

The latest Villafranchian – early Galerian small dogs of the Mediterranean area

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Abstract. This paper reports some preliminary results of the study of the latest Villafranchian – early and middle Galerian (latest Early Pleistocene and Middle Pleistocene) small sized fossil dogs from several European localities at Mediterranean latitudes and in Israel. The systematic position of these dogs is still doubtful, and they are therefore provisionally referred to *Canis* cf. *arnensis* or *Canis* aff. *arnensis* (advanced form). This latter dog probably represents a new species, for the definition of which we await further comparisons with the northern species. At present we do not exclude the possibility that at the transition Early-Middle Pleistocene, at least two different phyletic lineages were present, both paralleling wolf morphologies; one in the Mediterranean region, represented by *Canis arnensis*, the second in north and central Eurasia, represented by *Canis etruscus*, which gave rise to *Canis mosbachensis*. At the end of the Middle Pleistocene *Canis lupus* dispersed in Eurasia.

Key words: *Canis* aff. *arnensis*, latest Villafranchian, early and middle Galerian, latest Early Pleistocene, Middle Pleistocene.

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I. INTRODUCTION

The systematics of the Middle Pleistocene small dogs has been subject to varying interpretations. The Mosbach wolf, described as *Canis mosbachensis* (SOERGEL 1925), was considered by THENIUS (1954) as a sub-species of *Canis lupus*. BONIFAY (1971) synonymized *C. mosbachensis* with *Canis arnensis* and *Canis etruscus*. This interpretation was contended by TORRE (1974), who demonstrated that the Middle Pleistocene wolf is closer to *Canis lupus* than to the Villafranchian species.

The modern wolf *Canis lupus* is commonly thought to be derived from the evolutionary lineage *C. etruscus* - *C. mosbachensis* (MARTIN 1973; TORRE 1967, 1974, 1979; KURTÉN 1968; SOTNIKOVA 1989; ARGANT 1991). As already observed by KURTÉN & POULIANOS (1977) this interpretation presupposes a reversal in the size trend, as the late Villafranchian *Canis etruscus* (Olivola and Tasso faunal units) are on average significantly larger than the latest Villafranchian and early Galerian small dogs.

The Villafranchian and Galerian mammal ages are defined on macro-mammal fossil assemblages from Italy. They correspond to the Villanyian, Biharian and part of the Toringian (sensu

FEJFAR & HEINRICH 1990). The boundary between Villafranchian and Galerian is placed in the upper part of the early Biharian, at the Early-Middle Pleistocene transition (cfr. TORRE et al. 1992).

For this reason some authors do not exclude an origin of the Middle Pleistocene wolves from *Canis arnensis* (SOERGEL 1928; THENIUS 1954; DE BEAUMONT 1979, 1980; KURTÉN & POULIANOS 1977). This species was generally excluded from the ancestry of the wolf as it was believed to be closer first to jackals (TORRE 1967; KURTÉN 1968), then to coyotes (KURTÉN 1974). Close relationships between wolves and coyotes are however suggested by their tendency to hybridisation, rare in nature but possible under human influence (NOWAK 1979).

The relatively scanty fossil record of *Canis* in latest Villafranchian and post-Villafranchian localities, and the absence of a critical revision of its systematics, are responsible for the fact that dogs from this time span have been reported either as *Canis etruscus* (MORALES & SORIA 1979; TURNER 1992; BONIFAY 1986; ALCALÀ & MORALES 1989; MARTINEZ 1991), as *Canis etruscus mosbachensis* (PONS MOYÀ 1987; AGUSTÍ & MOYÀ SOLÀ 1992) or as *Canis mosbachensis* (KURTÉN & POULIANOS 1977; HAAS 1966; TSOUKALA 1989).

In the latest Villafranchian localities (late Early Pleistocene) of the Mediterranean region dogs are represented by large forms of *Canis (Xenocyon) gr. falconeri* (cfr. ROOK 1994) and by small dogs of a size comparable to the late Villafranchian *Canis arnensis*. Wolves of a size comparable to *Canis etruscus* have not been recorded.

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II. THE LATEST VILLAFRANCHIAN – EARLY GALERIAN SMALL DOGS

Fossil remains of the small dog have been recovered from Spain, Italy, Greece and Israel (Fig. 1).

Fossils from Cueva Victoria and Venta Micena (PONS MOYÀ 1981, 1987; MARTINEZ 1991) were described as *Canis etruscus etruscus* (Cueva Victoria) and *Canis etruscus mosbachensis* (Venta Micena) by PONS MOYÀ (1981; 1987). Recently, MARTINEZ (1991) described the specimens from Venta Micena as *Canis etruscus*, including a lower carnassial attributed by PONS MOYÀ (1987) to *Cuon priscus*.

Abundant macro- and micromammal remains have been recovered from the fissure fillings in the quarry area near Apricena (Fig. 1) in southern Italy (the so called Pirro Nord fauna; DE GIULI & TORRE 1984; DE GIULI et al. 1987; ROOK 1993). DE BEAUMONT (1979) refers an M^2 collected in this area to *Canis* cf. *arnensis*. DE GIULI et al. (1987) reported *Canis arnensis* from fissures PN 2 and PN 5 (excavated in 1984), and in the PIERI collection (collected in 1968 and stored in the Dipartimento di Geologia e Geofisica, Bari University). New material was collected in the course of field work organized during 1991-1992 by the Dipartimento di Scienze della Terra, University of Florence, with the support of Museo Civico di S. Severo (Foggia). The small dog material from this locality consists of: a left M_1 (Fig. 2: 1A,B), a left maxillary bone with M^1 , a right P^4 , a fragmentary left mandibular ramus with I_3-M_1 , a left M^2 , a juvenile right M^1 , a right maxillary bone with P^4-M^2 (Fig. 2: 3A,B), and a facial portion of skull with right and left I^{1-5} and C, right P^2-M^2 and left P^2 , P^4-M^2 (Fig. 2: 2A,B).

KOUFOS (1992) described material from Apollonia-1 (Fig. 1). The material consists of a left maxillary bone with I^2-P^3 , a fragmentary skull with right I^1-M^2 and left I^3-P^2 , a left mandibular

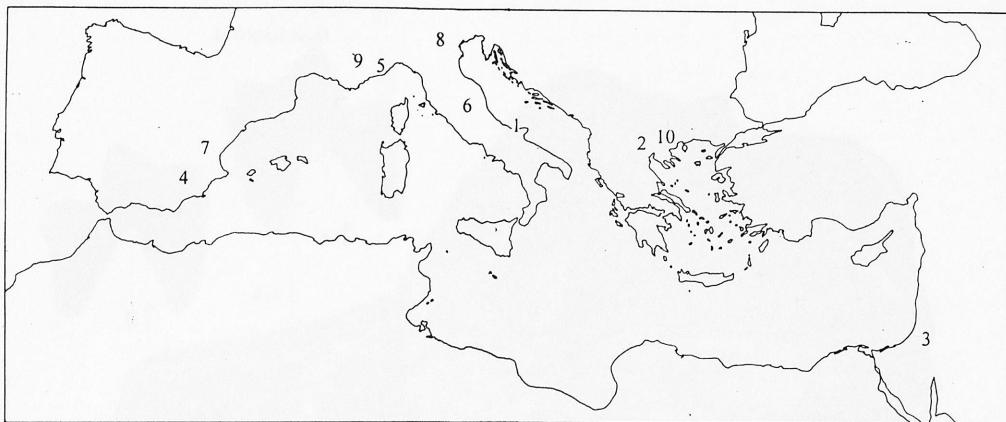


Fig. 1. Distribution of *Canis* cf. *arnensis* and *Canis* aff. *arnensis* (advanced form) in the Mediterranean area. *Canis* cf. *arnensis*: 1) Pirro Nord and Cava Dell'Erba, Gargano (Italy); 2) Apollonia-1, Mygdonia basin, Macedonia (Greece); 3) Oubeidiyeh, Jordan Valley (Israel); 4) Cueva Victoria and Venta Micena, Guadix-Baza basin, Granada (Spain). *Canis* aff. *arnensis* (advanced form): 5) Le Vallonnet, Roquebrune Cap-Martin (Monaco); 6) Colle Curti, Colfiorito basin, Macerata (Italy); 7) Huescar-1 and Cullar de Baza-1, Guadix-Baza basin, Granada (Spain); 8) Soave varoius sites (Castello, M. Tenda, Viatelle, Zoppega), Verona (Italy); 9) L'Escale, Saint-Estève-Janson (France); 10) Petralona, Chalkidiki peninsula (Greece).

ramus with C-M₃, and a left M₂. Comparing these fossils with *Canis etruscus* and *Canis arnensis* from Upper Valdarno, KOUFOS (1992) concludes that the Apollonia-1 sample shows morphological and metrical features intermediate between the two species, but considers it closer to *Canis arnensis* and assigns the Apollonia-1 dog to this species.

The material from Oubeidiyeh (Fig. 1; TCHERNOV 1986), a fragmentary maxillary bone, some fragmentary mandibular branches, and a few isolated teeth and postcranial remains, was attributed to *C. lupus mosbachensis* by HAAS (1966), while BALLESEO (1986) referred it to *Canis* cf. *arnensis*.

The fossil dogs from the above mentioned localities are here referred to *Canis* cf. *arnensis*. They are *arnensis*-sized dogs, showing some dental ratios suggestive of evolutionary change, such as the upper molars with a reduced L/W ratio (cf. DE BEAUMONT 1979) and relative trigonid length reduction (Fig. 3). The latter character could be due to size variation of the metaconid. However, given the high variability originating from the differing measurement sources (some data are from the literature) and the small differences, we are cautious in interpreting these results (ROOK 1993). Furthermore, the few mandibular fragments bearing premolars and carnassials from these latest Villafranchian localities (Pirro, Apollonia-1, Venta Micena) are, in this respect, closer to the morphologies present in the type population of *Canis arnensis*. The late Villafranchian dogs (*Canis etruscus* and *Canis arnensis*) are characterized by an M₁ paraconid that is relatively low, and does not rise over the main cusps of the premolars (TORRE 1967).

In Galerian faunas a small dog (size of *Canis arnensis*) is sometimes associated with the larger *Canis* (*Xenocyon*). Compared to the latest Villafranchian forms, these small dogs show more derived characteristics, with more pronounced "wolf-like" morphologies.

Among the sample reported by MOULLÉ (1992) from Le Vallonnet (Fig. 1; DE LUMLEY et al. 1988) it is worth mentioning a fragmentary skull, a fragmentary left mandibular ramus with M₁-M₂, a fragmentary right mandibular ramus with M₁-M₂, and a fragmentary right mandibular ramus

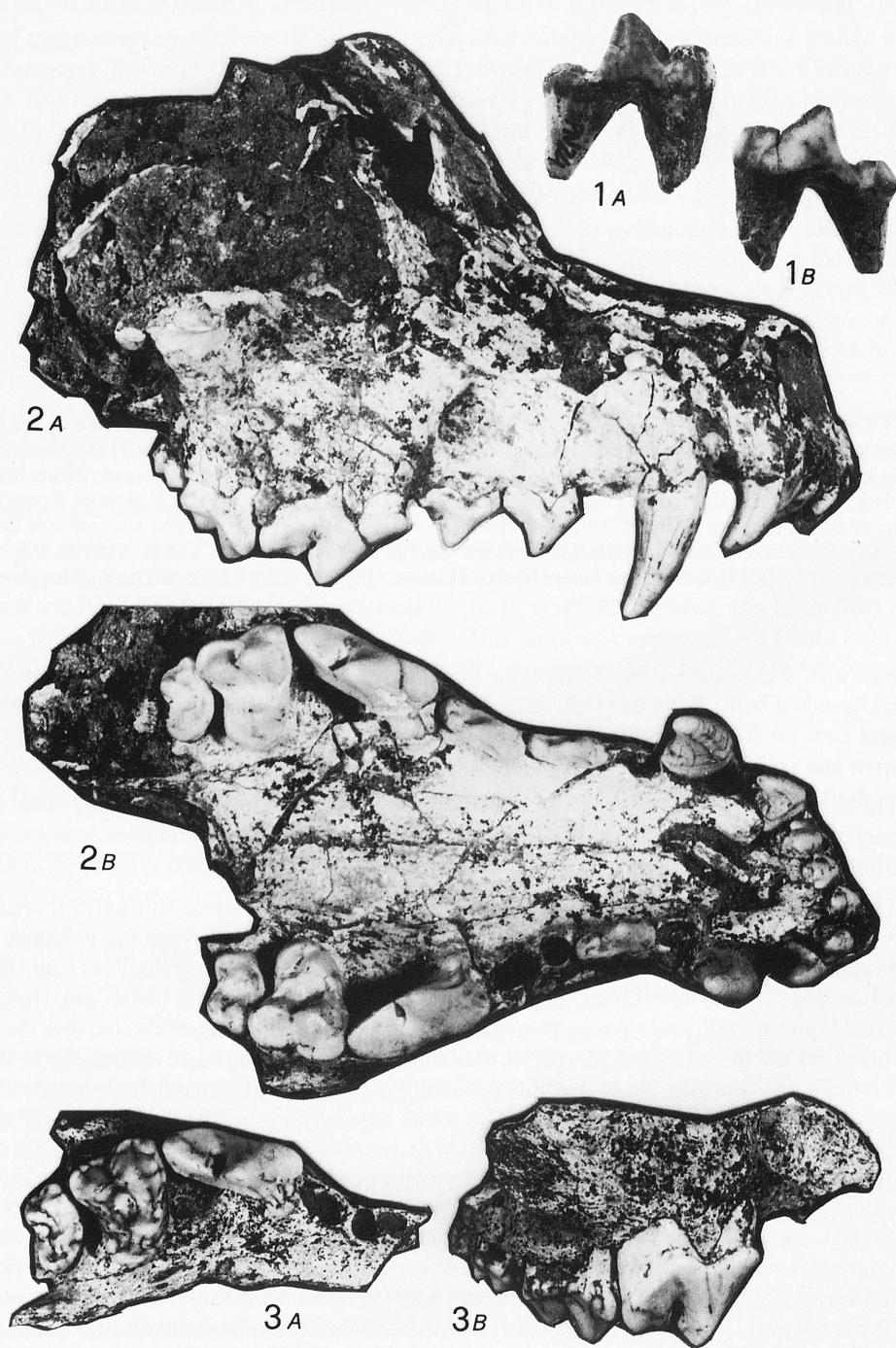


Fig. 2. *Canis* cf. *arnensis* from Pirro Nord. 1) PN 24, left lower carnassial; A, lingual view; B, labial view. 2) DE not numbered, fragmentary skull; A lateral view; B, ventral view. 3) DE 12-2, not numbered, Right maxillary bone with P^4 - M^2 ; A occlusal view, B Labial view. All figures natural size.

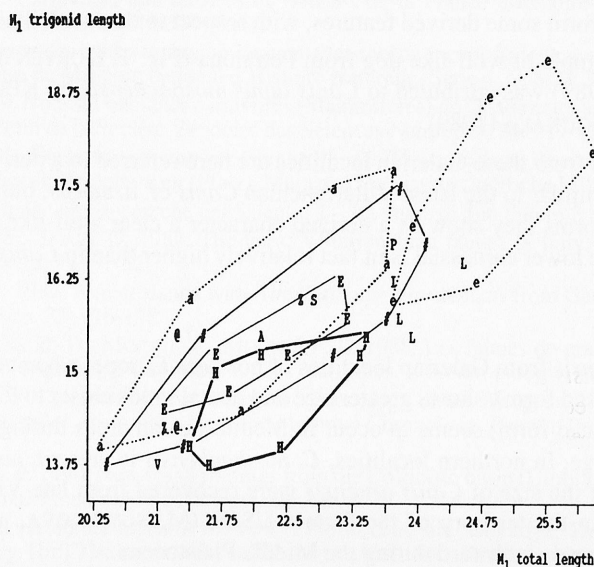


Fig. 3. Diagram of M_1 trigonid length versus M_1 total length for some fossil *Canis* species. *Canis etruscus*: from Upper Valdarno = e and dotted line; *Canis arnensis*: from Upper Valdarno = a and dotted line; *Canis cf. arnensis*: from Venta Micena = V (data from MARTINEZ 1991); from Pirro = P; from Apollonia-1 = A (data from KOUFOS 1992). *Canis aff. arnensis* (advanced form): from Le Vallonnet = L (data from MOULLÉ 1993); from Huescar-1 = I; from Cullar de Baza-1 = @; from Soave various sites, Soave Castello = S, Zoppega = Z; from L'Escafe, lower beds = E and thin line, upper beds = # and thin line; from Petralona = H and heavy line (data from KURTÉN & POULIANOS 1977, 1981).

with P_4 - M_1 , in addition to various fragments and isolated teeth. DE LUMLEY et al. (1988) and MOULLÉ (1992) compared the specimens from the cave of Le Vallonnet with the sample from Petralona and referred their fossils to *Canis lupus mosbachensis*.

FICCARELLI & MAZZA (1990) refer a tibia from the earliest Galerian locality of Colle Curti (Fig. 1) to *Canis cf. arnensis* on the basis of its dimensions.

Some fossil remains of a small dog were also recovered at Huescar-1 and Cullar de Baza-1 (Fig. 1; ALBERDI et al. 1989; ALCALÀ & MORALES 1989). Three specimens are known from Huescar-1, a right M^1 , a right M^2 and a left M_1 . From Cullar de Baza are recorded a fragmentary right mandibular ramus with C , P_1 , broken P_3 , P_4 , broken M_1 , M_2 , M_3 as well as isolated left P_3 , P_4 , and M_1 . After comparisons with the samples from L'Escafe, Petralona and Venta Micena, ALCALÀ & MORALES (1989) refer the material from these localities to *Canis etruscus*, although with some hesitation.

Fossil dogs from karst fissure fillings at the foothills of Lessini Mounts (Fig. 1; PASA 1947; BARTOLOMEI 1982) were described by PASA (1947) as *Canis sp. aff. mosbachensis*. Re-examination of the specimens (stored in the Museo Civico di Storia Naturale, Verona) allow us to attribute this material to *Canis aff. arnensis* (advanced form).

BONIFAY (1971) described as *Canis etruscus* the rich sample (at least 20 individuals are represented) from L'Escafe (Fig. 1). She considers *Canis mosbachensis* and *Canis arnensis* as

younger synonyms of *Canis etruscus*. This opinion was criticized by TORRE (1974), who recognized in the L'Escale form some derived features, with respect to the late Villafranchian species.

The abundant sample of wolf-like dog from Petralona (Fig. 1; KURTÉN & POULIANOS 1977, 1981; TSOUKALA 1989) was attributed to *Canis lupus mosbachensis* by KURTÉN & POULIANOS (1977, 1981) and TSOUKALA (1989).

The dog remains from these Galerian localities are here referred to a derived form, *Canis* aff. *arnensis*. They are similar to the latest Villafranchian *Canis* cf. *arnensis*, but in comparison with the Villafranchian forms they show as a derived character a clear wolf-like morphology of M₁. The paraconid of the lower carnassial is in fact relatively higher than in *Canis arnensis* and *Canis etruscus*.

Canis mosbachensis from Galerian localities of northern Europe, when compared with *Canis* aff. *arnensis* (advanced form), shows greater size and dental ratios closer to *Canis etruscus*. *Canis* aff. *arnensis* (advanced form) seems to occur in Mediterranean areas during the first part of the Galerian mammal age. In northern localities, *C. mosbachensis* is present, and it is interesting to note that no dogs of the size of *Canis arnensis* were recovered from late Villafranchian – early Galerian localities in the territory of the former USSR (M. SOTNIKOVA, pers. comm.). *Canis mosbachensis* dispersed southward during the Middle Pleistocene.

Canis aff. *arnensis* (advanced form) probably represents a new species, for the definition of which we await further comparisons with the northern species. At present we do not exclude the possibility that at the transition Early-Middle Pleistocene, at least two different lineages were present, both paralleling wolf morphologies: one in the Mediterranean regions, leading from *Canis arnensis* to *Canis* aff. *arnensis* (advanced form); the second, in the north and central areas of Eurasia, from *Canis etruscus* to *Canis mosbachensis*. In Asia a primitive wolf-like species, close to *Canis etruscus* [*Canis variabilis* (PEI, 1934)] seems to have survived for a longer time. It is reported at Choukoutien locality 1 and locality 13; at the former site it is associated with *Canis lupus*.

At the end of Middle Pleistocene *Canis lupus* dispersed in Eurasia. Even if it is possible that the modern wolf was derived from *Canis mosbachensis*, its abrupt arrival in middle holarctic latitudes, as well as its association with *Canis mosbachensis* in some post-Galerian Italian localities, such as Ceré (PASA 1949; ROOK unpublished) and S. Sidero 3 (DE GIULI 1983), suggest that this species had its origin in the north.

REFERENCES

- AGUSTÍ J., MOYÀ SOLÀ S. 1992. Mammalian dispersal events in the Spanish Pleistocene. *Courier Forschungs-Institut Senckenberg*, **153**: 69-77.
- ALBERDI M.T., ALCALÀ L., AZANZA B., CERDENO E., MAZO A. V., MORALES J., SESÉ C. 1989. Consideraciones biostratigráficas sobre la fauna de Vertebrados fósiles de la cuenca de Guadix-Baza (Granada, España). *Trabajos sobre Neogeno-Cuaternario*, **11**: 347-355.
- ALCALÀ L., MORALES J. 1989. Los carnívoros de Pleistoceno medio de Cúllar de Baza-1 y Huéscar-1 (Cuenca de Guadix-Baza). *Trabajos sobre Neogeno-Cuaternario*, **11**: 215-223.
- ARGANT A. 1991. Carnivores quaternaires de Bourgogne. *Documenta, Laboratoire de Géologie, Lyon*, **115**: 1-301.
- BALLESIO R. 1986. Les carnivores du gisement Pleistocene d'Oubeidiyeh (Israel). [In:] E. TCHERNOV (ed) – Les Mammifères du Pléistocène inférieur de la vallée du Jordain a Oubeidiyeh. *Mémoires et Travaux du Centre de Recherche Français de Jérusalem* n° 5. Association Paleorientale, Paris 1986, Pp: 63-91
- BARTOLOMEI G. 1982. Il limite Pleistocene Inferiore – Pleistocene Medio in Italia sulla base dei micromammiferi. *Geografia Fisica e Dinamica Quaternaria*, **5**: 243-245.

- BONIFAY M. F. 1971. Carnivores quaternaires du Sud est de la France. Mémoires du Museum national d'Histoire Naturelle, Série C, **21**: 43-377, Paris.
- BONIFAY M.F. 1986. Intérêt des études taphonomiques au Pléistocène ancien: Soleilhac et Ceyssaguet (Blanzac, Haute Loire). Bulletin du Museum national d'Histoire Naturelle, Série 4, C, **8**(2): 269-281.
- DE BEAUMONT G. 1979. Note sur quelques carnivores (Mammifères) du Quaternaire ancien de la Province de Foggia (Italie). Bulletin de la Société Vaudoise des Sciences Naturelles, **74**: 217-226.
- DE BEAUMONT G. 1980. Säugerfaunen von der Grenze Pliozän/Pleistozän aus Rheinessen 2. Les carnivores du Quaternaire ancien de Neuleiningen (Pfalz). Mainzer Geowissenschaftliche Mitteilungen, **8**: 7-16.
- DE GIULI C. 1983. Le faune pleistoceniche del Salento: 1 – La fauna di San Sidero 3. I Quaderni, **1**: 45-84.
- DE GIULI C., MASINI F., TORRE D. 1987. The latest Villafranchian faunas in Italy: the Pirro Nord fauna. Palaeontographia italica, **74**: 51-62.
- DE GIULI C., TORRE D. 1984. A microfauna with *Allophaiomys pliocaenicus* from Gargano (Southern Italy). Paleontographia italica, **73**: 116-128.
- DE LUMLEY H., KAHLKE H.-D., MOIGNE A., MOUILLÉ P. E. 1988. Les faunes de grands mammifères de la grotte du Vallonnet. Roquebrune Cap Martin, Alps maritimes. L'Anthropologie, **92**: 465-469.
- FEJFAR O., HEINRICH W. D. 1990. Muroid rodent biochronology of the Neogene. [In:] E. H. LINDSAY, V. FAHLBUSCH, P. MEIN (eds) – European Neogene Mammal Chronology. Plenum Press, New York, 91-117 pp.
- FICCARELLI G., MAZZA P. 1990. New fossil findings from the Colfiorito basin (Umbra-Marchean Apennine). Bollettino della Società Paleontologica Italiana, **29**: 245-247.
- HAAS G. 1966. On the vertebrate fauna of the Lower Pleistocene site 'Ubeidiya. The Lower Pleistocene of Central Jordan valley. [In:] The excavation at 'Ubeidiya 1960-1963. Israel Academy of Human Sciences, Jerusalem Central Press, 68 pp.
- KOUFOS G. D. 1992. Les carnivores Pléistocène du bassin de Mygdonia. Annales de Paléontologie, **78**(4): 205-227.
- KURTÉN B. 1968. Pleistocene mammals of Europe. Weidenfeld and Nicolson, London.
- KURTÉN B. 1974. A history of coyote-like dogs in North America (Canidae, Mammalia). Acta Zoologica Fennica, **140**: 1-38.
- KURTÉN B., POULIANOS A. N. 1977. New Stratigraphic and faunal material from Petralona Cave with special reference to the Carnivora. Anthropos (Athens), **4**: 47-130.
- KURTÉN B., POULIANOS A. N. 1981. Fossil carnivora of Petralona cave. Status of 1980. Anthropos (Athens), **8**: 9-56.
- MARTIN R. 1973. Trois nouvelles espèces de Caninae (Canidae, Carnivora) des gisements plio-villafranchiens d'Europe. Documenta, Laboratoire de Géologie, Lyon, **57**: 87-96.
- MARTINEZ B. 1991. Revisión sistemática y estudio cuantitativo de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada). Unpublished Doctoral Thesis, Universitat Autnoma de Barcelona. 264+XV pp.
- MORALES J., SORIA D. 1979. Nuevos datos sobre los carnivoros del area de Teruel: sintesis y bioestratigrafia. Estudios Geologicos, **35**: 497-540.
- MOUILLÉ P. E. 1992. Les grands mammifères du Pléistocène inférieur de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes). Etude paléontologique des Carnivores, Equidé, Suidé et Bovidé. Unpublished Doctoral Thesis, Muséum National d'Histoire Naturelle Paris, 356 pp.
- NOWAK R. M. 1979. North American Quaternary *Canis*. Monographs of the Museum of Natural History, University of Kansas, **6**: 1-154.
- PASA A. 1947. I mammiferi fossili delle antiche brecce veronesi. Memorie del Museo Civico di Storia Naturale di Verona, **1947**(1): 1-111.
- PEI W.C. 1934. On the Carnivora from the Locality I of Choukoutien. Paleontologia Sinica (C), **8**, Peking.
- PONS MOYÀ J. 1981. El *Canis etruscus* Major (Carnivora, Mammalia) del Villafranchiense terminal de la Cueva Victoria (Murcia, Espaa). Endins, Ciutat de Mallorca **8**: 43-46.
- PONS MOYÀ J. 1987. Los carnívoros (Mammalia) de Venta Micena (Granada, Espaa). Paleontologia i Evolució, Memoria Especial, **1**: 109-128.
- ROOK L. 1993. I cani dell'Eurasia dal Miocene Superiore al Pleistocene Medio. Unpublished Doctoral Thesis, Modena-Bologna-Firenza and Roma "La Sapienza" Universities, 154+XXIX pp.
- ROOK L. 1994. The Plio-Pleistocene Old World *Canis* (*Xenocyon*) gr. *falconeri*. Bollettino della Società Paleontologica Italiana, **33**: 71-82.
- SOERGEL W. 1925. Die Säugetierfauna des altdiluvialen Tonlagers von Jockgrim. Zeitschrift der Deutschen geologischen Gesellschaft, **77**: 405-438.
- SOERGEL W. 1928. Ein kleiner Wolf aus dem Kiesen von Süssenborn. Zeitschrift der Deutschen geologischen Gesellschaft, **80**: 227-255.

- SOTNIKOVA M.V. 1989. Late Pliocene – Early Pleistocene Carnivora stratigraphic significance. Academy of Sciences USSR, Transactions, **440**: 1-121. (In Russian with English summary).
- TCHERNOV E. (ed.). 1986. Les Mammifères du Pléistocène inférieur de la vallée du Jordain a Oubeidiyeh. Mémoires et Travaux du Centre de Recherche Français de Jérusalem no. **5**. Association Paleorientale, Paris 1986.
- THENIUS E. 1954. Die Caniden (Mammalia) aus dem Altquartär von Hundsheim (Niederösterreich) nebst Bemerkungen zur Stammesgeschichte der Gattung *Cuon*. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **99**: 230-286.
- TORRE D. 1967. I cani villafranchiani della Toscana. Palaeontographia Italica, **63**: 113-138.
- TORRE D. 1974. Affinità dentali del cane della grotta di "L'Escale". Rivista Italiana di Paleontologia e Stratigrafia, **80**: 147-156.
- TORRE D. 1979. The Ruscinian and Villafranchian dogs of Europe. Bollettino della Società Paleontologica Italiana, **18**(2): 162-165.
- TORRE D., FICCARELLI G., MASINI F., ROOK L., SALA B. 1992. Mammal dispersal events in the early Pleistocene of western Europe. Courier Forschungs-Institut Senckenberg, **153**: 51-58.
- TSOUKALA E. 1989. Contribution to the study of the Pleistocene fauna of larger mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave (Chalkidiki, N. Greece). Unpub. Doctoral Thesis, University of Thessaloniki, 360 pp.
- TURNER A. 1992. Villafranchian – Galerian larger carnivores of Europe: dispersions and extinctions. Courier Forschungs-Institut Senckenberg, **153**: 153-160.