dex Σ-462; proximal part of Metatarsal III-IV, Σ-1115.

Measurements & Description: M^3 is of medium size and very worn (L= 15.3, W= 16.8). The metatarsal III-IV has DTprox = 29.1 and DAPprox = 33.0 and typical cervid morphology (Heintz, 1970). The available material is not enough for valid morphological observations.

GERAKAROU

Synonymy: *Cervus* sp. (gr. «*pardinensis–philisi–perolensis*»), Kostopoulos (1996).

Material: Metacarpal III-IV, GER-280; Calcaneum, GER-324.

Measurements & Description: The metacarpal III-IV is moderately long (L=193.2, DTprox=27.1, DAPprox= 19.5, DTdia=16.6, DAPdia=18.0, DTdist=28.7, DAPdist= 19.1) and relatively short in comparison to the available calcaneum (L=99.7mm) but this is probably due to the scanty material.

Discussion: The morphological characters of the studied forms from Volakas and Dafnero are very close together, as well as to those of the medium sized cervids from West European "Villafranchian" localities. The Dafnero cervid appears more similar to *M. rhenanus* from St.Vallier and Cornillet (France) (Heintz, 1970; Heintz & Dubar, 1981). The material from Sesklo and Gerakarou is not enough for certain conclusions but it appears morphologically close to that from Volakas and Dafnero, allowing their determination as *Metacervoceros* aff. *rhenanus*. However, the Gerakarou metacarpal is smaller than the Dafnero and Senèze samples and probably closer to the Peyrolles and Valdarno ones.

Genus: ***Croizetoceros*** HEINTZ, 1970

Croizetoceros ramosus (CROIZET & JOBERT, 1828)

VOLAKAS

Material & Description: *in* Kostopoulos (1998a).

SESKLO

Synonymy: cf. *Croizetoceros ramosus*, Athanassiou (1996).

Material: P_2–M_3, Σ-200; P_3–M_3, Σ-465; P_2–M_2, Σ-490.

Measurements & Description: The P_2 and P_3 are triangular in shape and have well developed ribs and stylids. The P_2 has a well developed paraconid. P_4 is completely molarized (fig. 4). The molars are characterised by the presence of ectostylids, well developed lingual stylids and rather wrinkled enamel. The third lobe of M_3 expands labially. The hypsodonty index is 69.1–73.8 for M_2 and 53.7–54.5 for M_3, indicating relatively brachyodont molars. The length P_2–M_3 (Σ-200) is about 79 mm, with LM_1–M_3 = 48.5 mm. The premolar/molar ratio is 66%.

GERAKAROU

Material: part of antler, GER-268, 261, 262, 263, 264, 265, 266, 267, 268; dP^2–M^1, GER-200, 202; dP^3–M^1, GER-240, 248, 249, 252; P^2–M^3, GER-188, 194, 212, 213?, 185, 192, 193; P^3–M^3, GER-4, 205, 206, 217; P^2–M^2, GER-208; M^2–M^3, GER-203, 246; dP_2–M_1, GER-145, 146; dP_3–M_1, GER-1, 138, 216; dP_4–M_1, GER-143, 215; P_2–M_3, GER-220, 230, 231, 232, 234; P_3–M_3, GER-2, 182+237, 135, 234; P_4–M_3, GER-3, 224; P_2–M_2, GER-233; M_1–M_3, GER-183; distal part of Humerus, GER-300; prox. part of Radius, GER-311; dist. part of Radius, GER-309; Metacarpal III-IV, GER-278; prox. part of Metacarpal III-IV, GER-282; dist. part of Tibia, GER-313, 319; Metatarsal III-IV, GER-292; prox. part of Metatarsal III-IV, GER-285, 286, 297, 298.

Measurements: Lpedicle=12.3-14.0 (adults); DTpedicle=22.0-22.5, DAPpedicle= 21.5-23.1; DTburr= 26.0-30.3, DAPburr=29.2-35.5; L along the anterior face of the first tine=140-156; LP^2-M^3=64.7-72.9, LP^2-P^4= 28.2-32.5, LM^1-M^3=38.7-43.7; LP_2-M_3=73.6-78.0, LP_2-P_4= 28.4-31.5, LM_1-M_3=44.7-51.5; Radius DTprox=25-26.6, DAPprox=14.1-14.7, DTdist=23.0, DAPdist=13.9; Metacarpal III-IV L=172.4-187.2, DTprox=21.0-24.2, DAPprox=15.6-18.0, DTdia=13.9-16.6, DTdist=22.5-24.6, DAPdist=14.2-15.9; Tibia L=326.8, DTprox~46.5, DTdist= 26.0-28.1, DAPdist=21.3-22.7; Metatarsal III-IV L=202.9, DTprox=19.5-22.7, DAPprox=21.0-24.9, DTdia=12.7-13.7, DTdist=22.1-23.2, DAPdist=14.0-16.0.

Description: The pedicle is short and cylindrical shaped (fig. 5), longer in young individuals (18.6-20.2mm). The index "DT/DAP × 100"of the pedicle varies in the adult individuals from 95.2–104.6, while the index "$DAP_{pedicle}$/ DAP_{burr}" ranges from 67.9 to 69.6. The first tine is situated well above the burr, with a mean distance from it at about 68.6 mm in adult individuals. The insertion angle of the first tine is 90°, descending in the antero-external face of the beam (Fig. 6). The first tine configures an almost vertical angle, directed firstly antero-externally and then

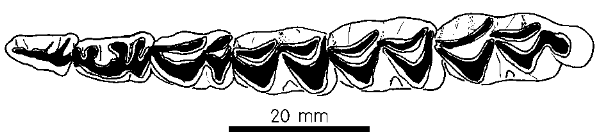

Figure 4: *Croizetoceros ramosus* lower toothrow (Σ-200) from Sesklo. Occlusal view.

Figure 4 : Denture inférieure de *Croizetoceros ramosus* (Σ-200) de Sesklo. Vue occlusale.

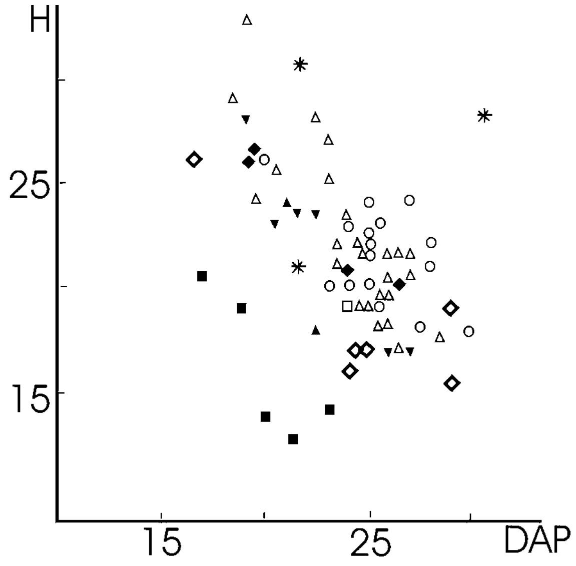

Figure 5: Scatter diagram of Height (H) against DAP of *Croizetoceros ramosus* pedicle. Closed squares: Gerakarou, open squares: Pardines, closed diamond: La Puebla de Valverde, open diamond: Coupet, closed triangle: Senèze, open triangle: Etouaires, closed inverse triangle: Villaroya, open circle: Saint Vallier, asterisk: Huelago (from Heintz 1970, modified).
Figure 5 : Diagramme de dispersion du pédicule (Hauteur /DAP) de *Croizetoceros ramosus*. Rectangle noir: Gerakarou, rectangle blanc: Pardines, losange blanc: Coupet, losange noir: La Puebla de Valverde, triangle noir: Senèze, triangle blanc: Etouaires, triangle inversé: Villaroya, cercle blanc: Saint Vallier, astérisque: Huelago (d'après Heintz 1970, modifié).

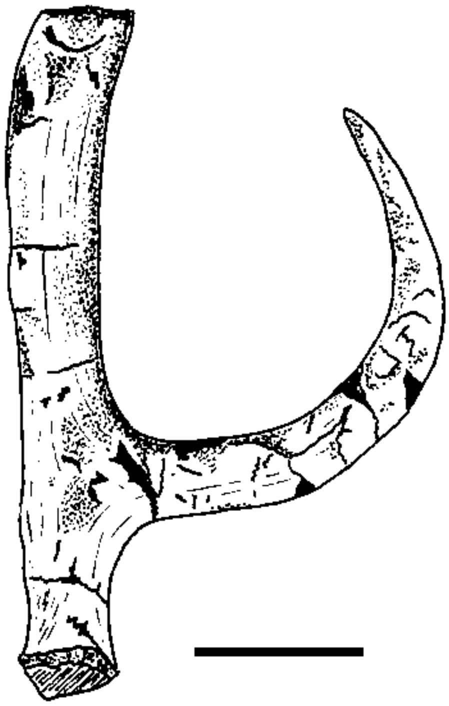

Figure 6: *Croizetoceros ramosus gerakarensis* holotype-antler (GER-268) from Gerakarou. Lateral view. Scale: 50mm.
Figure 6 : Bois de *Croizetoceros ramosus gerakarensis* holotype (GER-268) de Gerakarou. Vue laterale. Échelle: 50mm.

Figure 7: *Croizetoceros ramosus* upper toothrow (GER-188) from Gerakarou. Occlusal view. Scale: 10mm.
Figure 7 : Denture supérieure de *Croizetoceros ramosus* (GER-188) de Gerakarou. Vue occlusale. Échelle: 10mm.

upwards. Its uppermost part is usually curved backwards. The lower part of the beam is almost straight while between the first and the second tine it is slightly curved anteriorly (fig. 6). The beam is mediolaterally compressed and flattened at the level of the first bifurcation. The burr is well rounded. The dental morphology is generally similar to that referred to *Croizetoceros ramosus* (Heintz, 1970). The upper premolar row corresponds to 68.7–75% of the molar one; this percentage ranges from 61–65% in the lower tooth row. 47% of the studied M^1 have a protoconal fold, while 50% of them have a variably developed hypoconal fold (fig. 7). Both morphological structures are always present in $M^{2,3}$. Moreover, 4 of 18 M^1 (22%) have a slightly developed hypoconal fold. The mean height of the mandible behind M_3 is 26.5 mm with a respective mean width at about 10.7mm. 4 of 5 P_2 have a well-developed parastylid. P_3 and P_4 are molarized (stage c and d respectively, according to Heintz, 1970). The available postcranial material indicates a small *Croizetoceros ramosus* but the preservation status of the material permits just proportional comparison with the West European populations of the species.

Discussion. The general morphological and dimensional features of the Gerakarou small cervid completely follow those referred to *Croizetoceros ramosus* (Heintz, 1970: 94-95). However, some particular characters such as the slender antler with very short pedicle, the small distance between the burr and the first tine, the anteriorly curved beam between the first and the second tine, the short length of the first tine (148 mm) and its orientation, the short premolar row, the small P_2 with highly preserved paraconid (80%) and the small-sized postcranials, probably indicate a deviation from the known West European subspecies. According to Pfeiffer (1999) the reduction of size and the shortness of the premolar row could reflect a deterioration of the ecological conditions into a cervid species. This is probably true for the Gerakarou form which is chronologically placed at the very end of Pliocene. The plesiomorphic persistence of paraconid in P_2 in comparison with more or less contemporaneous populations of *Cr. ramosus* from Western Europe, could indicate a geographical isolation from the early "Villafranchian" stock, followed by an independent *in situ* evolution of the Greek population. The presence of the species in earlier Greek localities (Sesklo, Volakas) and the results of Heintz (1970, 1974) and Brunet & Heintz (1984) confirm these ideas. Based on these data Kostopoulos (1996) following the concept of Heintz (1970, 1974) proposes for the Gerakarou form a new subspecies:

Croizetoceros ramosus gerakarensis KOSTOPOULOS, 1996

Synonyms: *Croizetoceros ramosus* cf. *minor* Koufos & Melentis (1983).

Holotype: Part of antler, GER-268 (incorrectly labelled GER-264 in Kostopoulos, 1996).

Type locality: Gerakarou, Mygdonia basin, Greece.

Age: Latest Pliocene (MNQ18).

Etymology: from the name of the type locality Gerakarou.

Institution: Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki, Greece (LGPUT).

Differential Diagnosis: Smaller than the known forms of the species from France, Italy and Spain and even smaller that *Cr. ramosus minor* from Senèze; short pedicle; beam bend slightly forwards between the first and the second tine; first tine extremely short, inserted closer to the burr and diverging at nearly right angle from the beam, strongly curved upwards and terminally backwards with elliptical to rounded cross-section; flattened beam at the level of the first tine; short premolar row; P_2 with highly preserved paraconid; smaller post-cranials than *C. r. minor*.

The small cervid from Volakas appears morphologically similar to that from Gerakarou but larger and closer to the Sesklo one. In comparison to the West European representatives of the species the Sesklo *Croizetoceros ramosus* appears closer to those from Les Etouaires, St.Vallier (France), La Puebla de Valverde and Villaroya (Spain) (Heintz, 1970). Both the Volakas and Sesklo forms can attribute with some confidence to *Croizetoceros ramosus*.

Family: Giraffidae GRAY, 1821

Genus: *Mitilanotherium* SAMSON & RADULESCO 1966

Synonyms: *Macedonitherium* SICKENBERG, 1967.
Sogdianotherium SHARAPOV, 1974.

Type locality: Fîntîna lui Mitilan, Romania.

Type species: *Mitilanotherium inexpectatum* SAMSON & RADULESCO, 1966.

Reference localities: Dafnero, Sesklo, Libakos, Vatera (Greece), Kuruksay (Tajikistan),?Gülyazi (Turkey).

Age: Late Pliocene-Earliest Pliostocene.

Diagnosis: Medium sized giraffid, probably referred to the subfamily Palaeotraginae. Elongated skull with strong opisthocranial region, flat cranial roof and strong occipital condyles. Long ossicones with elongated-elliptical cross-section, situated exactly above the orbits, inclined towards the front and bent towards the rear. P^4 large and wide with strong hypoconal fold. M^3 with reduced and oblique distal lobe. M_3 with elongated talonid. Elongated and moderately slender limb bones, proportionally placed between *Palaeotragus* and *Samotherium*.

Mitilanotherium martinii (SICKENBERG, 1967)

VOLAKAS

Synonymy: *Macedonitherium martinii*, Sickenberg (1967).

Material: Cranial part with both ossicones; distal part of Humerus; distal part of Radius; Carpals II+III & IV; Metacarpal III-IV; Phalanx I; prox. part of Tibia; Calcaneum; Centrotarsal. All specimens are stored in the collection of the University of Athens, without catalogue number.

Description: *in* Sickenberg (1967).

SESKLO

Synonymy: cf. *Macedonitherium martinii*, Athanassiou (1996).

Material: dI_2, dI_3, dC dex, Σ-189; right mandibular part with dP_2–M_1 and left mandibular part with dP_2–dP_3, Σ-184; dist. part of Humerus dex, Σ-2010; prox. part of Radius and Ulna dex, Σ-670; dist. part of juvenile Tibia sin, Σ-50; Astragalus sin, Σ-1124; prox. part of Metatarsal III-IV sin, Σ-58.

Measurements: LdP_{2dex}=16, LdP_{2sin}=16, WdP_{2dex}=8, WdP_{2sin} =8.2; LdP_{3dex}=21, LdP_{3sin}=22.2, WdP_{3dex}=12, WdP_{3sin} =11.5; LdP_4=34.5, WdP_4=17; LM_1=29.9, WM_1~16.5, Height $M_1$25; Humerus DTdist= 99, $DAPdist_s$=86.1; Radius DTprox=105.5, DAPprox=50; Tibia DTdist=69, DAPdist=50; Metatarsal III-IV DTprox=59, DAPprox=55.5; Astragalus Lexternal=82.8.

Description: The mandible is elongated with long diastema (fig. 8). The deciduous incisors are wide and asymmetrical. The deciduous canine has the characteristic bilobe structure of the giraffids and it is wider than the incisors. The buccal teeth are very large and almost unworn. Their enamel is wrinkled. The morphology of dP_2 differs from that of cervids or bovids mainly by the presence of a well-developed paraconid. In the right dP_2 of Σ-184 the paraconid fuses to the metaconid in the middle of the crown's height; in the left one, the paraconid is much less developed and it fuses to the metaconid just at the base of the crown. The entoconid and the entostylid are long. The

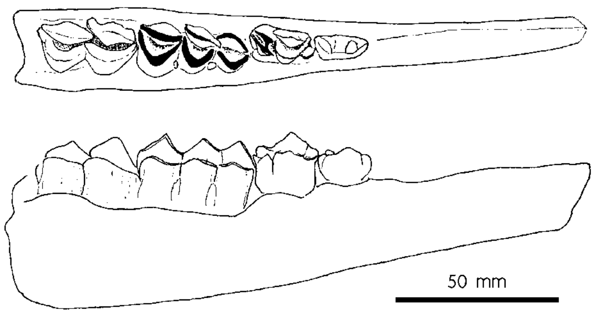

Figure 8: *Mitilanotherium martinii* lower toothrow (Σ-184) from Sesklo. Occlusal and buccal view.
Figure 8 : Denture inférieure de *Mitilanotherium martinii* (Σ-184) de Sesklo. Vue occlusale et labiale.

dP_3 has the morphology of a molarized premolar. It has a very strong metaconid, which, together with the protoconid, run parallel to the sagittal plane. The entoconid and entostylid are smaller, inclined towards the lingual wall of the tooth. dP_4 does not differ from the typical ruminant pattern, having three lobes with basal pillars. M_1 is completely fresh with strong lingual cuspids. The lingual stylids are not prominent, except of the well-developed mesostylid. There is no ectostylid between the buccal lobes.

The postcranial material is characterised by large size and moderately slender proportions. The proximal articulation of the radius is wide and less rounded medially in comparison to the radii of the smaller ruminants. The astragalus is long and narrow; its general appearance is more symmetrical than in Bovidae and Cervidae. The metatarsal diaphysis has concave palmar side, as in the Cervidae, though not so much expressed. The proximal articulation consists of three articular facets, two of which (for the scaphocuboid and the third cuneiform) are crescent shaped and of equal size, separated by a deep synovial fossa.

DAFNERO

Material: Part of maxilla with P^4–M^3, DFN-28; Radius, DFN-69; Tibia, DFN-150; Metatarsal III-IV, DFN-68.

Measurements: LP^4–M^3=87.6, LM^1-M^3=73.2; LP^4=19.5, WP^4=25.3, Height P^4=15.2, LM^1=29.1, WM^1=25.4; LM^2=28.5, WM^2=26.9; LM^3=24.4, WM^3=25.3; Radius: L= 525, DTprox=91.2, DAPprox=49.3, DTdia=55.5, DTdist=86.2, DAPdist=54.3; Tibia L=437.5, DTdia=44, DTdist=67.9, DAPdist=60.5; Metatarsal III-IV L=443.1, DTprox=56.6, DAPprox=56, DTdia=53.6, DTdist=70.2, DAPdist=42.3.

Description: All teeth are fairly hypsodont and have wrinkled enamel (fig. 9). The P^4 is very wide and large in comparison to the molars. It has well-developed styles and a hypoconal fold that divides the central fossette. The molars are also wide with well-developed styles, except for the metastyle. There is a cingulum along the labial wall of the teeth, as well as between the lobes. The distal lobe of M^3 is much reduced in size and oblique in relation to the sagittal plane. The post-cranial material has all the characters that have been considered as typical for the Giraffidae (Heintz, 1970; Geraads, 1986) and they are identical to those from Sesklo, previously described.

Discussion: Plio-Pleistocene giraffids were poorly documented from Eastern Europe and Asia. Sickenberg (1967) describes *Macedonitherium martinii* from the Greek locality of Volakas (Eastern Macedonia), while one year before Samson & Radulesco (1966), reviewing part of an earlier published material from Romania, establish the new giraffid genus and species *Mitilanotherium inexpectatum*. Later on, Sharapov (1974) describes another giraffid from the Late Pliocene of Kuruksay (Tajikistan), under the name *Sogdianotherium kuruksaense*. More recently Godina & Bajgusheva (1985) and Bajgusheva & Titov (2002) refer to another Pliocene form

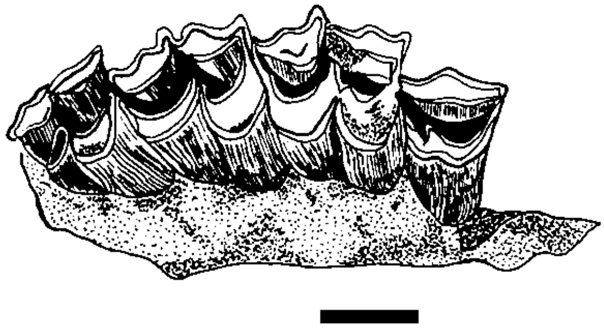

Figure 9: *Mitilanotherium martinii* upper toothrow (DFN-68) from Dafnero. Occlusal view. Scale: 20mm.
Figure 9 : Denture supérieure de *Mitilanotherium martinii* (DFN-68) de Dafnero. Vue occlusale. Échelle: 20mm.

Palaeotragus priasovicus from the Azov region, covering the geographical gap of the Pliocene giraffid distribution. Apart from the referred localities, *Macedonitherium* is also mentioned from the Turkish fauna of Gülyazi, (Sickenberg & Tobien, 1971).

Regarding the Greek record, Plio-Pleistocene giraffids present a vast repartition, mentioned from Western Macedonia (localities Libakos and Dafnero; Steensma, 1988; Kostopoulos & Koufos, 1994; Kostopoulos, 1996), Thessaly (locality Sesklo; Athanassiou, 1996) and recently on Lesbos Island (locality Vatera; de Vos *et al.*, 2002).

All Greek forms were generally attributed to the species *Macedonitherium martinii* Sickenberg, 1967, while Kostopoulos (1996) proposes the possible synonymy of the three genera *Mitilanotherium*, *Macedonitherium* and *Sogdianotherium*. In fact, the comparative study of the available material from Greece and Romania, permits the systematic revision of these forms, which represent a single genus: *Mitilanotherium* Samson & Radulesco, 1966.

The cranial fragment from Volakas (holotype of "*Macedonitherium*") is very similar morphologically to the skull from Kuruksay (holotype of "*Sogdianotherium*") described by Sharapov (1974). In both specimens the ossicones are long with elongated-elliptical cross section, situated above the orbits, inclined towards the front and bent towards the rear. The skull morphology also indicates affinities to the subfamily of Palaeotraginae (Sickenberg, 1967).

The teeth from Dafnero are very similar to those from Kuruksay (large P^4 with hypoconal fold, reduced and oblique distal lobe on M^3), but they are clearly smaller (almost 20%). The giraffid from Oubeidiyeh has similar M^3 morphology (Geraads, 1986), and it is metrically comparable with the Kuruksay specimen. The post-cranial material does not show major differences among the compared samples, indicating a quite large metrical variation (fig. 10). All specimens are grouped close together, placed between the two main Late Miocene genera *Palaeotragus* and *Samotherium* (fig. 11).

In our opinion *M. martinii* is most plausibly a junior synonym of the prior *M. inexpectatum*, but since the

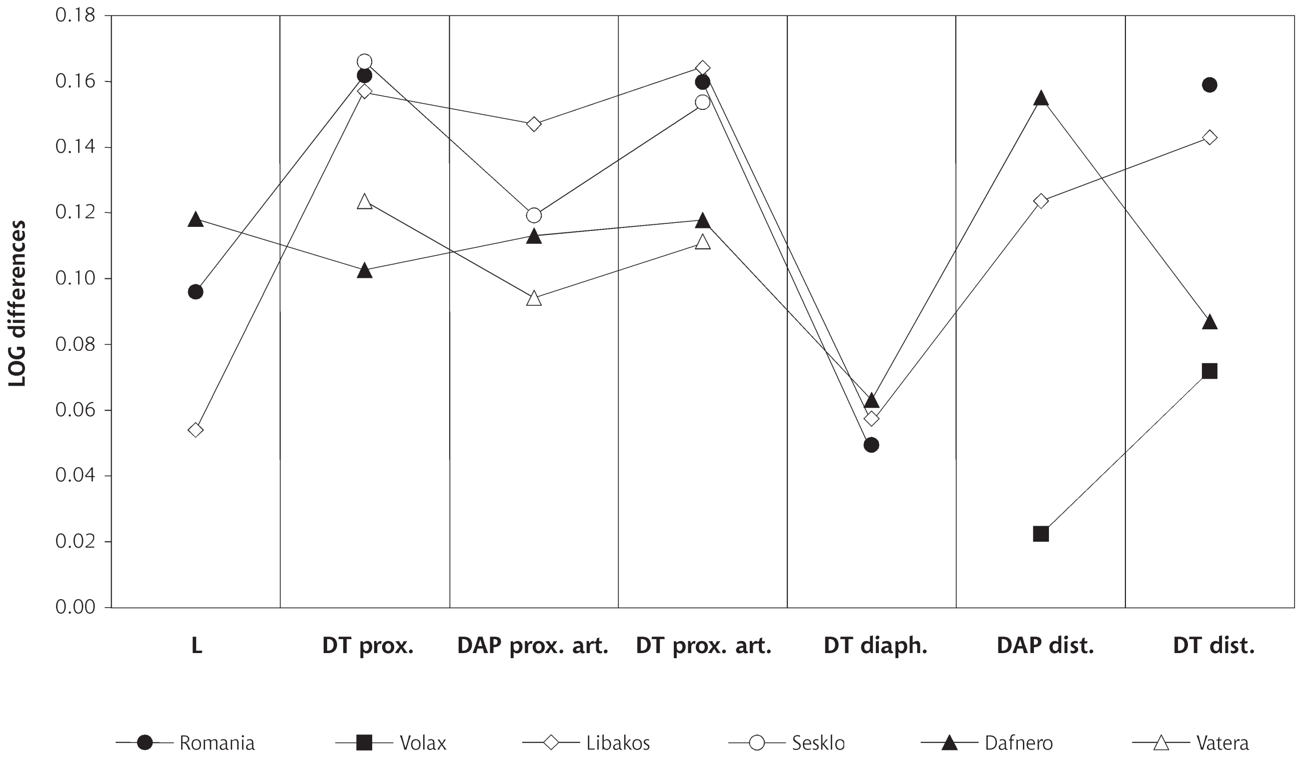

Figure 10: Logarithmic ratio diagram of *Mitilanotherium* radius from several localities (arbitrary standard).
Figure 10 : Diagramme des différences logarithmiques du radius de *Mitilanotherium* de différentes localités.

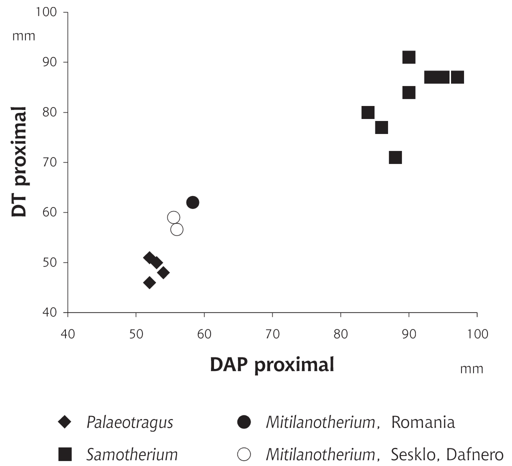

Figure 11: Scatter diagram of *Mitilanotherium* metatarsal III-IV (late Miocene data from Bohlin, 1926).
Figure 11 : Diagramme de dispersion du métatarse III-IV de *Mitilanotherium* (données du Miocène supérieur selon Bohlin, 1926).

available material does not allow a detailed comparison, we will still regard them as distinct species. *M. kuruksaense* is larger, while the relationships of *Palaeotragus priasovicus* with *Mitilanotherium* should be investigated. Interestingly, Arribas *et al*. (2001) refer lately cf. *Mitilanotherium* from the late Pliocene Spanish locality Fonelas, modifying our point of view, concerning the geographic expansion of this genus. If indeed the Fonelas giraffid belongs to this genus and no to a purely African immigrant into the Iberian Peninsula, it will be very interesting to investigate the reasons, time and ways of its distribution.

CONCLUSIONS

Despite their relative scarcity, suids, cervids and giraffids constitute an important part of the Greek Plio-Pleistocene faunas, mainly because of their biochronological and ecological significance (Kostopoulos & Koufos 2000). Though the bovid assemblage of the area is much different in relation to the West European associations of this time span, including forms of Asiatic origin and affiliations (Kostopoulos & Athanassiou, 1997; Kostopoulos 1998b; Kostopoulos *et al*. 2002; Athanassiou, 2002), suids and cervids clearly correlate the Greek faunas to those of SE Europe. The typical West European “Villafranchian” cervid assemblage *Croizetoceros-Metacervocerus-Eucladoceros* is also present in the Late Pliocene of Greece. Some minor differences, concerning mainly the size, do exist related probably to the climatic deterioration occurring at the end of Pliocene.

The presence of Plio-Pleistocene suids in Greece is very restricted. *Sus strozzii* certainly occurs in the latest Pliocene (MNQ 18) faunas of Northern Greece, while it is not mentioned from earlier or later associations of the area. The Greek form represents a large sized population similar with the contemporaneous from Western Europe (especially Senèze, France), and slightly different from the younger typical Italian *Sus strozzii*.

Until now less attention has been given on Plio-Pleistocene giraffids and their significance. In Eastern Europe giraffids occur in Greece, Romania, Turkey, Ukraine, Tajikistan and southernmost in Israel.

According to the available data most of the local samples represent a single genus, *Mitilanotherium (=Macedonitherium =Sogdianotherium)*, related to Palaeotraginae. The distribution of the genus remains however an open subject. In the Balkans at least, the giraffids seem to disappear at the very beginning of the Pleistocene.

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P.S. While this work was in press, several new data concerning the Plio-Pleistocene suids, cervids and giraffids appeared. We tried to include them all in the final version of the article.

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