



Remarks on the Messinian carnivores (Mammalia) of Italy

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ABSTRACT - The latest Miocene to earliest Pliocene is a period of remarkable changes in the geography and climate of the circum-Mediterranean area. Terrestrial ecosystems were strongly affected by these changes and several important mammal dispersal events took place during that period. Its geographic position in the Mediterranean region gives Italy a crucial role in the study of Messinian land mammal evolution. Carnivores are poorly represented in Italian Messinian faunal assemblages, but remains of several families are known (Viverridae, Hyainidae, Felidae, Mustelidae and Canidae) and provide valuable information for the study of the carnivore guild during the important turnover that occurred at the Mio-Pliocene transition.

RIASSUNTO - [Considerazioni sui carnivori (Mammalia) del Messiniano in Italia] - I cambiamenti climatici, geografici e ambientali che avvennero durante la transizione Miocene-Pliocene nella regione Mediterranea furono estremamente intensi. I movimenti tettonici e le conseguenti variazioni del livello del mare, dovute anche ai cambiamenti climatici, furono all'origine di un evento oggetto da decenni dell'interesse di studiosi di tutto il mondo: la Crisi di Salinità del Messiniano. Le condizioni geografiche stabilitesi in questo intervallo cronologico ebbero anche una notevole influenza sull'evoluzione dei mammiferi terrestri e su diversi eventi di dispersione. Per la sua posizione geografica al centro del Mediterraneo quella che oggi è l'Italia rappresenta un'area di studio cruciale anche a questo proposito. Nel Miocene Superiore erano presenti tre distinte bioprovince: l'area Tosco-Sarda, l'area Apulo-Abruzzese e la Calabro-Siciliana. Il record fossile a mammiferi terrestri delle prime due bioprovince (bacino di Baccinello-Cinigiano, Maremma, e cave di Apricena, Gargano, rispettivamente) presenta chiari caratteri endemici, legati al fatto che in queste aree esistevano arcipelaghi. La terza bioprovincia, quella Calabro-Siciliana, per contro, si caratterizza per una fauna a mammiferi bilanciata (Cessaniti). Verso la fine del Miocene, la Toscana perde le condizioni di isolamento e la fauna di Baccinello V3 testimonia l'avvenuto collegamento col resto d'Europa. Nel quadro delle trasformazioni che coinvolgono le faune a mammiferi terrestri nel corso del Messiniano il record fossile relativo ai carnivori, seppure non particolarmente ricco, fornisce importanti indicazioni per analisi paleoecologiche e ricostruzioni paleoambientali. Allo stato attuale delle ricerche sono rappresentate le famiglie Viverridae, Hyainidae, Felidae, Mustelidae e Canidae, provenienti da cinque diverse località: Gravitelli (Sicilia), Baccinello V3 e Casino (Toscana), Brisighella (Romagna) e Verduno (Piemonte). In questo lavoro è presentato un aggiornamento tassonomico sui carnivori italiani del Messiniano, con illustrazione di alcuni nuovi resti e il confronto con il record fossile di altri siti significativi dell'area Mediterranea (ad es. Venta del Moro, Spagna, e Sahabi, Libia) con faune riferibili all'unità MN13 della biocronologia a grandi mammiferi. Le differenze riscontrabili nella composizione faunistica dei carnivori tra le diverse località possono avere molteplici spiegazioni ed in particolare essere legata a differenze di età. Tuttavia il record italiano conferma il carattere di crocevia fra faune eurasiatiche ed africane al passaggio Mio-Pliocene, una fase che vede il declino delle iene dog-like e la diffusione dei Canidi del genere Eucyon.

FOREWORD

During the Miocene-Pliocene transition, from 7 to 4 Ma, remarkable changes in geography and climate took place in the circum-Mediterranean area. An interplay of tectonics and global sea level variations (dependent on climate changes) caused the event known as the Messinian Salinity Crisis. These changes strongly influenced the evolution and dispersal of land mammals. Made et al. (2006) identified four dispersal events in the Messinian. These authors pointed out that mammals adapted to dry or open environments widespread from Africa to SW Europe.

Due to its geographical position, the area where Italy is located today is of special interest and the study of the Late Miocene Italian fossil record provides valuable data for palaeobiogeographical reconstructions (see Rook et al., 2006).

Carnivores are poorly represented in Messinian Italian faunal assemblages, but several families are recorded (Viverridae, Hyainidae, Felidae, Mustelidae, and Canidae; Seguenza, 1902, 1907; Torre, 1989; Rook et al., 1991; Rook, 1992; Rook & Martínez Navarro, 2004).

In this paper the Italian record will be updated on the basis of available material and throughout the report of new material from the site of Verduno (Piedmont). This new material is stored at Museo Civico "F. Eusebio" of Alba (Piedmont, Northern Italy). In order to widen the discussion on a broader scale, the Italian record is compared with data from other important Late Miocene (MN13) localities, such as Venta del Moro (Spain) and Sahabi (Libya), where faunal assemblages including a diversified sample of carnivores have been discovered.

Late Miocene Italian palaeobiogeography

The pre-Messinian Late Miocene land mammal localities of Italy document the existence of three main distinct palaeobioprovinces (Abruzzi-Apulia, Tusco-Sardinia and Calabria-Sicily); the first two areas were characterised by vertebrate faunas with evident endemic features, thus attesting the occurrence of isolated emerged areas (Torre et al., 2000; Rook et al., 2006).

In particular, within the Abruzzi-Apulian bioprovince, a structural high was located where today Gargano-Murge (respectively Foggia and Bari districts) are. In this area an archipelago remained emerged until the Early

Pliocene, where typical endemic elements survived (Abbazzi et al., 1996 and bibliography therein; Rook et al., 2006). The only mammalian carnivore represented in this faunal assemblage is the mustelid *Paralutra garganensis* (Willemsen, 1983).

The Tusco-Sardinian bioprovince was located in the peri-Tyrrhenian side of Italy (Southern Tuscany and Sardinia). The Late Miocene faunal assemblages of the Tusco-Sardinia are referred to an endemic faunal complex (“*Oreopithecus* Zone Faunas [OZF]” in Bernor et al., 2001) including, in addition to the hominoid primate *Oreopithecus* and the antelope *Maremmia*, a few endemic carnivores referable to the subfamily Lutrinae: *Tyrrhenolutra helbingi* Hürzeler, 1987 (Baccinello V1), *Paludolutra maremmana* Hürzeler, 1987, and *Paludolutra campanii* (Meneghini, 1862) (Monte Bamboli; Ginsburg, 1999). On the other hand, the ursid *Indarctos anthracitis* Weithofer (1888) from Monte Bamboli has to be considered an invalid taxon, possibly a synonym of *Indarctos laurillardi* (Meneghini, 1863).

By Messinian time a dramatic reorganization in the palaeobiogeography of the Apennine chain resulted in a remarkable change in terrestrial ecosystems along the entire peninsula. All the taxa belonging to the OZF faunal complex disappeared and were replaced by a new faunal assemblage (Baccinello V3) including continental taxa with clear European affinities (Hürzeler & Engesser, 1976; Rook, 1999; Rook et al., 1999; Abbazzi, 2001; Benvenuti et al., 2001; Bernor et al., 2001). The V3 assemblage is characterized by non-endemic taxa, showing a definitive palaeobiogeographical connection with Europe. This faunal turnover is coupled with the documentation of correlatable faunas penetrated into the northern Apennines throughout Piedmont and Romagna as testified by the sites of Ciabòt Cagna (Alba, Piedmont; Cavallo et al., 1993), the recently discovered Verduno (Alba, Piedmont; Bonelli, personal communication), Brisighella (Faenza, Romagna; De Giuli et al., 1988; Sami, 2007), and several sites in Tuscany (Fine valley, Casino, Velona, and Baccinello V3; Kotsakis et al., 1997; Rook et al., 1999; Benvenuti et al., 2001).

Latest Miocene mammals are also reported from a site in southern Italy, at Cessaniti (Vibo Valentia, Calabria; Ferretti et al., 2003) and Gravitelli (Messina, Sicily; Seguenza 1902, 1907). Since some taxa from these sites (e.g. *Stegotetralodon syrticus* from Cessaniti; Ferretti et al., 2003) show clear affinities with taxa recorded in approximately coeval North African localities (e.g. Sahabi, Libya), the Calabria-Sicily area has been interpreted as a northern extension of the Late Miocene Mediterranean border of the African plate (Rook et al., 2006 and references therein). The Gravitelli fauna included, among the others, a rhino, different forms of bovids, a hexaprotodont hippopotamid and a colobine monkey (Rook, 1999). In addition the assemblage includes a suid referable to the genus *Propotamochoerus* (Gallai & Rook, 2006), thus evidencing at least in part an European affinity. Unfortunately the fossils from Gravitelli were destroyed during the Messina earthquake in 1908, and information on this fauna can be taken only from descriptions by Seguenza (1902, 1907).



Fig. 1 - Location of the fossiliferous localities.

THE ITALIAN CARNIVORE FOSSIL RECORD

At present, Messinian (MN13) carnivore remains have been discovered in Italy in the following localities (Fig. 1): Gravitelli (Sicily), Baccinello V3 (Tuscany), Casino basin (Tuscany), Brisighella (Romagna), and Verduno (Piedmont).

Family VIVERRIDAE

Viverra howelli Rook & Martínez Navarro, 2004
(Baccinello V3)

Viverrids are poorly represented in the Mio-Pliocene European fossil record. A viverrid mandible coming from the Baccinello V3 faunal assemblage has been described as *Viverra* sp. by Rook et al. (1991). Recently, Rook & Martínez Navarro (2004) compared this specimen to those of viverrid coming from the latest Miocene Northern and Eastern African localities. They pointed out strong affinities between the Baccinello V3 fossil, *Viverra* n. sp. “A” from Sahabi, Libya (Howell, 1987) and *Viverrinae* sp. indet from Lothagam, Kenya (Werdelin, 2003), thus erecting the species *Viverra howelli*. This species is characterized by a relatively small size and a lower carnassial with a short talonid. *Viverra howelli* is close to *Viverra pepratxi* (Early Pliocene of Europe) in general size. Moreover, Rook & Martínez Navarro (2004) on the basis of dental features (in particular of the lower carnassial) claim greater affinity between *V. howelli* and large-sized Late Miocene and Pleistocene species from Africa (*Viverra leakey* from Langeebanweg and the Omo Valley) than with European taxa (*V. pepratxi* and *Megaviverra*).

Family HYAENIDAE

The following hyaenid taxa have been collected from Italian Messinian localities: *Plioviverrops faventinus* Torre, 1989 (Brisighella; Fig. 2), *Plioviverrops orbignyi* (= *Ictitherium orbignyi*) (Gaudry & Lartet, 1856) (Gravitelli), *Hyaenictitherium hyaenoides* (Zdansky, 1924) (= *Ictitherium hipparionum*) (Gravitelli), *Hyaenictitherium* sp. (Verduno), *Lycyaena chaeretis* (Gaudry, 1861) (= *Thalassysctis (Lycyaena)* ex gr. *chaeretis-macrostoma*) (Brisighella), Hyaenidae indet. (coprolites) from Baccinello V3.

The fossil hyaenas from Brisighella have been studied in detail by Torre (1989) who erected the new species *Plioviverrops faventinus*. Later Rook et al. (1991) and Ferretti (2007) provided further data on the group.

Plioviverrops faventinus is the most abundant carnivore at Brisighella (Rook et al., 1991). It is the youngest species of this fox-sized genus. As stated by Torre (1989) the cranial features of this taxon are similar to that of viverrids, but the relative proportions between the muzzle and the braincase recalls that of *Vulpes*. The dentition of *Plioviverrops* is primitive in retaining four premolars (P1-P4/p1-p4) and two molars (M1-M2/m1-m2), a condition similar to that of viverrids (Ferretti, 2007). *Plioviverrops* was characterised by reduction of

the sectorial portion of the dentition and the growth of a number of high, puncture-crushing cusps on the jugal teeth, non-retractile claws and a skeleton with terrestrial adaptations (Werdelin & Solounias, 1996).

Brisighella yielded also a few specimens of a larger hyaenid, referred to as *Thalassysctis (Lycyaena)* ex gr. *chaeretis-macrostoma* by Rook et al. (1991). *Lycyaena* includes species with cursorial attitudes, as suggested by the evolution of a highly cursorial skeleton. They also are characterised by the development of the shearing component of the dentition with the presence of additional cusps on premolars, more compressed laterally than in extant bone-cracking hyaenas. *Lycyaena chaeretis* was a wolf-sized species, with slender skeleton and elongated skull, found in the Turolian faunas of Greece (Samos and Pikermi, MN12; Werdelin & Solounias, 1991 and references therein). This species seems to be very close to the Asian *L. dubia* Zdansky, 1924 and *L. macrostoma* (Lydekker, 1884). The specimens from Brisighella can be considered as the latest representative of the species in Europe (Fig. 3).

The Gravitelli hyaenids were figured by Seguenza (1902, 1907), but the original material was lost in the earthquake that struck Messina in 1908. The taxonomy of the Gravitelli specimens is updated following Werdelin & Solounias (1991).



Fig. 2 - Skull and mandible of *Plioviverrops faventinus* Torre, 1989 from Brisighella (Faenza, Romagna) (photo F. Liverani). Scale bar = 4 cm.

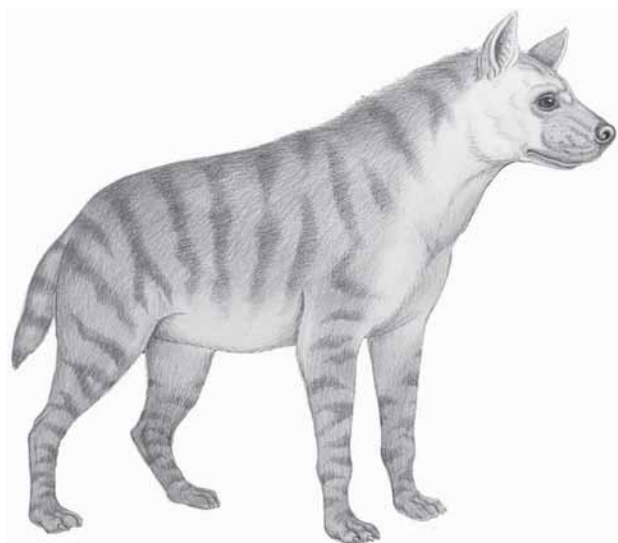


Fig. 3 - Reconstruction of the large hyaenid *Lycyaena chaeretic* (Gaudry, 1861) (drawing by M. Sami).

New evidence of the occurrence of hyaenids in a Messinian deposits in Italy is provided by the recent discovery of vertebrate remains from Verduno (Tanaro river basin, Alba, Piedmont; Bonelli, personal communication). Among them a left P3 has been collected (Fig. 4). Its morphology and size (L 22.5 mm; W 11.6 mm) recall those of a large dog-like hyaena. The tooth is broad, with a conical main cusp that has with a wear surface at the apex typical of bone-cracking carnivores. The specimen from Verduno (stored at museum "F. Eusebio" of Alba, catalogue number G.1591) is here referred to *Hyaenictitherium* sp.

Further field campaigns will hopefully clarify the status of *Hyaenictitherium* sp. from Verduno, and no further analyses can be stressed on the material from Gravitelli. *Hyaenictitherium* included different species ranging from jackal to brown hyaena size, as in the case of *Hyaenictitherium namaquensis* (Stromer, 1931). The dentition can be considered quite unspecialised, similar to that of canids, but with an evident tendency toward bone crushing. The skeleton was adapted to a terrestrial mode of life, but without cursorial adaptations. Dog-sized hyaenas have been discovered in coeval localities from the Mediterranean region: *Hyaenictitherium hyaenoides* (= *Thalassictis* aff. *hyaenoides*) from Venta del Moro (Spain; Montoya et al., 2006) and *Hyaenictitherium namaquensis* from Sahabi (Libya; Esu & Kotsakis, 1980; Werdelin & Solounias, 1991; Rook & Sardella, 2008).

Hyaenids were the most diversified group of carnivores in the Late Miocene of the Old World, reaching a diversity of 22 species between 9 and 5 Ma (Werdelin & Turner, 1996). Werdelin & Solounias (1996) grouped the Eurasian Hyaenidae, including the Ictitherinae, into six ecomorphological types:

1. Civet-like insectivore/omnivore morphology (*Protictitherium*).
2. Mongoose-like insectivore/omnivore morphology (*Plioviverrops*)

3. Jackal- to wolf-like meat- and bone-eaters (*Ictitherium*, *Hyaenotherium*, *Hyaenictitherium* and other genera). In a recent work, Zhang et al. (2002), *Hyaenotherium* has been synonymized with *Hyaenictitherium*.

4. Cursorial meat- and bone-eaters (*Lycyaena*, *Hyaenictis*, *Chasmaporthetes*). This group now also includes *Lycyaenops* (Werdelin, 1999).

5. Transitional bone-crackers (*Palinhyena*, *Ikelohyaena* and *Belbus*). This group previously included *Leecyaena* that is now known to be a synonym of *Pliocrocota* (Werdelin, pers. comm.).

6. Bone-crackers (*Pachycrocota*, *Pliocrocota*, *Crocota*, *Hyaena*, *Parahyaena* and *Adcrocota*).

Werdelin & Solounias (1991, 1996) consider the first three types as successive components in the Hyaenidae evolutionary trend. Most of the Miocene hyaenas belong to types 1-4, while Pleistocene and Recent hyaenas nearly all belong to type 6.

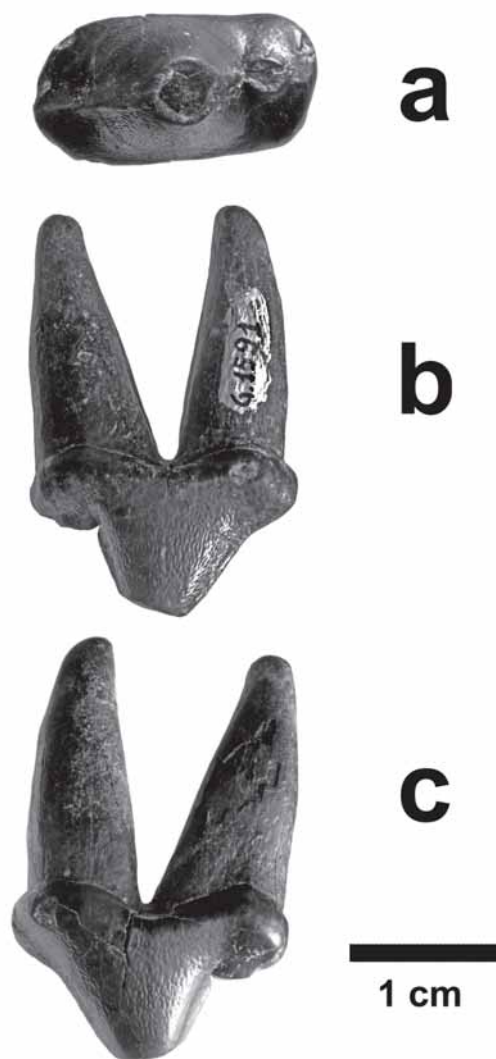


Fig. 4 - G.1591: left P3 of *Hyaenictitherium* sp. from Verduno (Alba, Piedmont) stored at the Museo Civico "F. Eusebio" of Alba, a) occlusal view; b) lingual view; c) labial view. (photo O. Cavallo).

The Hyaenidae from Messinian of Italy are diversified, being represented ecomorphological type 2, 3, and 4 by Werdelin & Solounias (1996).

Family FELIDAE

Felis attica Wagner, 1857 vel *Felis christoli* Gervais, 1848-1852 (Brisighella), *Metailurus major* Zdansky, 1924 (Baccinello V3), *Metailurus parvulus* (Hensel, 1862) (= *Machairodus ogygia*) - (Kaup, 1833) (Gravitelli), *Amphimachairodus* sp. (*Machairodus* ex gr. *giganteus*) (Baccinello V3), Felidae indet. (Casino basin).

Among the felids, the only true cat comes from Brisighella and the fossil sample is represented by a right mandible with M1, one metatarsus and one phalanx described by Rook et al. (1991). These authors referred these fossils to "*Felis*" ex gr. *attica-christoli*, including two groups of felids differing mainly for their size, and suggest the use of a single chronospecies. The smaller *Felis attica* and *Felis* sp. characterized European and Chinese MN12 faunas (Pikermi, Samos, and Lok. 49 of the *Hipparion* beds), while younger faunas (i.e. Venta del Moro and Montpellier) are characterized by the larger *Felis christoli* (see Rook et al., 1991 and references therein). For its size the specimen from Brisighella shows affinities with the second group. Recently, Montoya et al. (2006) suggested the occurrence of *Felis* n. sp. at Venta del Moro (Spain). Only further discoveries and studies will clarify the taxonomy of the small true cats (Felinae) at Mio-Pliocene transition.

The taxonomy of Neogene machairodontine cats has been discussed in a series of recent papers (Antón et al., 2004; Peigné et al., 2005; Sardella & Werdelin, 2007).

Sabertoothed cats have been recorded in the Baccinello V3 horizon faunas (Rook et al., 1991) and Gravitelli (Seguenza, 1902, 1907). The occurrence of *Metailurus major* in the late Messinian of Italy is testified by two mandibles with teeth having the typical size and morphological characters of this species, widespread in the Eurasian Late Miocene deposits. The taxonomic position of the medium-sized sabertoothed cat from Gravitelli (destroyed in 1908 during the Messina earthquake) has to be reconsidered. Rook et al. (1991) suggest that the attribution to *Paramachairodus ogygia* (= *Machairodus ogygia*) cannot be maintained because the Sicilian specimen has to be referred instead to *Metailurus parvulus*.

Metailurini show the typical sabertooth condition of laterally compressed canines, but they parallelized true cats in the relative elongation of the upper canines (Sardella, 1994 and references therein).

Finally, also the large sabertoothed cat referable to the genus *Amphimachairodus* (sensu Antón et al., 2004) has been recorded in Italy. Some isolated teeth from the Baccinello V3 horizon have been described by Rook et al. (1991) and referred to *Machairodus* ex gr. *giganteus* (see also Sardella, 1994). *Amphimachairodus giganteus* (Wagner, 1848) is a large sabertooth that characterizes the Turolian Eurasian faunas. As recent studies on Late Miocene Machairodontinae from Africa show, they represent a heterogeneous assemblage, with both small and large forms

(Sardella & Werdelin, 2007 and references therein). In particular, the specimen from Sahabi (Libya) belongs to the group of larger taxa, along with *Amphimachairodus kabir* from Toros Menalla (Chad; Peigné et al., 2005). Both the Sahabi and Chad specimens have relatively slender lower carnassials, similarly to the Plio-Pleistocene *Homotherium*, even if craniodental features suggest that they are not in the direct ancestry of that genus (Werdelin & Sardella, 2006; Sardella & Werdelin, 2007).

The occurrence of *Amphimachairodus kabir* (or closely related forms) in latest Miocene-earliest Pliocene European localities is possibly represented by an upper canine and right mandible recorded at Venta del Moro and stored at the "Museo Nacional des Ciencias Naturales" of Madrid (personal observations) (= *Amphimachairodus giganteus* in Montoya et al., 2006). The occurrence of this African sabertoothed cat in Europe has great palaeogeographic implications. The size and morphology of the isolated teeth from Baccinello V3 show differences between them and *Amphimachairodus kabir* group, but the scantiness of the remains suggests caution in taxonomic attribution and to refer them to *Amphimachairodus* sp.

The occurrence of a specimen attributable to Felidae indet. within the Casino Basin stored within the "Accademia dei Fisiocritici" collections in Siena has been identified by Gallai (2005).

Family MUSTELIDAE

Mellivora beinfieldi Hendey, 1978 (Brisighella), *Plesiogulo crassa* Kurtén, 1970 (Baccinello V3 horizon).

Mustelids are poorly represented in the Italian Messinian deposits. As pointed out before the only carnivore represented in Late Miocene (pre-Messinian) deposits of Italy are Lutrinae mustelids, according to the endemic features of Southern Tuscany and Gargano (Apulia) faunal assemblages.

At Brisighella Rook et al. (1991) referred a mandibular branch with teeth to *Mellivora beinfieldi*, evidencing the affinities of this specimen with the specimens from the Earliest Pliocene Quarry E at Langenbaanweg, in South Africa (Hendey, 1974).

Rook et al. (1991) described a fragmentary mandible with teeth of a wolverine coming from Cinigiano (Baccinello V3 horizon) and referred it to the species *Plesiogulo crassa*. *Plesiogulo* includes different species (from Late Miocene to Early Pliocene) with a wide distribution. Large specimens referable to *Plesiogulo monspessulanus* Viret (1939) have been reported from Venta del Moro (Spain; MN13), Montpellier (France; MN14; Montoya et al., 2006 and references therein).

Made et al. (2006) claim that *Plesiogulo* dispersal event is part of the dispersals occurred around 6.1 Ma, when mammals adapted to dry or open environments dispersing from Africa and SE Europe to SW Europe.

The occurrence of a specimen attributable to Mustelidae indet. within the Casino Basin stored within the "Accademia dei Fisiocritici" collections in Siena has been identified by Gallai (2005).

Family CANIDAE

Eucyon monticinensis (Rook, 1992) (Brisighella, Verduno)

The taxonomy and systematics of Late Miocene *Canis*-like forms of Eurasia and North America were debated until 1990's. Rook et al. (1991), Rook (1992, 1993), Tedford et al. (in press), pointed out that the fossils from the Late Miocene Holarctic localities could not be referred to *Canis*.

Finally, Tedford & Qiu (1996) erected the new genus *Eucyon*, which included several Neogene primitive *Canis*-like specimens. *Eucyon monticinensis* (Rook, 1992) from Europe and *Eucyon davisii* (Merriam, 1911) from North America can be considered as the earliest species of the genus, being the taxonomic position of "*Canis*" *cipio* Crusafont 1950, from Concud (Spain) (MN12) still unclear (Rook, 1993, 1992). *Eucyon* survived until the Late Pliocene in Asia (*Eucyon marinae*) (Spasov & Rook, 2006) and Africa (*Eucyon* is present at Ahl al Oughlam - *Canis* aff. *aureus* in Geraads 1997, p. 151).

Brisighella is the type locality of *Eucyon monticinensis*, which was also recorded in the coeval faunal assemblage of Venta del Moro (Spain; Montoya et al., 2006 with references therein) and possibly also in the Casino Basin (Rook, 1992). A left M1 (Fig. 5) referable to this species have been recently found at Verduno (Piedmont; Bonelli, personal communication). The fossil is stored at the museum "F. Eusebio" of Alba, catalogue number G.1590. The size (L 15.1 mm; W 10.7 mm) and the tooth morphology led to consider the fossil from Verduno as belonging to a large specimen of *Eucyon monticinensis*. The morphology of the paracone and metacone, similar in size, the occurrence of a crest connecting protocone to metaconule support such a taxonomic attribution.

Eucyon and the raccoon-dog *Nyctereutes* characterized the Early Pliocene (Ruscinian) faunas of Europe. True representatives of the genus *Canis* became widespread in Europe during the Late Pliocene; the so-called 'Wolf Event' (Azzaroli, 1983), previously supposed to have taken place at the Plio-Pleistocene transition, was already completed before the beginning of the Pleistocene (Rook & Torre, 1996; Sardella & Palombo, 2007 and references therein).

Finally, the recent identification of *Canis* in the Early Villafranchian faunal assemblage from Viallette (France; Lacombe et al., 2008) testifies that true dogs, even if probably rare, were part of the European terrestrial ecosystems already in Middle Pliocene.

CONCLUSIONS

The latest Miocene and earliest Pliocene is a period of remarkable changes in the geography and climate of the circum-Mediterranean area. The terrestrial ecosystems were strongly affected by these changes and several important mammal dispersal events took place during the period. Its geographic position in the Mediterranean region gives Italy a crucial role in understanding these events. The palaeogeographic changes that during the Messinian characterised the central Mediterranean area produced a dramatic reorganization in the Italian palaeobioprovinces distribution. In particular, Sardo-Tuscanian endemic vertebrates were completely replaced by a new faunal assemblage (Baccinello V3) including continental taxa with clear European affinities. This European fauna penetrated into the northern Apennines throughout Piedmont and Romagna and spread along the entire newly emerged Apennine chain.

Carnivores play an important role in understanding the composition and evolution of land mammal guilds. The fossil record of the Italian Messinian (MN13) deposits, even if not very rich, provides valuable information. Rook et al. (1991) already demonstrated differences in the faunal composition (also among carnivores) between Baccinello V3 and Brisighella. These authors pointed out that this could be due to different palaeoecological and taphonomic conditions, besides different ages, as Brisighella is younger than Baccinello V3. Further studies will clarify the age of the mammals recently found at Verduno. The Italian fossil record of Messinian

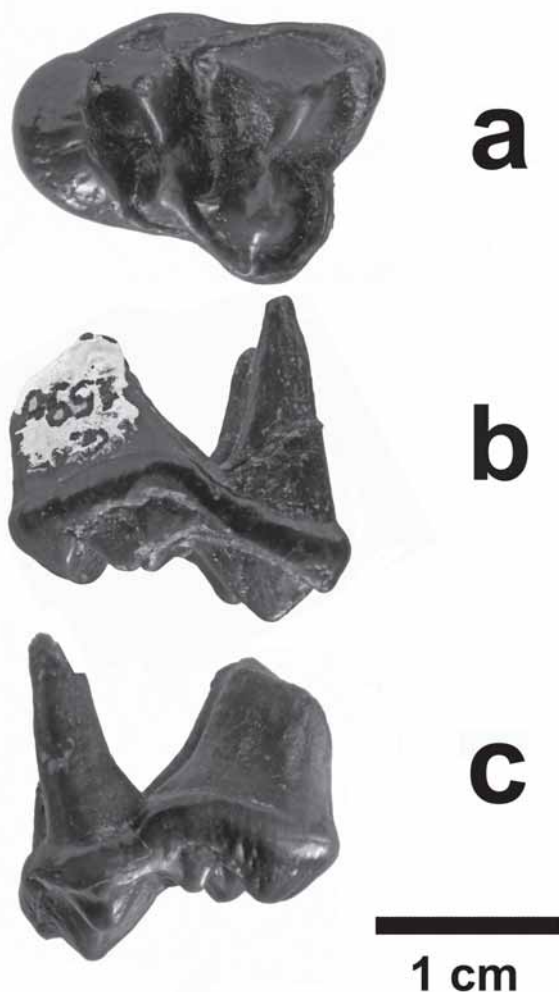


Fig. 5 - G.1590: left M1 of *Eucyon monticinensis* (Rook, 1992) from Verduno (Alba, Piedmont) stored at the Museo Civico "F. Eusebio" of Alba, a) occlusal view; b) anterior view; c) posterior view (photo O. Cavallo).

carnivores confirms the crossroad condition of the faunas between Africa and Asia.

Moreover, an important turnover in Old World hyaenid faunas, took place at the Miocene/Pliocene transition (Werdelin & Solounias, 1996; Werdelin & Turner, 1996), when type 2 (mongoose-like) and type 3 hyaenids (dog-like hyaenas) became extinct, followed by the dispersal of modern bone-cracking (type 6) hyaenas in Eurasia. Hyaenids were the dominant dog-like predators of the Old World Miocene, reaching a diversity of 22 species between 9 and 5 Ma with strong reduction to five species at 4 Ma. During the same time interval, the first canid of modern-type (*Eucyon*) dispersed to the Old World (Rook, 1992, 1993; Tedford & Qiu, 1996; Spassov & Rook, 2006). There is clearly a close ecological relationship between these events. Different species of hyaenids (including type 3 taxa) and *Eucyon* are included in Italian fossil record, documenting a crucial phase of the evolution of the carnivore guild in the Mediterranean region.

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