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**Pannonictis nestii** (Galictinae, Mustelidae), a new element in the vertebrate association of the human site of Pirro Nord (Italy, Early Pleistocene)

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**ABSTRACT**

Systematic excavations in the Early Pleistocene site of Pirro Nord (Apulia, southern Italy) yielded some remains of a relatively rare mustelid belonging to the subfamily of Galictinae Reig, 1956. The taxonomy of extinct genera within this clade is controversial, especially between *Pannonictis* Kormos, 1931 and *Enhydrictis* Forsyth-Major, 1901. Nevertheless, the Pirro Nord findings are very similar to the holotype of *Pannonictis nestii* (Martelli, 1906) from Upper Valdarno, and closely related to the specimens from Pietrafitta and Atapuerca.

**KEY WORDS**

Mustelidae,  
*Pannonictis*,  
Early Pleistocene,  
Pirro Nord,  
Italy.

**MOTS CLÉS**

Mustelidae,  
*Pannonictis*,  
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Pirro Nord,  
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Pannonictis nestii (Galictinae, Mustelidae), un nouvel élément dans l’association de vertébrés du site d’occupation humaine de Pirro Nord (Italie, Pléistocène inférieur). Les fouilles systématiques dans le site du Pléistocène inférieur de Pirro Nord (Pouilles, Italie du Sud) ont livré quelques restes d’un mustélidé relativement rare appartenant à la sous-famille des Galictinae Reig, 1956. La taxonomie des genres éteints de ce clade est controversée, en particulier entre *Pannonictis* Kormos, 1931 et *Enhydrictis* Forsyth-Major, 1901. Néanmoins, les fossiles de Pirro Nord sont très similaires à l’holotype de *Pannonictis nestii* (Martelli, 1906) de Valdarno supérieur, et étroitement liés aux spécimens de Pietrafitta et Atapuerca.

**RÉSUMÉ**
INTRODUCTION

The Early Pleistocene fossil vertebrates of Pirro Nord were discovered in the early 1970s (Freudenthal 1971) within the fillings of an extensive karstic network on the Gargano peninsula. Since its discovery, this site has been subjected to extensive palaeontological investigation. The vertebrate association found in the different fillings is very rich and diversified (Abbazzi et al. 1996; Arzarello et al. 2009). Some lithic artifacts have recently been found in association with the Early Pleistocene vertebrates testifying the presence of the genus Homo (Arzarello et al. 2007, 2009). The research at Pirro Nord is still in progress, with systematic excavations and studies of both vertebrate remains and lithic industry. During the excavation campaigns of the recent years (from 2007 until 2010), two hemimandibles, several isolated teeth and a humerus were found, attributable to the large-sized mustelid Pannonicitis nestii (Martelli, 1906).

The Pirro Nord locality

The Early Pleistocene site of Pirro Nord (also known in the literature as “Cava Pirro” or “Cava Dell’Erba”) is situated near Apricena (Foggia, southeastern Italy) on the west slope of the Gargano promontory (Figs 1; 2). This fossil site has been well known to the palaeontological community since its discovery in the early 1970s (Freudenthal 1971) and the following studies (Abbazzi et al. 1996; Arzarello et al. 2007, 2009; Pavia et al. 2012). It consists in a karstic network developed along the contact between the Mesozoic limestone and the Neogene calcarenite and filled in with continental sediment of various origins (Abbazzi et al. 1996; Pavia et al. 2010). The fissure fillings yielded a large number of fossil vertebrates, referable to two different faunal assemblages. The oldest one is referable to the Late Miocene/Early Pliocene, the other one to the Early Pleistocene. The Neogene vertebrate association, known as the “Mikrotia Fauna” is a not-balanced association characterized by strongly endemic taxa testifying the isolation of the Gargano during the Late Miocene (Masini et al. 2008). The Early Pleistocene vertebrate association is rich and highly diversified and contains more than 100 taxa of amphibians, reptiles, birds and mammals (Abbazzi et al. 1996; Arzarello et al. 2009 and references therein). This association defines the latest Villafranchian chronological unit (Pirro Nord Faunal Unit) in the Western European mammal biochronology (Gliozzi et al. 1997; Rook & Martínez-Navarro 2010). The mammal association found at Pirro Nord contains 14 carnivore taxa, with several species of Felidae Fischer von Waldheim, 1817, representing one of the richest Early Pleistocene carnivore associations known so far (Petrucci et al. in press). The rodent association found at Pirro Nord is poorly diversified but is characterized by the presence of Microtus (Allophaionmys) ruffoi (Pasa, 1947). The Microtus Schrank, 1798 assemblage of Pirro Nord has intermediate features between the type population of M. (A.) plocaenicus (Kormos, 1933) from the type population of Bettia II (Early Pleistocene, Hungary) and M. (A.) ruffoi (Marcolini et al. in press). This latter species is known from many Italian Early Pleistocene sites, all correlated with Late Villafranchian/Early Biharian biochronological unit and with “Mimomys savini-Mimomys pusillus” zone.

The palaeomagnetic analyses carried out during the 2007 and 2009 excavation campaigns revealed a reverse polarity. Thus the Pirro Nord sediments can be referred to the Muyama reverse polarity epoch, post Olduvay event, from 1.78 to 0.79 Ma (Napoleone et al. 2003; Tema et al. 2009; Pavia et al. 2012). Some authors (Arzarello et al. 2007, 2009; Pavia et al. 2012) stated that the age of Pirro Nord should be between 1.3 and 1.7 Ma, but others (Masini & Sala 2007; Bertini et al. 2010) suggest an age comprised between 1.2 and 1.5 Ma. Clearly, this debate is beyond the scope of our work. Nonetheless, the lithic industry found at Pirro Nord, composed by cores and flakes attributable to the Mode 1, testify that Pirro Nord is one of the European sites which can confirm the earliest presence of the genus Homo in the continent. Among the others localities we have to cite Lézignan-la-Cèbe (1.57 Ma, southern France; Crochet et al. 2009), Barranco Leon-5 (1.4 Ma); Fuente Nueva-3 (1.25 Ma, Orce Basin, Andalousia; Toro-Moyano et al. 2009) and la Sima del Elefante (c. 1.2 Ma, northern Spain; Carbonell et al. 2008). In Eastern Europe, important sites are those of Ko-
Pannonictis nestii (Galictinae, Mustelidae) from Pirro Nord (Italy, Early Pleistocene)

and some extant genera, i.e. Galictis Bell, 1826 and Lyncodon Gervais, 1844. Baskin (1998) considered this subfamily as a tribe under the name of Galictini Baskin, 1998 belonging to Mustelinae Fischer von Waldheim, 1817. However, recent paleontological findings and new phylogenetic research point to a more complex situation. As regards the extinct genera, we have to add the Mediterranean Mustelercta De Gregorio, 1925 and the Asian genera Eirictis Qiu, 2004 and Oriensictis Ogino & Otsuka, 2008. Moreover, in accordance with the phylogenetic analyses of Carnivora Bowdich, 1821 performed by Fulton & Strobeck (2006), Galictinae Reig, 1956 can be considered as a consistent clade composed by some extant species diffused in South America within the genus Galictis, but present in the Old World too with the genus Ictonyx Kraup, 1835. Nevertheless, other genera, such as Lyncodon, Poecilogale Thomas, 1883 and Vormela Blasius, 1884 are closely related (Bininda-Emonds et al. 1999; Flynn et al. 2005; Koepfl i et al. 2008). All of them possess “aposematically coloured pelage (i.e. black and white warning colours) combined with defence behaviours that include threat displays and excretion of pungent musk from enlarged anal

**Galictinae Historical Framework**

The name Galictinae Reig, 1956 was established to substitute the name Grisoninae Pocock, 1921, used until that moment to describe some extant and extinct species of Mustelidae (see also Pilgrim 1932). Indeed, the name Grison Oken, 1816, genus type of Grisoninae was considered invalid (Hershkovitz 1949) being the correct one Galictis Bell, 1826. Among the other reasons of its invalidity Hershkovitz (1949) stated that Grison appears as the vernacular name and it was never proposed by Oken as a generic name. So, in accordance with the principles of art. 40 of ICZN code (see in particular art. 40.2, but see also arts 11 and 12) the valid name of the subfamily should be Galictinae.

Following the work of some authors (Reig 1956, 1957; Bjork 1970; Ray et al. 1981; Martin 1989; Baskin 2011) the Galictinae subfamily includes some extinct genera, i.e. Enhydrictis Forsyth Major, 1902, Pannonictis Kormos, 1931 from the Old World, Lutravus Furlong 1932, Cernictis Hall, 1935, Trigonictis Hibbard, 1941, Stipanicicia Reig, 1956, and Sminthosinis Bjork, 1970 from the New World and some extant genera, i.e. Galictis Bell, 1826 and Lyncodon Gervais, 1844. Baskin (1998) considered this subfamily as a tribe under the name of Galictini Baskin, 1998 belonging to Mustelinae Fischer von Waldheim, 1817. However, recent paleontological findings and new phylogenetic research point to a more complex situation. As regards the extinct genera, we have to add the Mediterranean Mustelercta De Gregorio, 1925 and the Asian genera Eirictis Qiu, 2004 and Oriensictis Ogino & Otsuka, 2008. Moreover, in accordance with the phylogenetic analyses of Carnivora Bowdich, 1821 performed by Fulton & Strobeck (2006), Galictinae Reig, 1956 can be considered as a consistent clade composed by some extant species diffused in South America within the genus Galictis, but present in the Old World too with the genus Ictonyx Kraup, 1835. Nevertheless, other genera, such as Lyncodon, Poecilogale Thomas, 1883 and Vormela Blasius, 1884 are closely related (Bininda-Emonds et al. 1999; Flynn et al. 2005; Koepfl i et al. 2008). All of them possess “aposematically coloured pelage (i.e. black and white warning colours) combined with defence behaviours that include threat displays and excretion of pungent musk from enlarged anal
glands” (Koepfli et al. 2008). A very recent work (Wolsan & Sato 2010) groups together the genus Galictis with Poecilogale, Vormela and Ictonyx but refers to this clade as Ictonychinae Pocock, 1921. Nonetheless Wilson & Reeder (2005) include Galictis and Ictonyx in Mustelinae not recognizing the validity of the subfamily Galictinae.

The European remains of the Plio-Pleistocene Galictinae have recently been reconsidered (García et al. 2008; García & Howell 2008) in the wake of new discoveries from the paleoanthropological site of Sima de l’Elefante (García & Howell 2008). The first report of fossil Galictinae came from Forsyth-Major (1901). He described the new genus Enhydrictis and the new species E. galictoides based on a skull and a fragmentary mandible found in the Late Pleistocene deposits of Monte San Giovanni, Iglesias (Sardinia, Italy). Later, Kormos (1931) described the new genus Pannonictis based on several remains from the Plio-Pleistocene sites of Villany and Beremend (Hungary) establishing the type species Pannonictis pliocaenica Kormos, 1931. The new genus can be distinguished from Enhydrictis on the basis of the cranial morphology. Then Kormos (1933) separated the Hungarian material into two different species, Pannonictis pliocaenica and Pannonictis pilgrimi Kormos, 1933, the first being of a larger size. Later on, Schaub (1949) referred Mustela ardea Bravard, 1828 from Ardes, Perrier-Étouaires (2.5 Ma) to Pannonictis. In the same paper (Schaub 1949) the author indicated the synonymy of Propotorius olivolanus Martelli, 1906 from Olivola (Late Pliocene, Italy) with Pannonictis ardea (Bravard, 1828).

Describing the fossil mammals from Saint-Vallier, Viret (1950, 1954) focused on the cranium and the right hemimandible of a fossilized Mustelidae. He stated that they had characteristics in common with Enhydrictis galictoides Forsyth-Major, 1901, allowing him to use the same genus for his fossils. Then, Viret identified them as belonging to a species that could also include Pannonictis pilgrimi Kormos, 1933, Propotorius olivolanus Martelli, 1906 and Mustela ardea Bravard, 1828, synonymising all these forms in Enhydrictis ardea (Bravard, 1828).

Subsequently, Ficcarelli & Torre (1967) supported Schaub’s conclusions (1949) and indicated that Enhydrictis can be separated from Pannonictis on the grounds of its stronger post-orbital constriction. In the same paper (Ficcarelli & Torre 1967) the authors rejected the synonymy of Pannonictis pilgrimi with Enhydrictis ardea, because P. pilgrimi manifests a wider ascending ramus and a longer rostral length. In addition, the authors observed a great similarity between Pannonictis pilgrimi and Propotorius nestii Martelli, 1906, described from the Upper Valdarno (Late Pliocene, Italy) and no longer reported after its first description, and they suggest that it should be attributed to the genus Pannonictis, under P. nestii.

Later on, Kurtén (1968) and Willemsen (1988) again considered Pannonictis pilgrimi as synonymous with Enhydrictis ardea, while Rook (1995), studying the Galictinae from the Early Pleistocene of Pietrafitta (Italy), confirmed the validity of the characteristics pointed out by Ficcarelli & Torre (1967) and determined the Pietrafitta remains as Pannonictis nestii.

Burgio & Fiore (1997) reconsidered the type material of a mustelid assigned to Mustela (Mustela) arzilla by De Gregorio (1886, 1925). They recognized it as part of the extinct European Galictinae. In particular, they observed some significant similarities to the type specimen of Pannonictis nestii, suggesting that they could belong to the same genus.

Rabeder (1976) established the new species Pannonictis ? janossyi Rabeder, 1976 from some cranial and dentary remains from Villany-Kalkberg. This species can be distinguished from the others for the small dimensions, similar to the current Galictis cuja (Molina, 1782). In the same work, describing some carnivores from Deutsch-Altenburg 2 (Austria, Early Plesistocene), he stated that Enhydrictis ardea should appertain to Pannonictis. According to him P. pilgrimi should be considered as a junior synonym of P. ardea. Moreover, he noted that the bulla auditoria of the species belonging to Pannonictis, in particular that of P. pliocaenica and P. ardea, were substantially different from that of Enhydrictis galictoides.

This hypothesis has been also followed by Spassov in several papers (Spassov 1997, 1998, 1999, 2000). In particular he noted that the area en-
closed between the incisures of *os palatinum* and the pterygopalatine crests in *Enhydrictis galictoides* cranium is visibly narrower than in the crania of both “*E.* ardea” from Saint-Vallier and *Pannonictis plicaenica* from Villany (Spassov pers. comm., but see also Spassov 1999). According to him, this
character could be important for the subdivision at a generic level. Nonetheless, Sotnikova et al. (2002) stated that *E. ardea* and *E. galictoides* are chiefly similar, having a strong postorbital constriction of the skull. Also in the view of García & Howell (2008) the Saint-Vallier specimen described by Viret (1954) as *Enhydrictis ardea*, has a narrower postorbital constriction than *P. plicenica* from Villány and *P. nestii* from Pietrafitta, although not as narrow as the Sardinian individual attributed to *E. galictoides*. According to them *E. galictoides* should be considered the only valid species within the genus *Enhydrictis*.

García et al. (2008) seem to consider *Pannonictis nestii* (= *Enhydrictis ardea*) as a whole group, *Enhydrictis* being an endemic genus of the Late Pleistocene of Sardinia (as a matter of fact the use of “Tosco-Sardinian” bioprovince by the authors is incorrect being this paleobioprovince confined to the Late Miocene endemic complex; Rook et al. 2006) with the unique species *Enhydrictis galictoides*. It represents a derived and local form of the Galictinae, distinct from the Pliocene and Early Pleistocene *Pannonictis* (García & Howell 2008). In addition, *Pannonictis pilgrimi* is a synonym of *P. plicenica*, as the dimensional differences have been interpreted as sexual dimorphism (García & Howell 2008).

Fejfar et al. (2012) considered *P. pilgrimi* as a junior synonym of *P. ardea* and attributed some remains of mustelid from Ivanovce (Early Pliocene of Slovakia) to this species. According to them, the auditory bulla of “*ardea*” species is more analogous to the genus *Pannonictis* than to *Enhydrictys*.

Moreover, García et al. (2008) and García & Howell (2008) carried out a large scale revision of the entire Eurasian fossil Galictinae dividing them into five geographical regions (East and Central Asia, Black Sea and Transcaucasian region, Southeast Europe, North and Central Europe and Mediterranean area).

Fossil remains of the genus *Pannonictis* have also been found in Asia (García et al. 2008 and reference therein). The species *Pannonictis pachygnatha* (Teilhard de Chardin & Piveteau, 1930) was described from Nihewan, China; this species is different from other *Pannonictis* in its stoutness and in having the anterior margin of the P4 without any concavity. In addition, the remains of Mustelidae gen. et sp. indet. from the Upper Miocene of China (Zdansky 1927) were considered to be the oldest *Pannonictis* remains (Kormos 1931; Pilgrim 1932; Rook 1995; García & Howell 2008). The fossil remains from Nihewan were studied again and attributed to the new genus *Eirictis* (Qiu et al. 2004). García & Howell (2008) confirmed the validity of the morphological characteristic pointed out by Qiu et al. (2004) to distinguish *Pannonictis* from *Eirictis* on the basis of the P4 morphology.

Recently, Ogino & Otsuka (2008) have assigned some fossils from the Middle Pleistocene of Matsugae, Japan, to the new genus *Oriensictis*, belonging to Galictinae.

**MATERIAL AND METHODS**

The *Pannonictis* fossil remains have been found in the various levels of the succession of the P10 fissure at Pirro Nord (Pavia et al. 2012). The specimens are kept in the Museo di Geologia e Paleontologia of the Torino University (PU).

Fossil remains have been compared with recent skeletal material of recent Mustelidae (*Martes martes* Linnaeus, 1758; *M. foina* Erxleben, 1777; *Mustela nivalis* Linnaeus, 1766; *Meles meles* Linnaeus, 1758), Canidae Fischer Von Waldheim, 1817 (*Vulpes vulpes* Linnaeus, 1758; *Canis lupus* Linnaeus, 1758), Felidae (*Felis sylvestris* Schreber, 1777; *Lynx lynx* Linnaeus, 1758) preserved at Museo Civico di Storia Naturale di Carmagnola (MCC) and Museo Regionale di Scienze Naturali di Torino (MRSN).

**SYSTEMATIC PALEONTOLOGY**

**Family MUSTELIDAE**

Fischer Von Waldheim, 1817

**Subfamily GALICTINAE** Reig, 1956

**Genus Pannonictis** Kormos, 1931

**Type species.** — *Pannonictis plicaeana* Kormos, 1931 by original designation.
Fig. 3. — A, B, *Pannonictis nestii* (Martelli, 1906), holotype: left hemimandible (IGF 916) from Upper Valdarno in lingual (A) and labial (B) views; C-G, *Pannonictis nestii* from Pirro 10: left hemimandible (PU 120257) in lingual (C) and labial (D) views; juvenile right hemimandible (PU 126946; reversed pictures) in lingual (E), occlusal (F) and labial (G) views; H-P, *Pannonictis nestii* from Pirro 10: H, I, left lower canine (PU 118847) in lingual (H) and labial (I) views; J, K, right lower canine (PU 118848) in lingual (J) and labial (K) views; L, M, right upper canine (PU 118846) in lingual (L) and labial (M) views; N-P, left P4 (PU 120242) in labial (N), lingual (O) and occlusal (P) views. Scale bars: 10 mm. Photos of elements A and B, courtesy of Saulo Bambi (Museo di Storia Naturale, Firenze).
**Pannonictis nestii** (Martelli, 1906)  
(Figs 3; 4)

**Proputorius nestii** Martelli, 1906: 598.

**Pannonictis nestii** – Ficcarelli & Torre 1967: 141. — Rook 1995: 856.  
**Pannonictis cf. nestii** – García & Howell 2008: 9.

**Holotype.** — Left hemimandible bearing P₃-M₂, from Upper Valdarno (Tuscany, Italy), housed in the Museo di Geologia e Paleontologia of the University of Florence and labeled as IGF 916.

**Material examined.** — Adult left hemimandible, almost complete (PU 120257); uncomplete juvenile right hemimandible (PU 126946); left lower canine (PU 118847); right lower canine (PU 118848); right upper canine (PU 118846); left P₄ (PU 120242); left humerus (PU 129095).

**Description**

**Adult left hemimandible**

The specimen (Fig. 3C, D) is not complete in all of its parts. It lacks the coronoid process and, in the anterior part, it completely lacks the symphysis and the alveoli of the incisors are entirely absent. M₁ and P₄ are the only teeth present. The horizontal branch presents a fracture, which reaches the P₄ damaging the protoconid and moderately rotating the anterior part of the mandible.

The hemimandible appears stout and low. The ascending ramus is relatively wide. The angular process is somewhat thick especially in the lower part. It curves towards the medial side which presents a deep concavity. The mandibular condyle is low, slightly tilted to the dental side. No incisor is present. The canine alveolus is not complete but it suggests the presence of a large and deep root. The inferior mandibular margin descends slightly until it meets an inflection point just beneath the M₁ talonid, where it rises again gently. The masseteric fossa is deep, but shorter and more shallow than in the fully developed specimen. The inferior mandibular margin is slightly bended but we cannot observe a clear inflection point. The alveolar ridge is preserved from the posterior part of the canine alveolus. Even if the canine alveolus is partially preserved, it appears large and deeply set in the mandibular body. Slightly distally, a tiny alveolus is present on the buccal side. More lingually, we can notice the erupting P₃. Posteriorly two alveoli are present. Subsequently an M₁ in eruption is observable. The alveolar ridge ends with the M₂ alveolus. The M₁ paraconid is well developed even if lower than the protoconid. The metaconid is not in line with the protoconid but slightly posterior. The talonid is deep and we can observe well developed both the hypoconid and the hypoconulid. On the lingual side a tiny cusp is present developing from a low lapping of these two teeth. As we have said, P₄ is partially damaged in such a way that the anterior part of the tooth is shifted ahead, not permitting the measurement of the dental element. It has a well-pronounced protoconid, as well as a relatively well-pronounced projection of the posterior basal area where a tiny cusplet rises from enamel swells. The M₁ is very worn, with low cusps. The M₁ protoconid is stout and well developed. The paraconid is well developed too, but it shows a higher degree of wear. The metaconid is not in line with the protoconid but slightly posterior. The talonid is worn and we cannot see other accessory cusps except for a very light sign of the hypoconid. The talonid appears as a concavity with the lingual side being more consumed so that it seems to be inclined towards that part.

**Juvenile right hemimandible**

The specimen is not complete. It lacks completely the coronoid process. The anterior part is broken at the level of the distal part of the alveolus of the inferior canine. The hemimandible has a lighter structure compared to the adult specimen. The ascending ramus is less large than it appears in the adult form. The angular process is barely developed. The mandibular condylus is not present and we can observe only a partially preserved tiny swelling of the bone. The massteric fossa is deep, but shorter and more shallow than in the fully developed specimen. The inferior mandibular margin is slightly bended but we cannot observe a clear inflection point. The alveolar ridge is preserved from the posterior part of the canine alveolus. Even if the canine alveolus is partially preserved, it appears large and deeply set in the mandibular body. Slightly distally, a tiny alveolus is present on the buccal side. More lingually, we can notice the erupting P₃. Posteriorly two alveoli are present. Subsequently an M₁ in eruption is observable. The alveolar ridge ends with the M₂ alveolus. The M₁ paraconid is well developed even if lower than the protoconid. The metaconid is not in line with the protoconid but slightly posterior. The talonid is deep and we can observe well developed both the hypoconid and the hypoconulid. On the lingual side a tiny cusp is present developing from a low
margin that encloses the basin of the molar. The talonid is inclined towards the lingual side.

By comparison with the adult specimen (PU 120257) we can see that the alveolar ridge has comparable size while the posterior part is much shorter, being the whole structure less stout. This condition is also observable in the minor highness of the mandibular body, while the width has closer measures (Table 1).

**Lower canines**
The two lower canines show a very similar morphological pattern (Fig. 3H-K) but different dimensions (Table 1).

They have a bent shape with stout and lightly curved root. A high cingulum is clearly visible at the base of the enamel and on the internal side we can see a modest longitudinal depression that continues on the root. The enamel appears crumpled with typical wrinkles and little furrows.

**Upper canine**
The upper canine has a very modest degree of bending (Fig. 3L, M). Like the inferior canines, it appears crumpled and wrinkled. An anterolateral depression is present and extends for about ¼ longitudinally. A more evident groove can be observed on the anterior side, departing from the cingulum up to almost the point of the tooth. The high cingulum decreases on the lingual side.

**P4**
The upper carnassial has three roots (Fig. 3N-P). The tooth is completely unworn suggesting that it could belong to a young, sub-adult individual. The paracone is the most developed cusp. It rises in the middle of the tooth, slightly displaced on the labial side. The blade departs from the paracone, gently descending and reaching the metastyle after forming a slightly curved margin. The protocone area is better represented as a
concavity surrounded by enamel swelling forming a cingulum. A very little cusplet rises from the enamel. The cingulum continues on the lingual side creating a very low hypocone. When the cingulum reaches the medial point of the tooth, it descends rapidly and then rises up again, forming an evident inflectional point. Then it almost reaches the metastyle. On the buccal side there is a light cingulum that follows the lower margin of the dental crown.

Left humerus
A magnificently preserved left humerus (Fig. 4) provides further evidences on the postcranial skeleton anatomy of *Pannonictis*.

The diaphysis has a straight appearance in anterior view, while in lateral (and medial) view it is markedly curved backwards and, in its distal end, frontally. The latter curvature is given by the expanded epicondylar (or supinator) crest (Fig. 4).

The proximal epiphysis has a round articular head, projected cranially. The diaphysis is transversely compressed and marked by strong ridges: the deltidoid ridge is distinct and strong. The pectoral ridge is less stronger than the deltidoid one and is present almost throughout the length of the diaphysis. The lateral epicondylar (or supinator) crest is laterally very expanded and extends proximally from the margin of the lateral ecycondyle to reach about 2/3 of the diaphysys. In medial and lateral views it contributes the pronounced curved lateral profile (Fig. 4C, D).

On the proximal end, the lesser tuberosity is large and is separated from the greater tuberosity by a marked deep intertubercular groove.

The articulation of the distal epiphysis is wide. The capitulum (or medial condyle; for articulation with the radial head) is relatively wide on the anterior face. The trochlea (or lateral condyle) is

| Table 1. — Measurements (in mm) of *Pannonictis nestii* (Martelli, 1906) from Pirro Nord (Pirro 10) and other European localities. Abbreviations: HMaM₁, mandibular height at M₁ level; WMaM₁, mandibular width at M₁ level; C-M₂, distance from anterior part of canine alveolus to the posterior part of M₂ alveolus; M₁-M₂, distance from anterior part of M₁ alveolus to the posterior part of M₂ alveolus; LCI, maximum length of inferior canine; WCI, maximum width of inferior canine; LM₁, maximum length of M₁; WM₁, maximum width of M₁; LT₃M₁, trigonid length of M₁; W₄alM₁, talonid width of M₁; LCS, maximum length of superior canine; WCS, maximum width of superior canine; LP₄, maximum length of P₄; WP₄, maximum width of P₄; *, juvenile individual. Data are from: ¹, Rook (1995); ², Sotnikova et al. (2002); ³, García & Howell (2008). |
|---------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| **Pannonictis nestii**          |     |     |     |     |     |     |     |     |     |     |     |     |
| Upper Valdarno                 | 14.8| 6.35| 40.15| –   | –   | 11.75| 5.2 | –   | –   | –   | –   | –   |
| IGF 916¹ (holotype)            | –   | –   | –   | 7.5 | 4.8 | –   | –   | –   | –   | –   | –   | –   |
| Pirro Nord PU 120242           | 13.9| 6.6 | 41.2 | 16.2| –   | 12.6 | 5.6 | 8.4 | 5.2 | –   | –   | –   |
| Pirro Nord PU 120257           | 11.0| 6.2 | –   | 16.05| –   | 12.25| 5.4 | 8.2 | 5.15| –   | –   | –   |
| Pietrafita 1745¹               | 13.25| 6.7 | –   | –   | –   | 12.6 | 5.55| –   | –   | –   | –   | –   |
| Pietrafita 1749¹               | 14.5| 7.05| 42.95| –   | –   | 12.5 | 5.25| –   | –   | –   | –   | –   |
| Pietrafita 1776¹               | 11.95| 5.35| –   | –   | –   | 11.50| 4.8 | –   | –   | –   | –   | –   |
| Liventsovkova RSU 98²          | 15.1| 7.1 | 17.3 | –   | 13.5 | –   | –   | –   | –   | –   | –   | –   |
| **Pannonictis cf. nestii**     |     |     |     |     |     |     |     |     |     |     |     |     |
| Elefante                       | 13.3| 7.3 | 41.7 | 16.2| 8.3 | 5.6 | 12.6 | 5.1 | 9.0 | 5.2 | –   | –   | 10.6 | 6.9 |
| ATA98-TE-J30-19³               | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   |
| Elefante                       | 14.5| 7.7 | 46.2 | 17.9| 10.0| 6.4 | 14.0 | 5.2 | 9.7 | 5.2 | –   | –   | –   | –   |
| ATA00-TE9a-k30-10³             | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   |
| Elefante                       | 14.5| 7.7 | 46.2 | 17.9| 10.0| 6.4 | 14.0 | 5.2 | 9.7 | 5.2 | –   | –   | –   | –   |
| ATA00-TE9-L30-54³              | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   | –   |
narrow and relatively deep. The olecranon fossa is deep and wide. The supracondylar foramen is large, elongated proximo-distally. The radial fossa is deep and wide. The lateral epicondyle is much less laterally extended than the medial one, but it is antero-posteriorly developed and prominent due to the distal extension of the above-mentioned well-developed epicondylar crest. The medial epicondyle is well developed and extended medially.

**COMPARISON AND DISCUSSION**

In accordance with García & Howell (2008), the presence of a small hypocone on P4 of the Pirro Nord specimen allows excluding the Asian genus *Eirictis*.

The genus *Oriensictis* from the Middle Pleistocene of Matsugae, Japan (Ogino & Otsuka 2008) is clearly different from the Pirro Nord specimen. Indeed, in the Matsugae remains we cannot observe a basal cingulum on the lingual side of M1 while the talonid has distinct rounded marginal cusps as hypoconid and entoconid. Beside the M2 seems to be in a higher position so that the height of the horizontal ramus is greater than in the Pirro Nord specimen (Ogino & Otsuka 2008: fig 2). The P4 has a very well-distinguished hypocone that in our specimen is just a tiny swelling of the enamel.

With regards to the differences between “*Enhydriticus* ardea” and *Pannonictis nestii*, we can observe that the two forms have similar dimensions (Tables 1; 2), even if *Pannonictis nestii* is generally slightly larger. Nevertheless, our scanty material cannot produce absolutely a decisive evidence to the putative synonymy of these two forms as García et al. (2008) seem to have suggested considering *Pannonictis nestii* (= *Enhydriticus ardea*) as a whole group. Besides, even if there was a possibility that the “*ardea*” form appertain to *Pannonictis* rather than *Enhydriticus*, these conclusions should be beyond the scope of our work. Nonetheless, as pointed out by many authors (see Ficcarelli & Torre 1967; Rabeder 1976; Rook 1995; Spassov 1999; Sotnikova et al. 2002; García & Howell 2008) the morphological differences between the two genera *Enhydriticus* and *Pannonictis* should be found in the neurocranial and facial bones of the cranium especially in the shape of the *bulla auditoria*, in the area enclosed between the incisures of *os palatinum* and the pterygopalatine crests and in the postorbital constriction. In any case, the adult left mandible of Pirro Nord shows a robust mandibular body (Table 1) with a wide ascending ramus thus resulting very similar to the hemimandibles from Pietrafitta (Rook 1995), Upper Valdarno (Martelli 1906) and Atapuerca (García & Howell 2008), all assigned to *Pannonictis nestii*.

Following Kormos (1931), in one mandible of *Enhydriticus galictoides* “collected by Forsyth-Major at San Giovanni probably after having published the description of the skull” the M1 has the metaconid placed in one line with the protoconid, which is not the case of the Pirro Nord specimen where the first cusp is more posteriorly placed. In addition, *Enhydriticus galictoides* has to be excluded after the endemic characteristics showed by this species (Ficcarelli & Torre 1967), and its limited distribution to insular Sardinia.
The Pirro Nord fossils and *Pannonictis pachygnatha* (Teilhard de Chardin & Piveteau 1930) present different features especially for the size which is larger in the latter. Besides, the anterior edge of P4 of *P. pachygnatha* is straight while in the specimen from Pirro Nord it is divided in two lobes.

*Pannonictis* ? *janossyi* from Villany-Kalkberg (Rabeder 1976) is clearly distinguishable from the Pirro Nord remains for the smaller size (Table 2).

The fossil remains from Pirro Nord are similar in dimension to *Pannonictis pilgrimi* (*P. pliocaenica* according to García & Howell [2008]) (Fig. 5), while they are clearly smaller than *P. pliocaenica* (Kormos 1931, 1933) (Table 2). In accordance with García & Howell (2008), *P. pilgrimi* has to be considered a synonym of *P. pliocaenica* as no morphological differences have been found and size differences have to be regarded as sexual dimorphism.

None of the Galictinae remains from the Mediterranean area show similar dimension to *Pannonictis pliocaenica* (Kormos 1931, 1933; García &

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### Table 2

Measurements (in mm) of “Enhydrictis” *ardea* (Bravard, 1828), *Pannonictis pliocaenica* Kormos, 1931 and *P. ? janossyi* Rabeder, 1976 from various European localities. Abbreviations: see Table 1. Measurements of bones that are slightly worn or damaged are indicated with an asterisk (*). Data are from: 1, Rook (1995); 2, Rabeder (1976); 3, Viret (1954); 4, Willemse (1988); 5, Schaub (1949); 6, Fejfar et al. (2012).

| Species                  | Measurement | HMa | WMa | M1       | Ci-M1 | LCI | WCi | LM1 | WM1 | LTri | WTal | LCS | WCS | LP4 | WP4 |
|--------------------------|-------------|-----|-----|----------|-------|-----|-----|-----|-----|------|------|-----|-----|-----|-----|
| **Pannonictis pliocaenica** |             |     |     |          |       |     |     |     |     |      |      |     |     |     |     |
| Beremend U.P. 6061       |             | 13.3| 6.25| 38.9     | –     | –   | 11.8| –   | –   | –    | –    | 10.5| –   |     |     |
| Villany O.B. 35961       |             | 15.9| 50.0| –        | –     | –   | 15.3| 6.8 | 9.7 | –    | –    | 13.2| 8.3 |     |     |
| Villany O.B. 3601        |             | –   | –   | –        | –     | –   | 15.4| 6.3 | 10.7| –    | –    | –   | –   |     |     |
| Villany-Kalkberg U.P. 1291|           | 13.65| 50.4| –       | 15.9 | –  | –   | –   | –   | –    | –    | 11.5| –   |     |     |
| Villany-Kalkberg U.P. 1321|           | –   | –   | –       | –     | –  | –   | –   | –   | –    | –    | 12.55 | 8.7 |     |     |
| Villany-Kalkberg U.P. 1341|           | 18.35| 9.7 | –       | –     | –  | 15.45| 6.35| 10  | –    | –    | –   | –   |     |     |
| Villany-Kalkberg U.P. 1351|           | 13.15| 7.05| 45.15  | –     | –  | 13.5| 5.35| 8.05| –    | –    | 12.0| 7.6 |     |     |
| Villany-Kalkberg U.P. 1491|           | –   | –   | –       | –     | –  | –   | –   | –   | –    | –    | 11.2| 7.25|     |     |
| Villany-Kalkberg U.P. 7611|           | –   | –   | –       | –     | –  | 10.95| 6.55| 11.05| –    | –    | 10.7| 7.8 |     |     |
| Villany-Kalkberg U.P. 7612|           | 17.9| 9.55| 54.0   | –     | –  | 15.95| 6.55| 11.05| –    | –    | 12.0| 7.6 |     |     |
| Villany-Kalkberg U.P. 7613|           | 14.55| 7.55| 45.15  | –     | –  | 13.55| 5.35| 8.85| –    | –    | 13.2| 7.55|     |     |
| Villany-Kalkberg U.P. 7614|           | 16.4| 9.0 | 53.6   | –     | –  | 15.7| 6.6 | 10.85| –    | –    | 11.2| 7.25|     |     |
| **Pannonictis? janossyi** |             |     |     |          |       |     |     |     |     |      |      |     |     |     |     |
| Villany-Kalkberg V61/13902|           | –   | –   | –       | –     | –  | 11.8| –   | –   | –    | –    | –   | –   |     |     |
| **“Enhydrictis” areda**   |             | 13.3| –   | 8.1     | 5.5   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| Saint Vallier QVS 1493    |             | –   | –   | 7.4     | 4.5   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| Saint Vallier QVS 1503    |             | –   | –   | 12.7    | 5.2   | 12.0| 6.0  | –    | –    | –    | –    | –   | –   |     |     |
| Tegelen ZMA              |             | –   | –   | 11.6    | 4.96  | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| Tegelen 537964           |             | –   | –   | 7.4     | 4.5   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| Tegelen 7211584          |             | –   | –   | 12.7    | 5.2   | 12.0| 6.0  | –    | –    | –    | –    | –   | –   |     |     |
| Côte d’Arde U.P. 7495    |             | –   | –   | 11.6    | 4.96  | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| **Deutsch-Altenburg**    |             | 13.3| –   | 12.6    | 5.2   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| 22275/141242            |             | –   | –   | 12.2    | 5.1   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| 22275/141272            |             | –   | –   | 12.2    | 5.1   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| 22275/141292            |             | –   | –   | 9.3     | 5.6   | –   | –   | –   | –   | –    | –    | –   | –   |     |     |
| Ivanovce Z264612         |             | 12.9| –   | 7.1     | 5.3   | 12.0| 5.0  | 6.7 | 5.0 | –    | –    | –   | –   |     |     |
| Ivanovce Z264636         |             | 10.5| –   | 11.4    | 4.8   | 5.4 | 4.8  | –   | –   | –    | –    | –   | –   |     |     |
| Ivanovce Z264694         |             | –   | –   | –       | –     | –  | 7.0  | 4.8 | –   | –    | –    | –   | –   |     |     |
| Ivanovce Z264695         |             | –   | –   | –       | –     | –  | 6.4  | 5.0 | –   | –    | –    | –   | –   |     |     |
Howell 2008; Table 2), testifying that this species is distinctive of the Pannonian Basin.

The adult specimen from Pirro Nord (PU 120257) is fully comparable to the holotype mandible (IGF 916) of Proputorius nestii Martelli, 1906 (Fig. 3A, B), later referred to Pannonictis (Ficcarelli & Torre 1967). Indeed, there is an almost perfect congruence in every structure such as the stoutness of the mandibular body, the width of the ascending ramus, the position of the inflection point of the horizontal branch in the mandible, placed at the level of M1 talonid and the position of dental elements. The measurements of the two specimens are also very similar (Table 1). Moreover, the Pirro Nord specimens are not distinguishable from the specimens of Pannonictis nestii described from the Early Pleistocene of Pietrafitta (Rook 1995) and they have much in common with the material recently reported from the Early Pleistocene of Atapuerca and attributed to Pannonictis cf. nestii (García & Howell 2008), with the exception of minor details, as the cusp of P4, which is more centrally placed in the Spanish specimen.

On the basis of our comparative analysis, the Pirro Nord specimen can be referred to Pannonictis nestii (Martelli, 1906).

De Gregorio (1886) described a fossil vertebrate association with some endemic mammals and reptiles from the Early Pleistocene of Monte Pellegrino, Sicily (Burgio & Fiore 1997). Among them there is a Galictinae species, described as Mustela (Mustelercta) arzilla by De Gregorio (1886, 1925) and then analyzed again by Burgio & Fiore (1997). In particular, the latter authors underlined the similarities of the samples with Pannonictis nestii from Upper Valdarno, comparing directly the fossil specimens (Burgio & Fiore 1997: fig. 3). Upon comparison of the mandible from Pirro Nord with the one described from the Sicilian locality, the width of the ascending ramus, the height of the horizontal branch and the dimension of the dental elements are similar. Nevertheless, some details are different, for example the lower margin of the horizontal branch is less curved. The differences between the continental specimens and the insular forms can be explained with reference to the endemic characteristics of the latter one, which shares with the whole Monte Pellegrino vertebrate association (Kotsakis 1985). In accordance with the arguments by Burgio & Fiore (1997), we recognize that the two forms belong to the same genus. Nonetheless, we suggest to maintain the subgeneric distinction for the endemic Sicilian form of Monte Pellegrino which should be indicated as Pannonictis (Mustelercta) arzilla (De Gregorio, 1886).

Locomotion interpretation based on postcranial characters of extinct carnivores is always a difficult task (Van Valkenburgh 1985, 1987; Peigné et al. 2008). Inferring the locomotion of Pannonictis would require a revision of the entire available postcranial material for this taxon, in order to describe and revise all postcranial characters particularly specialized for habit and locomotion specialization. The anatomical characteristics of the complete humerus recently collected at Pirro Nord allow us to evidence the occurrence of some “aquatic” characters such as marked curvature of the diaphysis (the strong curvature of the humerus provides a better mechanical strength for resistance against flexion; Willemsen 1992). Such a character, however, contrasts with other non-aquatic humerus traits like, e.g., the slenderness of humerus, the large size of the supinator crest, and the development of medial epicondyle (large medial epicondyles are characteristic of carnivorans that climb and dig; Taylor 1974).

**CONCLUSIONS**

The specimens of Pannonictis nestii here described add a new element to the very rich and diversified
Pirro Nord vertebrate association (Arzarello et al. 2009). Remains of this taxon are not common. It has been previously reported from the Late Pliocene of Upper Valdarno (Martelli 1906) and from the Early Pleistocene of Pietrafitta (Rook 1995). The Pirro Nord specimens represent the last occurrence of the taxon in Italy.

With regards to palaeoecological aspects, Rook (1995) had hypothesized an aquatic adaptation and a lifestyle linked to humid habitats as it happens in extant Galictinae in South America. Nevertheless, García & Howell (2008) did not find reliable evidence of an aquatic lifestyle in the cranial features. The revised anatomical characteristics of Pannonictis humerus does not allow however to definitely exclude an aquatic lifestyle for his taxon. The question of locomotor adaptations and lifestyle of Pannonictis is, in our view, a still open question.

A taxonomic revision of extinct Galictinae is required in order to construct a clear phylogenetic history of this mustelid group. In particular, it would be necessary to analyze the relationships between the European genera Enhydrictis and Pannonictis which are clearly close to each other.

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