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This is the author's manuscript

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/126812 since

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08 November 2026

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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Colombero S., Pavia M. & Rook L. 2012. — *Pannonictis nestii* (Galictinae, Mustelidae), a new element in the vertebrate association of the human site of Pirro Nord (Italy, Early Pleistocene). *Geodiversitas* 34 (3): 665-681. http://dx.doi.org/10.5252/g2012n3a11

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.

RÉSUMÉ
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.

MOTS CLÉS
Mustelidae,
Pannonictis,
Pléistocène inférieur,
Pirro Nord,
Italie.

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 *Pannonictis 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* (*Allophaiomys*) *ruffoi* (Pasa, 1947). The *Microtus* Schrank, 1798 assemblage of Pirro Nord has intermediate features between the type population of *M.* (*A.*) *pliocaenicus* (Kormos, 1933) from the type population of Betfia 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 Matuyama 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-

zarnika (1.4 or 1.2-0.9 Ma, NW Bulgaria; Sirakov *et al.* 2010; Kahlke *et al.* in press) and Bogatyri/Sinyaya Balka and Rodniki (1.2-1.6 Ma, southern Azov Sea region, Russia; Shchelinsky *et al.* 2010).

The excavation campaigns carried out during the past four years (2007-2010) were focused on two single fissures, P10 and P13, characterized by the large number of fossil vertebrates and lithic industry, the last one particularly abundant at P13. The two fissures are located on the south slope of the limestone quarry exploited by Casale s.r.l. and already known as Cava Pirro. In addition the two fissures are quite large and display a stratigraphic complexity, so that their exploitation allows us to collect some important information about the genesis of the deposits and the ways in which the fossil remains have accumulated. The campaigns gave us the opportunity to collect a large amount of fossil vertebrate material, particularly from the P10 fissure. This fissure is characterized by a four-meter succession of yellowish clay sands with a one-meter conglomerate on the top, separated by a discontinuity surface (Pavia *et al.* 2012).

FIG. 1. — Location map of the Apricena quarries area, Italy.

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; Koepfli *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 *Proputorius 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, *Proputorius 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 *Proputorius 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* (*Mustelercta*) *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-

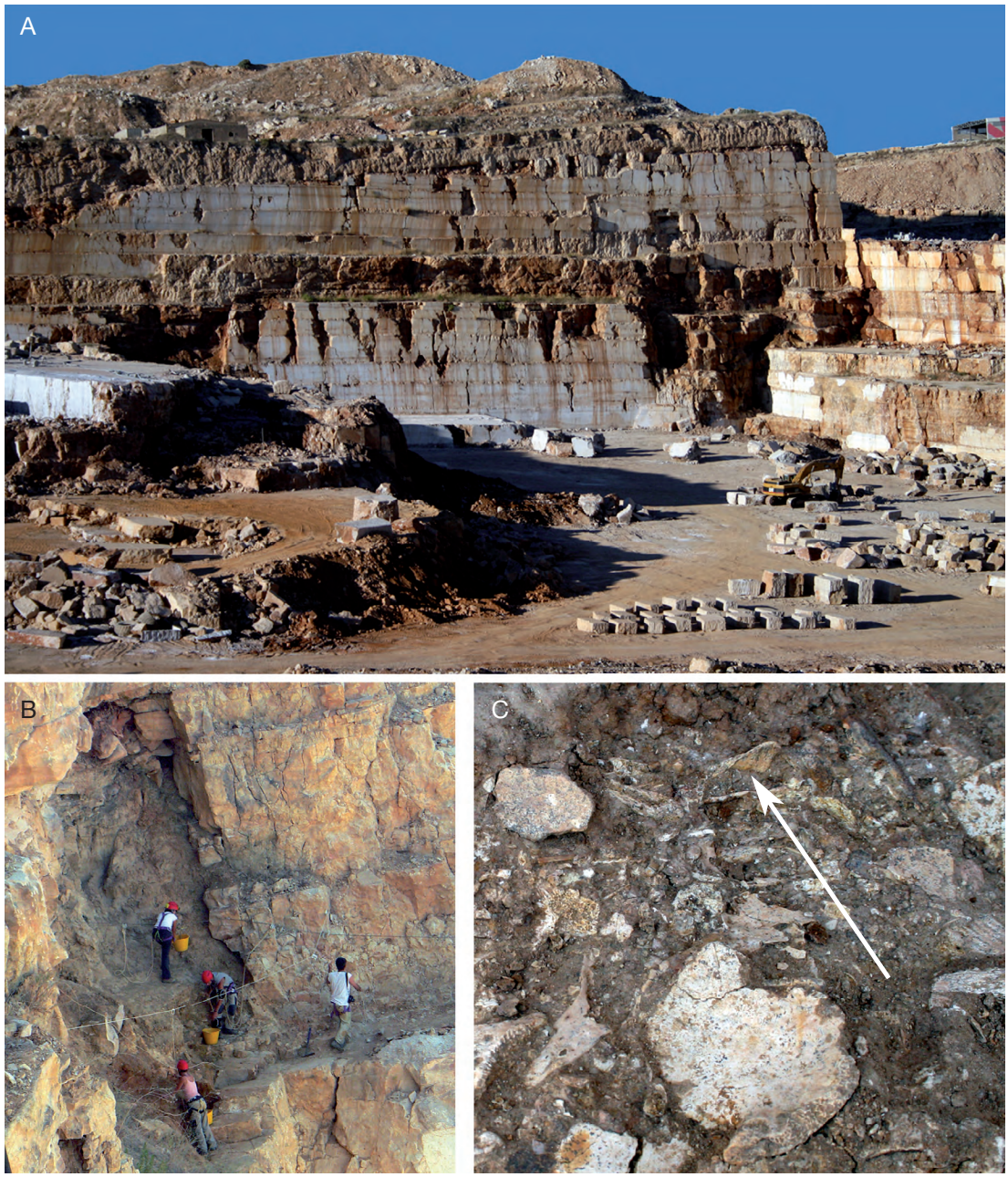

FIG. 2. — View of the Dell'Erba quarry (**A**) and details on the Pirro 10 fissure (**B**) during the excavation campaign of 2007; the hemimandible of *Pannonictis nestii* (Martelli, 1906) still in the sediment before removing (**C**, white arrow).

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 pliocaenica* 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. pliocenica* 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. pliocaenica*, 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 *Enhydrictyis*.

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 P^4 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 P^4 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 of Carmagnola (MCC) and Museo Regionale di Scienze Naturali of Torino (MRSN).

SYSTEMATIC PALEONTOLOGY

Family MUSTELIDAE
Fischer Von Waldheim, 1817
Subfamily GALICTINAE Reig, 1956

Genus *Pannonictis* Kormos, 1931

TYPE SPECIES. — *Pannonictis pliocaenica* 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 P^4 (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 P_3-M_2, 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 P^4 (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. M_1 and P_4 are the only teeth present. The horizontal branch presents a fracture, which reaches the P_4 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 M_1 talonid, where it rises again gently. The masseteric fossa is very deep and extends further on the M_2 alveolus, almost reaching the M_1.

Although P_2 and P_3 are not present, we can observe the alveoli of these teeth occupied by the remains of their roots. They do not lie on the same line, but are slightly clockwise rotated. Thus, the posterior root of P_2 is almost at the same level of the anterior root of P_3, suggesting a partial overlapping of these two teeth. As we have said, P_4 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 M_1 is very worn, with low cusps. The M_1 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 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 P_3. Posteriorly two alveoli are present. Subsequently an M_1 in eruption is observable. The alveolar ridge ends with the M_2 alveolus. The M_1 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

FIG. 4. — *Pannonictis nestii* (Martelli, 1906) from Pirro 10, left humerus (PU 129095) in anterior (**A**), posterior (**B**), lateral (**C**) and medial (**D**) views. Scale bars: 10 mm.

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 ⅓ 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.

P^4

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

TABLE 1. — Measurements (in mm) of *Pannonictis nestii* (Martelli, 1906) from Pirro Nord (Pirro 10) and other European localities. Abbreviations: **$HMaM_1$**, mandibular height at M_1 level; **$WMaM_1$**, mandibular width at M_1 level; **$C\text{-}M_2$**, distance from anterior part of canine alveolus to the posterior part of M_2 alveolus; **$M_1\text{-}M_2$**, distance from anterior part of M_1 alveolus to the posterior part of M_2 alveolus; **LCi**, maximum length of inferior canine; **WCi**, maximum width of inferior canine; **LM_1**, maximum length of M_1; **WM_1**, maximum width of M1; **$LTriM_1$**, trigonid length of M_1; **$WtalM_1$**, talonid width of M1; **LCS**, maximum length of superior canine; **WCS**, maximum width of superior canine; **LP^4**, maximum length of P^4; **WP^4**, maximum width of P^4; *****, juvenile individual. Data are from: **1**, Rook (1995); **2**, Sotnikova *et al.* (2002); **3**, García & Howell (2008).

	HMa M_1	WMa M_1	$C\text{-}M_2$	$M_1\text{-}M_2$	LCi	WCi	LM_1	WM_1	LTri M_1	WTal M_1	LCS	WCS	LP^4	WP^4
Pannonictis nestii														
Upper Valdarno IGF 916[1] (holotype)	14.8	6.35	40.15	–	–	–	11.75	5.2	–	–	–	–	–	–
Pirro Nord PU 120242	–	–	–	–	–	–	–	–	–	–	–	–	10.8	6.2
Pirro Nord PU 120257	13.9	6.6	41.2	16.2	–	–	12.6	5.6	8.4	5.2	–	–	–	–
Pirro Nord PU 118846	–	–	–	–	–	–	–	–	–	–	6.0	4.6	–	–
Pirro Nord PU 118847	–	–	–	–	7.5	4.8	–	–	–	–	–	–	–	–
Pirro Nord PU 118848	–	–	–	–	8.7	5.5	–	–	–	–	–	–	–	–
Pirro Nord PU 126946*	11.0	6.2	–	16.05	–	–	12.25	5.4	8.2	5.15	–	–	–	–
Pietrafitta 1745[1]	13.25	6.7	–	–	–	–	12.6	5.55	–	–	–	–	–	–
Pietrafitta 1749[1]	–	–	–	–	–	–	–	–	–	–	–	–	10.45	5.9
Pietrafitta 1750[1]	14.5	7.05	42.95	–	–	–	12.5	5.25	–	–	–	–	–	–
Pietrafitta 1776[1]	11.95	5.35	–	–	–	–	11.50	4.8	–	–	–	–	–	–
Liventsovka RSU 98[2]	15.1	7.1	–	17.3	–	–	13.5	–	–	–	–	–	–	–
Pannonictis* cf. *nestii														
Elefante ATA98-TE-J30-19[3]	13.3	7.3	41.7	16.2	8.3	5.6	12.6	5.1	9.0	5.2	–	–	10.6	6.9
Elefante ATA00-TE9a-k30-10[3]	–	–	–	–	–	–	–	–	–	–	–	–	11.4	7.4
Elefante ATA00-TE9-L30-54[3]	14.5	7.7	46.2	17.9	10.0	6.4	14.0	5.2	9.7	5.2	–	–	–	–

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 deltoid ridge is distinct and strong. The pectoral ridge is less stronger than the deltoid 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 ⅔ of the diaphisys. 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

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 P^4 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 M_1 while the talonid has distinct rounded marginal cusps as hypoconid and entoconid. Beside the M_2 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 P^4 has a very well-distinguished hypocone that in our specimen is just a tiny swelling of the enamel.

With regards to the differences between "*Enhydrictis*" *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* (= *Enhydrictis ardea*) as a whole group. Besides, even if there was a possibility that the "*ardea*" form appertain to *Pannonictis* rather than *Enhydrictis*, 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 *Enhydrictis* 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 hemimandible 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 *Enhydrictis galictoides* "collected by Forsyth-Major at San Giovanni probably after having published the description of the skull" the M_1 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, *Enhydrictis galictoides* has to be excluded after the endemic characteristics showed by this species (Ficcarelli & Torre 1967), and its limited distribution to insular Sardinia.

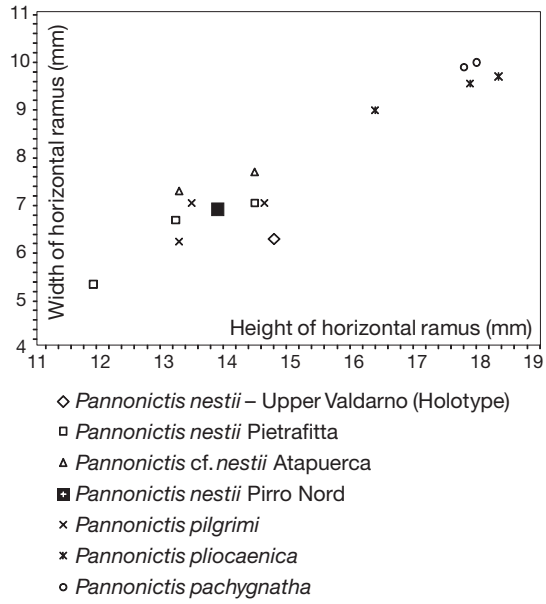

FIG. 5. — Scatter diagram of hemimandibles of different specimens. Measures (in mm) taken at M_1 level. Measurements of *Pannonictis nestii* (Martelli, 1906) holotype, *P. nestii* from Pietrafitta are from Rook (1995). Measurements of *P.* cf. *nestii* from Atapuerca are from García & Howell (2008). Measurements of *P. pilgrimi* Kormos, 1933 and *P. pliocaenica* Kormos, 1931 are from Kormos (1931, 1933-1934). Measurements of *P. pachygnatha* (Teilhard de Chardin & Piveteau, 1930) are from Teilhard de Chardin & Pivetau (1930).

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 indicate with an asterisk (*). Data are from: [1], Rook (1995); [2], Rabeder (1976); [3], Viret (1954); [4], Willemsen (1988); [5], Schaub (1949); [6], Fejfar *et al.* (2012).

	HMa M_1	WMa M_1	Ci-M_2	LCi	WCi	LM_1	WM_1	LTri M_1	WTal M_1	LCS	WCS	LP^4	WP^4
Pannonictis pliocaenica													
Beremend U.P. 606[1]	13.3	6.25	38.9	–	–	11.8	–	–	–	–	–	10.5	–
Villany O.B. 3594[1]	–	–	–	–	–	–	–	–	–	–	–	13.2	8.3
Villany O.B. 3596[1]	15.9	–	50.0	–	–	15.3	6.8	9.7	–	–	–	–	–
Villany O.B. 3600[1]	–	–	–	–	–	15.4	6.3	10.7	–	–	–	–	–
Villany-Kalkberg U.P. 129[1]	13.65	–	50.4	–	–	15.9	–	–	–	–	–	11.5	–
Villany-Kalkberg U.P. 132[1]	–	–	–	–	–	–	–	–	–	–	–	12.55	8.7
Villany-Kalkberg U.P. 134[1]	18.35	9.7	–	–	–	15.45	6.35	10	–	–	–	–	–
Villany-Kalkberg U.P. 135[1]	13.15	7.05	45.15	–	–	13.5	5.35	8.05	–	–	–	–	–
Villany-Kalkberg U.P. 149[1]	–	–	–	–	–	–	–	–	–	–	–	12.0	7.6
Villany-Kalkberg U.P. 765[1]	–	–	–	–	–	–	–	–	–	–	–	11.2	7.25
Villany-Kalkberg U.P. 766[1]	–	–	–	–	–	–	–	–	–	–	–	10.7	7.8
Villany-Kalkberg U.P. 767[1]	17.9	9.55	54.0	–	–	15.95	6.55	11.05	–	–	–	–	–
Villany-Kalkberg U.P. 768[1]	14.55	7.55	45.15	–	–	13.55	5.35	8.85	–	–	–	–	–
Villany-Kalkberg U.P. 769[1]	16.4	9.0	53.6	–	–	15.7	6.6	10.85	–	–	–	–	–
Pannonictis*? *janossyi													
Villany-Kalkberg V61/1390[2]	–	–	–	–	–	–	–	–	–	–		7.0	–
"*Enhydrictis*" *ardea*													
Saint Vallier QVS 149[3]	–	–	–	–	–	11.8	–	–	–	–	–	–	–
Saint Vallier QVS 150[3]	–	–	–	–	–	–	–	–	–	–	–	10.4	–
Tegelen ZMA[4]	–	–	–	8.1	5.5	–	–	–	–	–	–	–	–
Tegelen 53796[4]	–	–	–	7.4	4.5	–	–	–	–	–	–	–	–
Tegelen 721158[4]	–	–	–	–	–	12.7	5.2	12.0*	6.0*	–	–	–	–
Côte d'Arde U.P. 749[5]	–	–	–	–	–	11.6	4.96	–	–	–	–	–	–
Deutsch-Altenburg 22275/14124[2]	13.3	–	–	–	–	12.6	5.2	–	–	–	–	–	–
Deutsch-Altenburg 22275/14127[2]	–	–	–	–	–	12.2	5.1	–	–	–	–	–	–
Deutsch-Altenburg 22275/14129[2]	–	–	–	–	–	–	–	–	–	–	–	9.3	5.6
Ivanovce Z26392[6]	12.9	–	–	7.1	5.3	12.0	5.0	6.7	5.0	–	–	–	–
Ivanovce Z26393[6]	10.5	–	–			11.4	4.8	5.4	4.8	–	–	–	–
Ivanovce Z26394[6]	–	–	–	–	–	–	–	–	–	7.0	4.8	–	–
Ivanovce Z26395[6]	–	–	–	–	–	–	–	–	–	6.4	5.0	–	–

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 P^4 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 &

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 M_1 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 P_4, 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).

TABLE 3. — Measurements (in mm) of *Pannonictis nestii* from Pirro Nord (Pirro 10) (Humerus). Abbreviations: **GL**, greatest length of the humerus; **Bp**, greatest breadth of the proximal end; **Bd**, greatest end of the proximal end; **SD**, smallest breadth of diaphysis. Measures were taken following Von der Driesch (1976).

	GL	Bp	Bd	SD
Pannonictis nestii				
Pirro Nord PU 129095	84.82	18.85	26.09	7.55

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.

Acknowledgements
This study was financially supported by University Ministry grants MIUR PRIN 2009MSSS9L_002 (resp. G. Pavia, Torino) and by Italcementi Group, Cassa di Risparmio di Torino Foundation, Compagnia di San Paolo Foundation. Field works at Pirro Nord were also supported by the Municipality of Apricena and by the quarry owner, particularly V. Zuccarino (Major of Apricena), A. Verni, L. Gervasio, F. Dell'Erba and G. Dell'Erba. Appreciation is expressed to Elisabetta Cioppi (Museo di Storia Naturale sezione Geologia e Paleontologia, Firenze) for facilitating access to the holotype of *Pannonictis nestii*, and Saulo Bambi (Museo di Storia Naturale, Firenze) for the photos in Figure 3, particularly A and B.

We also would like to thank the referees Nikolai Spassov, Stéphane Peigné and Annemarie Ohler for their peer review and the useful suggestions, which definitely improved the manuscript.

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Submitted on 13 July 2010;
accepted on 6 May 2011.