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NYCTEREUTES MEGAMASTOIDES (CANIDAE, MAMMALIA) FROM THE EARLY AND MIDDLE VILLAFRANCHIAN (LATE PLIOCENE AND EARLY PLEISTOCENE) OF THE LOWER VALDARNO (FIRENZE AND PISA, TUSCANY, ITALY)

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Abstract. Among living canids, the genus *Nyctereutes* Temminck, 1838 was the first to appear in the Western European fossil record. In the Italian Peninsula, scanty remains from a few Plio-Pleistocene localities of central Italy, referable to the Triversa Faunal Unit (FU) and the Montopoli FU, were historically attributed to *Nyctereutes megamastoides* (Pomel, 1842). Here we describe the partially unpublished *Nyctereutes* remains from two localities of the Lower Valdarno (Tuscany), S. Giusto (Florence; early Villafranchian) and Montopoli (Pisa; middle Villafranchian), and compare them with both extant and fossil species of this genus. The material described herein most closely resembles the remains from Spain, France and other European sites previously attributed to *N. megamastoides* in proportions and morphological features, hence confirming the presence of this relatively widespread species in Italy from the Pliocene to the Early Pleistocene. Besides the scanty material, the Lower Valdarno record of *N. megamastoides* represents one of the earliest of the species in Europe and allows to report, for the first time, the occurrence of a derived form of *Nyctereutes* in the Late Pliocene of Italy. This early record confirms that the evolutionary pattern of Asia, where the advanced *N. sinensis* is associated with the primitive *N. tingi*, was different in the Pliocene of Europe.

INTRODUCTION

The earliest fossil record of the genus *Nyctereutes* Temminck, 1838 in Eurasia dates back to the Early Pliocene with the presence of two contemporary species: *Nyctereutes tingi* Tedford & Qiu, 1991 in the Yushe Basin, China, and *Nyctereutes donnezani* (Depéret, 1890) in Western Europe (Ruscinian time, Tedford & Qiu 1991). Other European findings were ascribed to *N. tingi*, e.g., those of the Bulgarian site of Varshets (see Spassov 1997; 2003) and those of Megalo Emvolon (Greece; see Koufos 1997). Tedford & Qiu (1991) suggested that these two species may represent a single taxon with a wide Paleoartic distribution.

In some Chinese localities, together with *N. tingi*, there is also a more derived species, *Nyctereutes sinensis* (Schlosser, 1903) (see Tehilhard de Chardin & Pei 1941). This larger and more evolved taxon was replaced during the Early-Middle Pleistocene by *Nyctereutes* sp. (see Tedford & Qiu 1991). *N. sinensis* in some respects resembles the European taxon recovered from French and Spanish sites like Senèze and Villaroya, *Nyctereutes megamastoides* (Pomel, 1842), which is considered the phyletic descendant of *N. donnezani*. In their review of the Pliocene *Nyctereutes* species of Eurasia, Soria & Aguirre (1976) identified two subspecies of *N. megamastoides*: *N. megamastoides megamastoides* from western European sites like Perrier-Etouaires, Perrier-Pardines, Senèze (France), Chilhac, Villaroya (Spain) and Csárnota (Hungary); and *N. megamastoides vulpinus* from St. Vallier (France), suggesting the possible attribution of the material from La Puebla de Valverde (Spain) to this subspecies. This distinction is based on differences in dental proportions (e.g. the elongation of the premolars and of the carnassials and the M2 reduced length in comparison to *N. m. megamastoides*). Recently, Monguillon et al. (2004), revised the abundant material of St. Vallier, proposing to raise the subspecies *N. m. vulpinus* to the rank of species as the differences with *N. megamastoides* (sensu *N. m. mega-*

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mastoides of Soria and Aguirre 1976) testify to adaptations to a more carnivorous diet. The authors considered the hypothesis that *N. vulpinus* evolved from the European population of *N. tingi* more plausible. There is a consistent hiatus in the Eurasian fossil record of *Nyctereutes* during the Early Pleistocene. Nowadays *Nyctereutes procyonoides* (Gray, 1834) is the only living species of its genus. Its geographic distribution is composed of an original Asian range (Eastern Siberia, Northern China, North Vietnam, Korea and Japan) and a European range (Finland, Sweden, Norway, Poland, Germany, France and Hungary), where they were introduced between the 1930s and the 1950s. The earliest record of the extant *N. procyonoides* is in Zhoukoudian localities 1 and 13: these fossil specimens differ from the living individuals only by the larger size (see Tedford & Qiu 1991). The phylogenetic relationship of *N. procyonoides* to the other Eurasian forms is still unclear, though it is reasonable to consider *N. sinensis* the closest fossil species to the living raccoon-dog, as suggested by Tedford & Qiu (1991).

The Villafranchian (Late Pliocene to Early Pleistocene) fossil record in Italy records three occurrences of *Nyctereutes* (Gliozzi et al. 1997; Rook & Martinez Navarro 2010). One is from the Collepardo local fauna (Anagni Basin, Latium; Montopoli FU, Gliozzi et al. 1997) two from the Lower Valdarno (Tuscany; Triversa FU and Montopoli FU). The latter (two specimens housed in the Museum of Natural History of the University of Florence) are the subject of this paper.

NYCTEREUTES FROM LOWER VALDARNO

The Lower Valdarno basin has yielded *Nyctereutes* remains from two different localities: San Giusto (Triversa FU, early Villanyian, early Villafranchian, Late Pliocene; Florence), and Montopoli (Montopoli FU, middle Villafranchian, Early Pleistocene, Pisa).

San Giusto - San Giusto is a well-known early Villanyian (Late Pliocene) locality that yielded the type specimen of the vole *Mimomys stehlini* (Kormos 1931; Masini & Torre 1987). Together with other Italian early Villanyian sites (Cascina Arondelli, Asti, Piedmont; Arcille, Grosseto, Tuscany) this fauna is coeval with the large mammal assemblages of the early Villafranchian Triversa FU and are correlated to the Gauss Chron (Sala & Masini 2007).

An unpublished *Nyctereutes* hemimandible fragment from S. Giusto is kept in the collections of the Natural History Museum, Geological and Paleontological section, of the University of Florence with inventory number IGF 10132. The specimen was recovered during a sampling excavation in 1916 and later donated to the Museum by Prof. A. Fucini.

Montopoli - Montopoli is an important large mammal fauna site since it is the first middle Villafranchian (Early Pleistocene) large mammal assemblage. Montopoli is stratigraphically superposed on the fauna of the Triversa unit and shallow-water marine sediments of Early Pleistocene age (Middle Pliocene in papers prior to the IUGS 2009 decision; cf. Benvenuti et al. 1995). This fauna is celebrated in the literature for its important signs of environmental change given by the dispersals of a primitive species of the genus *Mammuthus* (Palombo & Ferretti 2005), the monodactyl horse *Equus* cf. *livenzovensis*, the large deer *Eucladoceros tegulensis*, and *Gazella borbonica*, as well as the disappearance of some taxa with subtropical affinities still characterizing the previous early Villafranchian assemblages (Pradella & Rook 2007).

The Montopoli Faunal Unit (corresponding to unit MN16b in the European MN sub-division) was originally included in the early Villafranchian (Azzaroli 1977; Azzaroli et al. 1988), but the marked faunal turnover characterizing the transition from the early Villafranchian Triversa FU to the Montopoli FU suggested considering Montopoli as the basal unit of the middle Villafranchian (Caloi & Palombo 1996; Gliozzi et al. 1997). Montopoli, and the related faunal unit, occurs at the Gauss–Matuyama transition (Lindsay et al. 1980) thus correlating with the recently redefined Plio/Pleistocene boundary (Gelasian Stage, GSSP at Monte san Nicola Section, Sicily; Rio et al. 1994; Gradstein et al. 2004).

Del Campana (1913) discussed the attribution of a right maxillary fragment (IGF 10131) from Montopoli to *Vulpes alopecoides* (Major, 1875). The specimen, later relabeled in the Florence Museum inventory as *N. megamastoides*, has never been described in detail, although the occurrence of the species has been reported in faunal lists from Montopoli in all the general papers dealing with the biochronology of Italian mammalian faunas (e.g. Azzaroli et al. 1982; Caloi & Palombo 1996; Gliozzi et al. 1997; Palombo et al. 2002).

MATERIALS AND METHODS

The described material is stored in the collections of the Natural History Museum, Geological and Paleontological section, University of Florence (Italy). A comparative fossil sample considered is that of Dafnero 1 and Megalon Emvolon (Macedonia, Greece) housed in the Department of Geology, Aristotle University of Thessaloniki (Greece). Extant specimens used for morphological and statistical consideration [*N. procyonoides*, the raccoon-dog; *Vulpes vulpes* (Linnaeus, 1758), the red fox; and *Vulpes lagopus* (Linnaeus, 1758), the arctic fox] are housed in 'La Specola', Zoology section of the Natural History Museum of Florence. Additional comparative material of Villafranchian canids has been taken from the literature (Boule 1889; Depéret 1890; Viret 1954; Vekua 1972; Ficcarelli et al. 1984; Tedford & Qiu 1991; Geraads 1997; Geraads et al. 2010; Argant 2004; Monguillon et al. 2004).

Measurements of studied specimens have been taken with digital calipers to the nearest 0.1 mm. Cranial and dentognathic measurements follow Von Den Driesch (1976), even though slightly modified. Nomenclature of cusps is modified from Biknevicius & Van Valkenburgh (1996).

Log-ratio diagrams (Simpson 1941; Simpson et al. 1960) were used to visualize the mensural differences between different types of *Nyctereutes* species. Mean values of these species come from the literature (e.g., Monguillon et al. 2004), whereas values for *N. sinensis* are derived from drawings in Tedford & Qiu (1991: fig. 2 and 3).

Site and Institutional abbreviations

DFN, Dafnero 1, Western Macedonia, Greece; **IGF**, Museum of Natural History, Geological and Paleontological section, University of Florence (Italy); **LV**, Lower Valdarno; **MZUF**, Collection of the Natural History Museum, 'La Specola', Zoology section, of the University of Florence (Italy).

Anatomical abbreviations

Upper dentition. **dac**: distal accessory cusp(s); **hyp**: hypocone; **met**: metacone; **metl**: metaconule; **mets**: metastyle; **par**: paracone; **pars**: parastyle; **prot**: protocone; **protl**: protoconule.

Mandible and Lower dentition. **BM m1**: breadth of the mandible at m1; **H R**: Height of the Mandible Ramus.

Other abbreviations. **L**: Length; **W**: Width.

SYSTEMATIC PALEONTOLOGY

Order **Carnivora** Bowditch, 1821
Family Canidae Fischer von Waldheim, 1817
Genus *Nyctereutes* Temminck, 1838

Nyctereutes megamastoides (Pomel, 1842)

Fig. 1, Tab. 1

Referred material: San Giusto (Late Pliocene; Triversa FU): IGF 10132, left, edentulous mandibular fragment.

Montopoli (Early Pleistocene; Montopoli FU): IGF 10131_1, right maxillary fragment with P2-P4; IGF 10131_2, right maxillary fragment with M1 (probably same individual of IGF 10131_1).

Description

Cranial fragments – The second and third upper premolar in the specimen IGF 10131_1 (Fig. 1) are rather bucco-lingually flattened, and lack a distal accessory cusp. They are separated by short diastemata. In the P4, the protocone is large and directed mesio-lingually. It has a long and low metastylar blade. The M1 (IGF 10131_2) is rather elongated mesio-distally (Fig. 1). As the occlusal surface is highly worn, the only feature that can be confidently assessed is that the paracone and metacone are of equal size.

Mandible – The hemimandible (Fig. 1) is broken anteriorly at the level of the alveoli of the p4 and posteriorly slightly above the alveolus of m3. It does not have any teeth. The angular region is only partially preserved but the high-angled subangular lobe is well-preserved. The corpus is quite thick under the m1.

Comparisons

Montopoli - The morphology of the upper carnassial differs greatly from the extant *N. procyonoides*, *N. tingi* and *N. donnezani*, especially regarding the enlarged protocone and it mesial position relative to the anterior margin of the P4. In *N. sinensis* from the Yushe basin, the protocone of the P4 lies far mesial of the mesial margin of the paracone, much more so than in IGF 10131_1, whereas the upper carnassial of *N. megamastoides* is very similar to the Montopoli specimen. Focusing on the European species, Fig. 2 schematically points out the features of the upper carnassials of *N. donnezani* (from Depéret 1980), *N. vulpinus* (from Viret 1954), *N. megamastoides* (from Boule 1889 and DFN-17) and IGF 10131_1. As shown in the figure, the P4 of IGF 10131_1 does not show the embayment on the mesial margin of the tooth that separates the protocone from the rest of the paracone in *N. donnezani*-type specimens reported in Depéret (1890). On the contrary, the mesial margin of P4 of IGF 10131_1 is straight like in *N. vulpinus* and *N. megamastoides*,

Catalog. No.		P2		P3		P4		M1	
		L	W	L	W	L	W	L	W
IGF 10131_1	R	6,9	3,0	7,5	3,6	12,9	6,4	-	-
IGF 10131_2	R	-	-	-	-	-	-	10,6	12,3

Tab. 1 - Upper teeth measurements of *Nyctereutes megamastoides* of the Lower Valdarno.

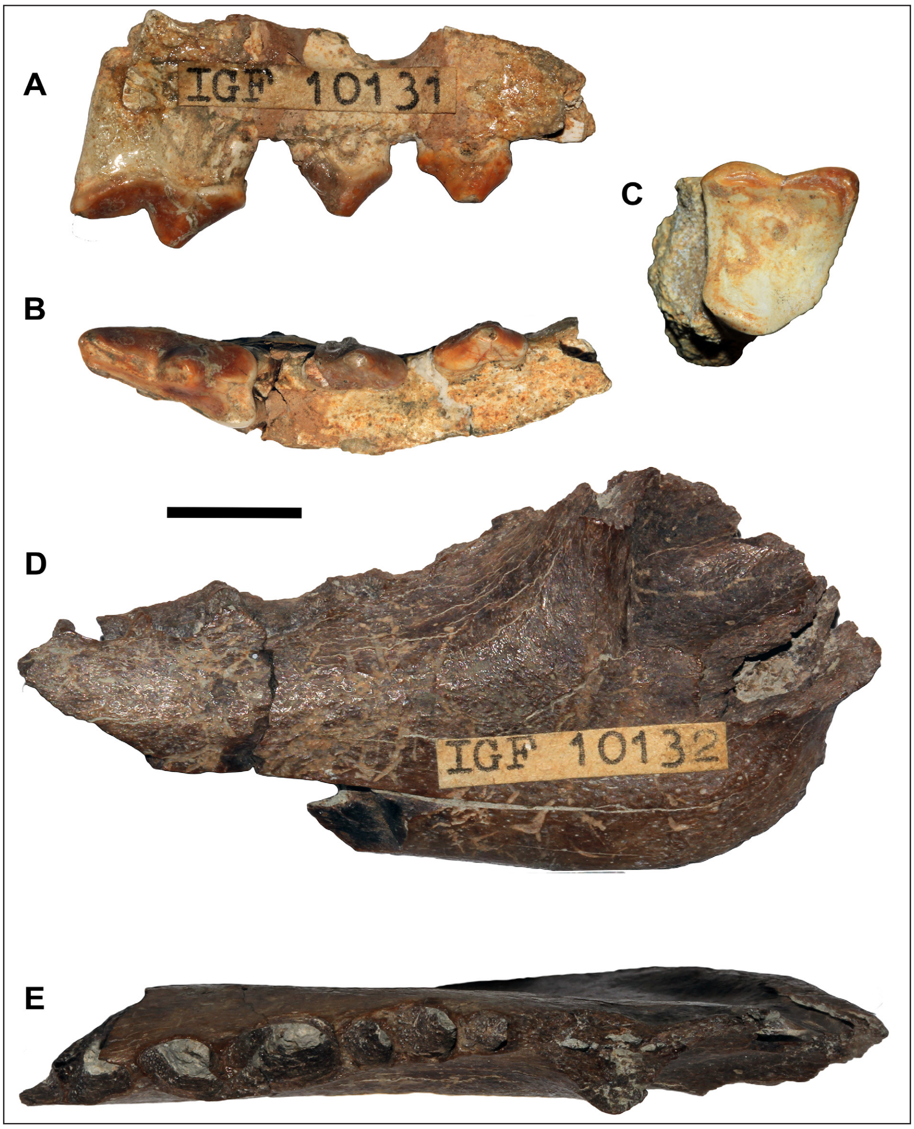

Fig. 1 - *Nyctereutes megamastoides* from the localities of S. Giusto and Montopoli. IGF 10131_1, right maxillary fragment: A, lateral view; B, occlusal view. IGF 10131_2, right maxillary fragment with M1: C, occlusal view. IGF_10132, left mandibular fragment: D, lateral view; E, occlusal view. The scale bar equals 10 mm.

especially like DFN-17. Unlike *N. donnezani* and *N. vulpinus*, the P4 of IGF 10131_1 has a mesio-distally short paracone and an elongated metastylar blade. This resembles the condition seen in the holotype of *N. megamastoides* in Boule (1889). Even though the M1 of IGF10131_2 is heavily worn, its buccal margin resembles that of *N. sinensis* and *N. megamastoides*.

The log-ratio diagram of upper teeth measures (Fig. 3) shows that IGF 10131_1 is close in size to *N. megamastoides*, *N. donnezani*, *N. vulpinus* and *N. sinensis*, whereas *N. procyonoides* and *N. tingi* are on average, respectively, smaller and larger. Although P4 L-P4 W proportions show a trend similar to that of *N. donnezani*, all the other proportions bear resemblance to *N. megamastoides* (e.g., P3L-P4 L of IGF 10131_1 and the standard *N. megamastoides* are identical in proportions, and the P4 W-M1 L-M1 W points of IGF 10131_1 show only a slight difference between them).

San Giusto - The caudoventral curvature of the subangular lobe is more marked in comparison with primitive forms like *N. donnezani* and *N. tingi*, in which the strong curvature of this part of the mandibular body is missing. In contrast, IGF 10132 resembles *N. megamastoides*, *N. sinensis* and, to some extent, *N. procyonoides*. *Nyctereutes vulpinus* from St. Vallier does not have such a high angle-curvature, being somewhat intermediate between primitive and derived forms.

Discussions and conclusions

Taxonomic remarks and importance of the material from Lower Valdarno - The morphological features of the *Nyctereutes* remains from the sites of S. Giusto and Montopoli here described (such as the morphology of the P4 of the Montopoli specimen and the high-angled caudoventral curvature of the corpus of the San Giusto mandible) point to a substantial

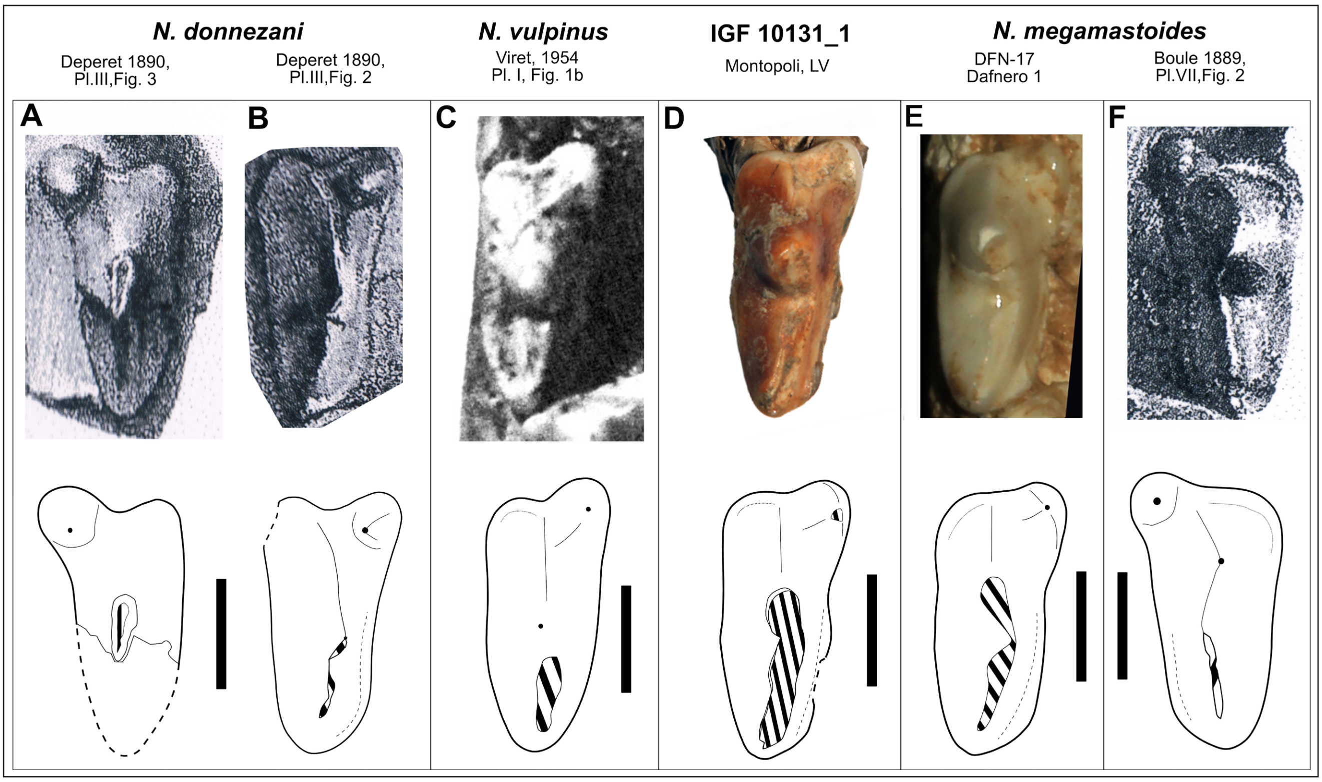

Fig. 2 - Comparison between P4 morphologies of the European species of *Nyctereutes*, in occlusal view: *N. donnezani* from Depéret (1890), Plate III, Fig. 3 (A) and Fig. 2 (B). *N. vulpinus* from Viret (1954), Plate I, Fig. 1b (C). IGF 10131_1 from Montopoli (D). *N. megamastoides* from Dafnero 1 (Western Macedonia, Greece), DNF-17 (E) and Boule (1889), Plate VII, Fig. 2 (F). All scale bars equal 5 mm.

affinity with the Late Pliocene-Early Pleistocene *N. megamastoides* (Pomel, 1842) of Europe. This is also consistent with the stratigraphic history of Pliocene canids. The first record of the family Canidae of Western Europe is from the Turolian (Late Miocene) of Concud (Teruel Basin, Spain; Late Miocene,

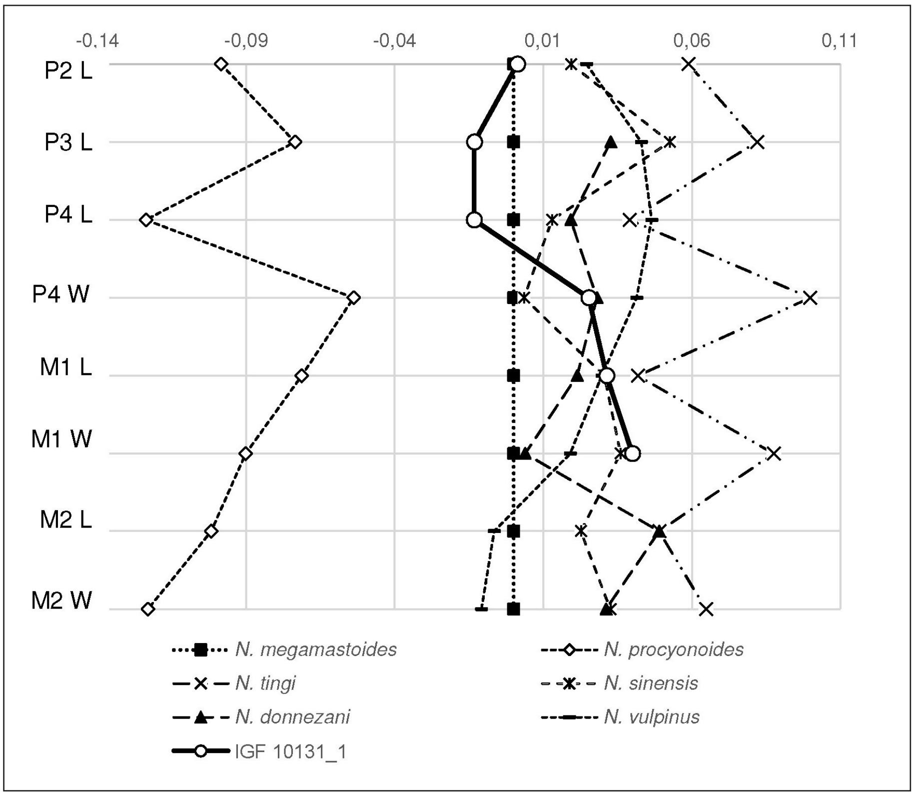

Fig. 3 - Log-ratio diagram based on log-transformed mean of upper teeth measurements of *Nyctereutes* spp. *Nyctereutes megamastoides* (Pomel, 1842) is used as a reference. Tooth measurements taken into consideration are shown on the left side.

MN12) with the species '*Canis*' *cipio* (see Crusafont Pairó 1950). The scarcity of the material and its peculiar features have led many researchers (e.g. Rook 1992; Wang & Tedford 2007) to question the taxonomic attribution of the specimens and, recently, Rook (2009) re-assigned the species to the genus *Eucyon* Tedford & Qiu, 1996. Other species of the latter genus characterized Late Miocene-Early Pliocene times in Europe: *Eucyon debonisi* Montoya et al., 2009 in the Late Miocene of Spain; *Eucyon monticinensis* (Rook, 1992) from the Messinian Monticino gypsum quarry of Brisighella (Ravenna, Italy); *Eucyon odessanus* (Odintzov, 1967) in the Early Pliocene of Southeastern Europe; and the Early Pliocene *Eucyon adoxus* (Martin, 1973) from the French site of Perpignan. During the Early Pliocene we have the appearance of the earliest *Nyctereutes* species, *N. donnezani*, in Spanish sites like La Gloria 4 (MN14) and Layna (MN 15) (Alcalá Martínez & Montoya 1989-1990). Subsequently, this primitive form is replaced by the more derived forms *N. megamastoides* and *N. vulpinus*. Indeed, from the Latest Pliocene, these two species are the only representatives of the genus in Europe (Monguillon et al. 2004). The presence of a fossil of *Nyctereutes* (IGF 10132) with derived features in the Late Pliocene locality of S. Giusto fits with the European panorama of raccoon-dog like canids. Even the maxillary fragment (IGF 10131) recovered from an Early Pleistocene locality of the same basin, shows morphological and mensural affinity to derived forms *Nyctereutes*. All things considered, the fossil material from the Lower Valdarno basin can be reasonably attributed to *N. megamastoides*.

In conclusion, the study of the *Nyctereutes* material of the Lower Valdarno highlights two points: the Montopoli specimen (IGF 10131) confirms the taxonomic attribution of this fossil to *N. megamastoides* (Pomel, 1842), a relatively widespread taxon in the earliest Pleistocene of Europe, whereas the described and figured specimen from San Giusto (IGF 10132) demonstrates the occurrence of an advanced *Nyctereutes* form in the Late Pliocene of Italy for the first time. It also represents one of the earliest records of the species *N. megamastoides* in all of Europe. This early occurrence of a derived *Nyctereutes* species in the Late Pliocene (early Villafranchian) of western Eurasia reveals an evolutionary pattern of the genus different from the one documented in the Early Pliocene of China, where a more advanced species is associated with the primitive *Nyctereutes tingi*.

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