

**THE FIRST WORKSHOP ON EUROPEAN FOSSIL PRIMATE RECORD
(SIENA AND GROSSETO, SEPTEMBER 11-13, 2008), WITH AN UPDATE
ON ITALIAN STUDIES IN PALAEOPRIMATOLOGY**

**IL PRIMO WORKSHOP EUROPEO SUI PRIMATI FOSSILI (SIENA E GROSSETO, 11-13 SETTEMBRE 2008), E UN AGGIORNAMENTO SUGLI STUDI DI
PALEOPRIMATOLOGIA IN ITALIA**

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Abstract. A colloquium on european fossil Primate record has been organised within the 2008 "Giornate di Paleontologia" of the Italian Paleontological Society, aimed to offer to the scientific community an occasion to discuss the status of the art on the wide spectrum of studies centered on the fossil primate record. In addition, the coincidence of the 50th anniversary of the recovery of the *Oreopithecus bambolii* skeleton at Baccinello by J. Hürzeler (August 2nd 1958) was further an opportunity to celebrate one of the most intriguing primates of the European fossil record. A report on the "colloquium" is provided herein, together with an update on recent studies about the Italian Primate fossil record.

The fossil catarrhines of the Italian record provide important documentation for the study of primate populations in Europe during the Neogene. Compared with the overall distribution of the European fossil primates only four genera are documented in Italy representing two superfamilies: Hominoidea and Cercopithecoidea. The first one is represented by the endemic Late Miocene *Oreopithecus*, while the second one is represented by three genera, the colobine *Mesopithecus*, and the cercopithecines *Macaca* and *Theropithecus*. The last decade has recorded a huge increase in our knowledge of the Italian fossil primate record, its geological and palaeobiological context, as well as taxonomy, anatomy and functional morphology. An overview of these discoveries and results are offered here.

Riassunto. Il primo workshop europeo sui primati fossili si è tenuto in occasione delle "Giornate di Paleontologia 2008" organizzate dalla Società Paleontologica Italiana. Questo workshop è stato organizzato con l'intento di offrire alla comunità scientifica una occasione per discutere lo stato dell'arte su tutti i campi di studio che interessano il record fossile dei Primati. Inoltre, coincidendo con il 50^{mo} anniversario della scoperta dello scheletro di *Oreopithecus bambolii* a Baccinello da parte di J. Hürzeler (2 Agosto 1958), il workshop è stata una ulteriore opportunità per discutere sulle recenti ipotesi e scoperte di quello che è stato definito come uno dei primati più problematici del record fossile europeo. Questa nota riporta una sintesi delle attività svolte durante il workshop ed offre inoltre un aggiornamento sugli studi di paleoprimateologia in Italia.

Il record fossile italiano dei primati fornisce una documentazione essenziale per lo studio del popolamento a primati dell'Europa durante il Neogene. In confronto con la più ampia documentazione del resto del continente europeo, nelle località fossilifere italiane sono presenti solamente quattro generi appartenenti a due superfamiglie, Hominoidea e Cercopithecoidea. La prima è rappresentata esclusivamente nel Miocene superiore dal genere endemico *Oreopithecus*, la seconda è invece rappresentata, a partire dal Messiniano, da tre generi, la colobina *Mesopithecus* (Messiniano-Pliocene medio), e due cercopithecine *Macaca* (Pliocene-Pleistocene superiore) e *Theropithecus* (Pleistocene inferiore). Nell'ultimo decennio le nostre conoscenze sul record dei primati fossili italiani sono aumentate in maniera considerevole. Questo grazie non solo a nuovi ritrovamenti, ma anche ad approfondimenti sui contesti geologici e paleobiologici di questi primati, e a nuovi studi di tassonomia, anatomia e morfologia funzionale. Il presente contributo vuole offrire una rassegna sulle nuove evidenze e sugli ultimi risultati delle ricerche di paleoprimateologia in Italia.

INTRODUCTION

The Italian fossil Primate record

The Italian Primate fossil record, although not extensive, hosts some outstanding samples. In the past, Italian paleontologists did not paid much attention to this mammal group. A look at the literature concerning the Italian primate record shows, in fact, a peculiar chronologic pattern: the largest amount of literature available on Italian fossil primate record dates from 1870's to the beginning of twentieth century with reports and descriptions of new findings (GERVAIS 1872; COCCHI 1872; FORSYTH MAJOR 1872a, 1872b, 1875, 1914; OTTOLENGHI 1898; SEGUENZA 1902, 1907; MERCIAI 1907; PORTIS 1917). Most of these studies have been made by researchers in Tuscan universities or Institutions. Especially Florence has been the center for the development of mammal paleontology in Italy, thanks to the collections of central Apennines basins including the extensive record of the Upper Valdarno, the type locality for *Macaca florentinus* (Cocchi, 1872). In addition, the industrial exploitation of Late Miocene lignites in several sites of southern Tuscany (among with the famous Montebamboli mine) produced the large sample of the fauna associated with *Oreopithecus bambolii* Gervais, 1872 (fig. 1).

After those first decades of enthusiastic interest, no Italian paleontologist has been working on the primate record for a long time. The only exception was the "first" scientific paper by a young Augusto Azzaroli (today in its 88, professor emeritus at the University of Florence) who described the endemic macaque from Sardinia (*Macaca majori*) in 1946. Since the late 1900's, a renovated interest on fossil primate record is "back in Tuscany" with a number of studies in paleoprimatology developed at the Florence University in the last decade (e.g. ROOK 1993, 1999; GENTILI et al. 1998; ROOK et al. 1996, 1999, 2001, 2004a, 2004b; MOYÁ SOLÁ et al. 1999 etc.).

The colloquium on European fossil Primate record

A colloquium on European fossil primate record has been organised within the 2008 "Giornate di Paleontologia" of the Italian Paleontological Society, aimed to offer to the scientific community an occasion to discuss the status of the art on the wide spectrum of studies centered on the fossil primate record. In addition, the coincidence of the 50th anniversary of the recovery of the *Oreopithecus bambolii* skeleton at Baccinello by J. Hürzeler (August 2nd 1958; ENGESSER 2000) was further an opportunity to celebrate one of the most intriguing primates of the European fossil record.

The workshop call, organized by the writer in collaboration with Sarah Elton (HYMS, Hull-York University, UK), received an enthusiastic interest within the scientific community. More than thirty researchers from various countries (Austria, France, Germany, Greece, Italy, Spain, United Kingdom, USA) attended the workshop.

The first scientific session of the meeting has been held on September 11th 2008 in Siena in the venues of the celebrated Accademia dei Fisiocritici. In this occasion invited and key lectures have offered an overview on the status of the art on European fossil primates studies and on new recent discoveries. Marc Godinot (Paris) presented an overview on the Paleogene primate record in Europe; David Martinez-Alba (Barcelona) offered an overview on the new impressive finds from the Late Miocene Catalan basins; Raymond L. Bernor (Washington DC) discussed the paleogeographic and paleozoogeographic context of fossil primate record in the Old World, focusing on the ongoing debate on the geographic origin of the African apes / Human clade; Paul O'Higgins (Hull-York) offered an overview of exciting results from innovative approaches developed in the field of functional morphology and biomechanics thanks to the use of new analytical methodologies like geometric morphometric and finite elements analyses; finally, Roberto Macchiarelli (Poitiers) presented the latest news

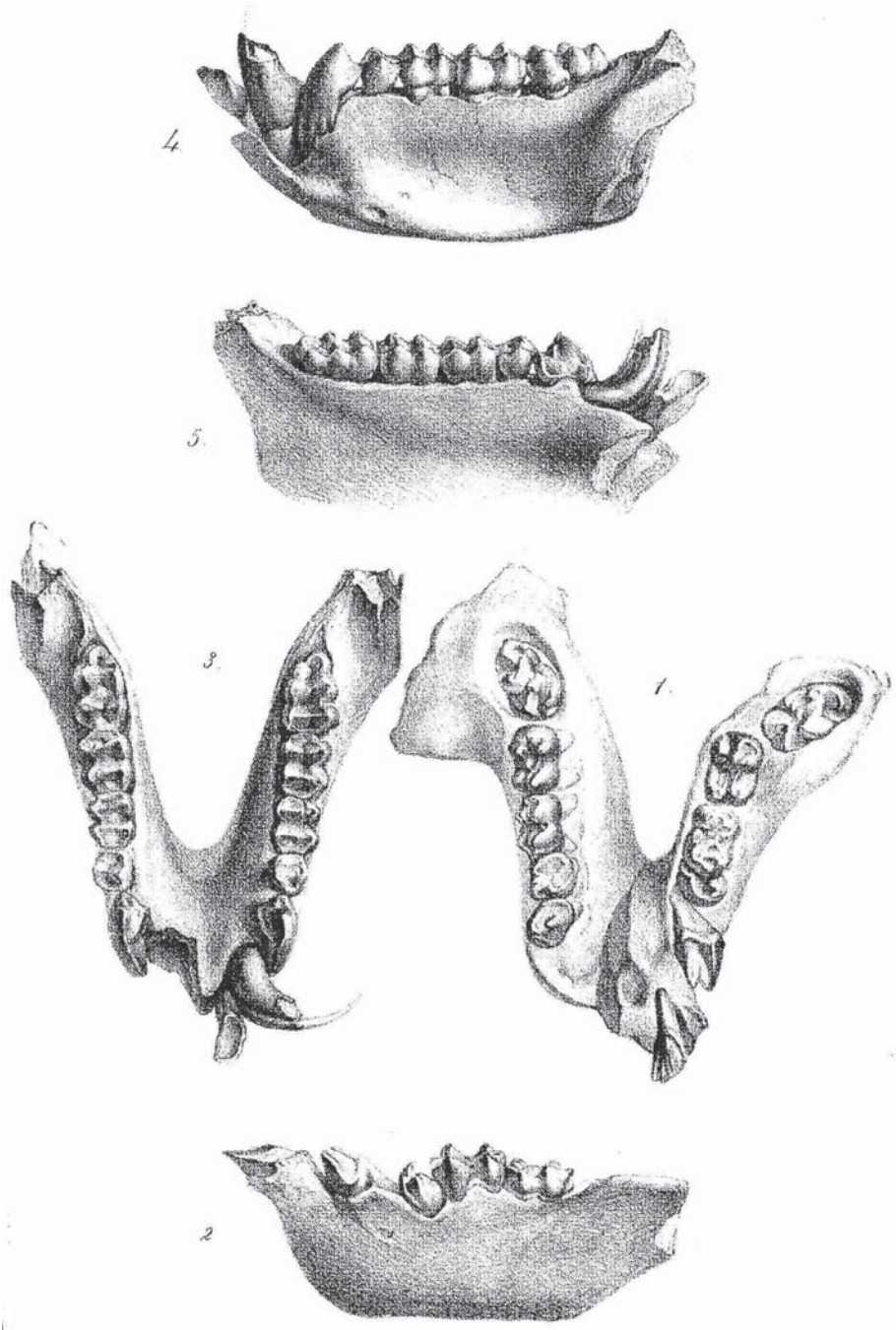


Fig. 1 – The type specimens of *Oreopithecus bambolii* Gervais, 1872 from Montebamboli (1-3) and of *Macaca florentinus* Cocchi, 1872 from Upper Valdarno (4-5) from the original plate by Igino Cocchi (1872).

on the study of *Oreopithecus bambolii* dental elements examined throughout the use of high-resolution microCTscan available at the “European Synchrotron Radiation Facility” in Grenoble (France).

The second day (September 12th 2008) the workshop moved to Grosseto in the venues of the renewed Museo di Storia Naturale della Maremma. Welcomed by Emilio Bonifazi (Town Major) and by Andrea Sforzi (Museum Director), participants appreciated visiting the new Museum exhibit with the life-sized 3D diorama of *Oreopithecus* in its reconstructed environment and enjoyed the warm hospitality offered by the town and by the Museum. The Museo di Storia Naturale della Maremma conference hall was a wonderful space for lectures and scientific discussion among participants. Podium and poster presentations were organised in different sessions: “Cercopithecoids”, “Hominoids: chronology and taphonomy”, and “Hominoids and Hominids: paleobiology, taxonomy and anatomy”.

On September 13th 2008, most of participants took part to a field excursion to the late Miocene outcrops of the Baccinello basin (fig. 2). Under the guidance of M. Benvenuti (Florence) and the writer, we visited the area and noted the main geologic and sedimentologic characteristics of the Baccinello sedimentary succession. Apart the small inconvenience of “hostile” weather at lunch time (a huge rain made wet the barbecue lunch offered by the Scansano town administration), the excursion has been the best way to conclude the workshop, highly appreciated by all the participants.

UPDATING THE ITALIAN FOSSIL PRIMATE RECORD

GENTILI et al. (1998) provided a summary of the Italian fossil primate record. Since then, a number of new discoveries and new studies have been published and an update is offered here. The fossil primates (other than *Homo*) from the Late Neogene (sensu LOURENS et al. 2004) of Italy belong to two superfamilies: Hominoidea and Cercopithecoidea. The first one is represented by the endemic *Oreopithecus bambolii*, while the second one is represented by three genera, the colobine *Mesopithecus* (Messinian to mid-Pliocene), and the cercopithecines *Macaca* (Pliocene-Late Pleistocene) and *Theropithecus* (Early Pleistocene).

Hominoidea

Oreopithecus bambolii

The occurrence of the peculiar large-bodied hominoid *Oreopithecus bambolii* and the associated endemic mammal fauna from several mines exploiting Late Miocene lignite deposits in southern Tuscany has been known since the nineteenth century (GERVAIS 1872; ROOK et al. 2000) (fig. 1). Among these localities, the geology and palaeontology of the Baccinello area are the best known, thanks to the efforts of J. Hürzeler (HÜRZELER 1958; LORENZ 1968) who recovered abundant faunal remains from different stratigraphic levels and the famous almost complete adult male of skeleton *O. bambolii*.

The Baccinello-Cinigiano basin consists of four biochronological units, spanning the Late Miocene (biochronologically calibrated between 9.5-8.7 Ma and 6.5-5.5 Ma). The oldest three units (V0, V1 and V2) represent an endemic fauna. Units V1 and V2 include *Oreopithecus* fossils. The youngest unit (V3) reflects a faunal turnover with the arrival of typical European fauna and the end of endemism, including the extinction of *Oreopithecus* (BENVENUTI et al. 1995, 2001; ROOK et al. 2000). In recent years, fieldwork activity has increased our knowledge of the geology and sedimentology of the area, allowing a better understanding of the sedimentary/environmental evolution of the basin (BENVENUTI et al. 1995, 2001), including the geochronological calibration with Ar/Ar dating of an ash layer identified within the sedimentary suc-

cession (ROOK et al. 2000). The chronological constraints of the basin chronology have been further improved through new palaeomagnetic research that allowed the placement of this succession in a firmer chronological placement and to better define the chronology of the *Oreopithecus*-bearing succession at Baccinello. Among other details, OMS et al. (2008) palaeomagnetic data support the hypothesis of *Oreopithecus* being the latest Eastern European Late Miocene ape, surviving well longer after the so-called “mid-Vallesian Crisis” (ROOK et al. 2000).

In addition to the localities from Tuscany classically related to the discoveries of *O. bambolii* and associated fauna, a new *Oreopithecus*-bearing site has been discovered in the early 1990s in Sardinia (ROOK et al. 2006; ABBAZZI et al. 2008). The site of Fiume Santo (Sassari) represents the most recent documentation available of the extinct insular fauna of the so-called Tusco-Sardinian palaeo-bioprovince (*Oreopithecus* Faunal Zone; cfr. BERNOR et al. 2001). The site yielded a rich assemblage of fossil vertebrates. About fifteen taxa have been identified, including the highly derived ape *Oreopithecus*, six bovids (including *Maremmia* and *Tyrrhenotragus*), the giraffid *Umbrotherium*, and the suid *Eumaiiochoerus*. The occurrence of these taxa characterises also the levels V0-V2 of the well-known Tortonian faunas (Turolian Mammal Age) from the Baccinello-Cinigiano basin in southern Tuscany. Since September 2001, the University of Florence is responsible for the excavation and study of the site and fauna. Preliminary results on the fossil vertebrate assemblage have been recently summarised by ROOK et al. (2006) and ABBAZZI et al. (2008).

Recent studies on the postcranial anatomy of this endemic hominoid (KÖHLER & MOYÁ-SOLÁ 1997; MOYÁ-SOLÁ et al. 1999, 2005; ROOK et al. 1999) re-launched the discussion on the peculiar adaptations of this fascinating insular fossil primate. Two opposing hypotheses have been proposed. The classical view holds that the basic orthograde pattern of *Oreopithecus* is an adaptation to climbing and below-branch locomotion (HARRISON 1987; SUSMAN 2004). The more recently proposed hypothesis suggests that *O. bambolii* shows, superimposed on these basic orthograde features, specific adaptation to bipedal locomotion (KÖHLER & MOYÁ-SOLÁ 1997; MOYÁ-SOLÁ et al. 1999; ROOK et al. 1999, 2004a). These adaptations have been interpreted in the context of evolution under insular conditions (MOYÁ-SOLÁ & KÖHLER 1997; KÖHLER



Fig. 2 – Participants on September 13th 2008 at the “Hürzeler’s bench” located within the small Baccinello public park. From left: Cornelia Fitsch, Sherry von Nelson, Jerome Prieto, Amanda Smith, George Koufos, Oriol Oms, Olga Panagiotopoulos, David Martínez-Alba, Gianni Gallai, Sergio Almécija, Marc Furiò, Marco Benvenuti, Jan van der Made, Isaac Casanovas-Villar, Lorenzo Rook, Flora Groening, Sarah Elton, Wendy Dirks, Raymond L. Bernor, Wolfgang Raba, Madleine Boeme, Marc Godinot, Nicole Preussner, Andrea Sforzi.

& MOYÁ-SOLÁ 2003).

In addition to postcranial anatomy, the dentition of *Oreopithecus bambolii* has been also a matter of discussion since the early descriptions by GERVAIS (1872) and SCHLOSSER (1887), who reported a number of resemblances to the cercopithecids for the permanent lower crowns. Later on, a reassessment of the *Oreopithecus* dental evidence in a broader evolutionary perspective has been performed, among the others, by HÜRZELER (1949, 1958), BUTLER & MILLS (1959) and SZALAY & DELSON (1979). As a whole, the majority of the studies have primarily considered external crown size and morphology, while only minor attention has been devoted to the *Oreopithecus* endostructural dental variation, notably in terms of tissue proportions (ANDREWS & MARTIN 1991; SMITH et al. 2003; OLEJNICZAK et al. 2004; ROSSI et al. 2004). These aspects are the focus of ongoing projects, whose results have been preliminarily presented at the first workshop on European fossil primate record (MACCHIARELLI et al. 2008).

The peculiar *Oreopithecus* cranial morphology has been also basis for different interpretations of *Oreopithecus* phylogenetic position. Some authors (BEGUN 1997, 2001; BEGUN & KORDOS 1997) consider it a relatively primitive ape, while MOYÁ-SOLÁ & KÖHLER (1997) and HARRISON & ROOK (1997) consider it to be a form more closely allied to *Dryopithecus* (now *Hispanopithecus*). ALBA et al. (2001a) explain this in further detail, with particular emphasis on MOYÁ-SOLÁ & KÖHLER's (1997) hypothesis that the cranium of *Oreopithecus* is paedomorphic.

Cercopithecoidea (Colobinae)

Mesopithecus

Mesopithecus is a small to medium-sized “colobine” monkey, known from the Late Miocene to the Early and Middle Pliocene deposits in Europe. The genus has its largest and outstanding record in several localities from Greece but it is also well known in a wider area, having been recovered from Late Miocene to Pliocene sites from Bulgaria (KOUFOS et al. 2003; DELSON et al. 2005), Romania (RADULESCU et al. 2003), Italy (ROOK 1999; PRADELLA & ROOK 2007), France (GERVAIS 1849; DELSON 1973, 1974), Germany (ANDREWS et al. 1996), Hungary (KORDOS 2000), Iran (ANDREWS et al. 1996), Afghanistan (HEINTZ et al. 1981) and Pakistan (HARRISON & DELSON 2007). A distinction is currently drawn between two species, which differ in their chronological range and body size (JABLONSKI 2002): the Late Miocene *Mesopithecus pentelicus*, and the smaller Pliocene *M. monspessulanus*. The later Pliocene species differs from *M. pentelicus* also by its narrower molars and less terrestrial adaptations. A third species, *M. delsoni*, has been described on some larger remains from the Late Miocene of Greece (BONIS et al. 1990; KOUFOS 2006; KOUFOS et al. 2004). Although the taxonomic status of the latter has been questioned (ZAPFE 1991; DELSON 1994; ANDREWS et al. 1996; ROOK 1999), recent studies based on new fossils from Bulgaria and Greece provide further evidence in favour of a specific distinction for this species (KOUFOS et al. 2003; KOUFOS 2006).

The latest Miocene Italian record of *Mesopithecus* has been described and discussed by ROOK (1999). The genus is present in several Messinian (MN 13) fauna; Baccinello V3 and Casino Basin in Tuscany, Monticino gypsum quarry (Brisighella) in Emilia-Romagna, and Gravitelli in Sicily. Specimens from Monticino quarry and Casino have been identified as *M. pentelicus*, while the sample from Gravitelli (re-examined only on the basis of the original literature), as well as the specimens from Baccinello V3, are not allocated at specific level (*Mesopithecus* sp.). The situation at Baccinello fits that reported for the latest Miocene sample from Ditiko (Macedonia, Greece; BONIS et al. 1990), with some specimens allocable to *M. pentelicus*, others to *M. monspessulanus*. All these finds could confirm the occurrence in the Mediterranean area of latest Miocene populations showing evidence of transition from *M. pentelicus* to *M. monspessulanus*. In light of the probable climatic instability in southern Europe

during the Messinian, the possibility of an evolutionary modification in (different?) populations of *Mesopithecus*, leading on one side toward the smaller-toothed *M. monspessulanus* and (perhaps) on the other toward the larger-bodied thus *Dolichopithecus* might well render more precise identification of local isolates problematical.

The last occurrence of the genus *Mesopithecus* within the Italian fossil record is reported in the early Villafranchian faunal assemblage of Villafranca d'Asti in north-western Italy (HÜRZELER 1967; PRADELLA & ROOK 2007). In this locality, *Mesopithecus* is associated with cercopithecoid remains belonging to the genus *Macaca* (ROOK et al. 2001). The Villafranca *Mesopithecus* specimens have been described by PRADELLA & ROOK (2007), within a study on the palaeoenvironmental context of *Mesopithecus* extinction, at the early–middle Villafranchian transition. The palaeoecological analyses show that the extinction of the genus is related to a faunal turnover and a change of the palaeoenvironment at the time of this biochronological transition (PRADELLA & ROOK 2007). This is consistent with the faunal turnover known as “Elephant-*Equus* event” (AZZAROLI 1983), that occurred at 2.5 Ma in Europe. Extinction of *Mesopithecus* coincides with one of the major shifts among the $\delta^{18}\text{O}$ isotopic oscillations (cf. MILLER et al. 2005) and this may support the suggestion that this taxon had woodland-oriented adaptations, particularly in association with the locomotory patterns inferred for *M. monspessulanus* (CIOCHON 1993).

Cercopithecoidea (Cercopithecinae)

Macaca

The Barbary macaque, *Macaca sylvanus* is nowadays distributed in North Africa and Gibraltar, although it was much more widely distributed throughout Europe during the Plio-Pleistocene (SZALAY & DELSON 1979; DELSON 1980; ARDITO & MOTURA 1987; FLADERER 1987), extending into Europe as far north as Untermassfeld in Germany (ZAPFE 2001) and Hoxne in the UK (SINGER et al. 1982). Its fossil record begins in the Late Miocene although, early fossil remains of this genus are rare (KÖHLER et al. 2000). Due to its conservative morphology, distinguishing fragmentary fossils of *Macaca* from other primitive papionins or defining a firm alpha-taxonomy is a difficult task. European fossil macaques are usually considered as belonging to the *M. sylvanus* lineage, but there is some uncertainty regarding their specific taxonomic status. Three subspecies are classically recognised in the fossil record of continental Europe: the Pliocene *M. sylvanus prisca* Gervais, 1859; the Late Pliocene to Early Pleistocene *M. sylvanus florentina* Cocchi, 1872 (fig. 1); and the Middle to Late Pleistocene *M. sylvanus pliocena* Owen, 1846 (SZALAY & DELSON 1979; DELSON 1980). No operational diagnoses for the several subspecies are available: according to DELSON (1980), *M. s. florentina* is basically comparable to *M. s. sylvanus* and larger than *M. s. prisca*, while *M. s. pliocena* is very close to *M. s. florentina* except for its “slightly wider” dentition (DELSON 1980). In most cases, the specific or subspecific designation of the fossil remains is only tentative until the taxonomic distinction between European Pleistocene macaques (*M. s. florentina* and *M. s. pliocena*) will be better clarified (ALBA et al. 2008).

Fossil remains attributable to the genus *Macaca* from the Italian continental Pliocene and Pleistocene deposits have long been known (COCCHI 1872; FORSYTH MAJOR 1872a; RISTORI 1890; PORTIS 1917) (fig. 1). Until recently, fossil remains were fragmentary and consisted only of cranio-mandibular fragments, isolated teeth or fragmentary postcranial bones (GENTILI et al. 1998; ROOK et al. 2001; MAZZA et al. 2005). This scarcity and the extremely conservative characters of the specimens made it difficult the above mentioned taxonomic assessment. An exception to this general picture of “patchy” and fragmentary Plio-Pleistocene macaque record is the outstanding sample from Early Pleistocene lignite deposits of Pietrafitta (Perugia, Umbria, Central Italy). This sample is made up by a total of about 80 fossils representing at

least 8 individuals. It includes isolated teeth, upper and lower jaws, a hip bone, hind limbs and tarsal bones. This important late Villafranchian sample has not yet been described in detail, although a preliminary description has been offered in GENTILI et al. (1998) and a few specimens have been made available for functional morphology studies (hip bone in MACCHIARELLI et al. 2001; mandibles in TINALLI & ROOK 2007).

Among the Middle Pleistocene record, SANZO & SARDELLA (2008) recently reported *Macaca* remains from two sites in Central Italy: several isolated teeth and postcranial bones at Casal Selce (Rome; dated to 0.6 Ma) and a fragmentary ulna at Fontana Ranuccio (Frosinone; dated approximately to 0.45 Ma). The preliminary analysis of the fossils, falling within the range of the living Barbary macaque (GENTILI & MOTTURA 2007), allows SANZO & SARDELLA (2008) to attribute the Middle Pleistocene remains to *Macaca sylvanus*.

The only clear extinct species within the European fossil record of the genus is the latest Pliocene to Early Pleistocene macaque from Sardinia, *Macaca majori* (AZZAROLI 1946; ROOK & O'HIGGINS 2005). The first suggestion of a primate occurring in the fossiliferous breccias at Capo Figari (north-eastern Sardinia, Italy) was made by DEHAUT (1911). Between 1910 and 1914, C.J. Forsyth Major recovered an abundant fossil assemblage from this locality through systematic excavation and among these fossils was a rich collection of primate remains which were classified as belonging to the genus *Macaca* by FORSYTH MAJOR (1913, 1914). The first detailed study of this *Macaca* assemblage was carried out by AZZAROLI (1946) who erected the new species *M. majori* as an endemic dwarf macaque. This species *M. majori* is represented by a large sample (quite an exceptional case for the fossil record of a primate): more than 250 specimens (most fragmentary) were recovered from the bone breccias at Capo Figari. In addition to Capo Figari, fossil remains of this species are known from two more sites: Is Oleris in the south-western part of the island (COMASCHI CARIA 1970) and the fissure fillings at Monte Tuttavista quarries in the area of Orosei (ROOK et al. 2003; ABBAZZI et al. 2004). *M. majori* is comparable in size with the smallest extant macaque species of insular and peninsular areas of south-eastern Asia and is characterized by reduced cranial dimensions, relative to body size, and, with regard to facial morphology, by a reduced anteroposterior palatal length, relative to extant species.

Since AZZAROLI's paper, no specific study has dealt with this species for a long time. DELSON (1974, 1975, 1980), JABLONSKI (2002) and especially SZALAY & DELSON (1979) cast doubts on the supposed insular dwarfism of this Sardinian macaque and consider this form as a subspecies of the extant macaque *M. sylvanus* (*Macaca sylvanus majori*). Recent studies focusing on morphology of the face in *M. majori* from Capo Figari (ROOK & O'HIGGINS 2005; SMITH et al. 2008) and from other Sardinian sites (MANTA et al. 2007) in a comparative ontogenetic context indicate that *M. majori* manifests a facial morphology no more similar to the extant *M. sylvanus* than to some Asian species. These analyses fail to indicate any aspects of facial morphology or ontogeny that particularly align this fossil taxon with its geographically nearest extant relative *M. sylvanus* (ROOK & O'HIGGINS 2005; MANTA et al. 2007). It is difficult from these findings to support the view that the fossils represent a subspecies of *M. sylvanus* (*M. sylvanus majori*) (SZALAY & DELSON 1979). Rather, the results point to a distinct specific status for the Sardinian fossil macaque. Furthermore, a new unique characteristic of *Macaca majori* has been recently evidenced in the dental eruption pattern (TINALLI & ROOK 2007). The tooth eruption sequence in *M. majori* has been traced using the maturation of the permanent teeth germs within the mandible. The observed permanent tooth eruption sequence of the P3-M1 shows a pattern apparently different from those available in literature for any extant species of the genus *Macaca* (TINALLI & ROOK 2007 and literature therein). The *M. majori* eruption pattern of permanent dentition is M1, P3 (and only later on M2), while in the extant *Macaca* species the pattern of permanent dentition eruption is M1, M2 and only later P3 (TINALLI & ROOK 2007 and literature therein). Since dental eruption sequence is considered very stable, the *M. majori* unique dental eruption pattern would stand as an unique case in

the patterning of dentition eruption among higher primates (and especially within the genus), and further characterise the life history of this endemic species.

A still open question is if the features of dental anatomy, facial morphology and facial ontogeny in *M. majori* are related to dietary adaptations. It is possible that these features represent an adaptation to the Early to Middle Pleistocene environments of Sardinia, and more detailed functional anatomical and palaeoecological analyses are called for. In order to provide the palaeoecological frame of *M. majori*, an ongoing project is focusing on dietary reconstructions through the study of stable isotopes in dental remains. Preliminary results on the phosphate carbonate values from *M. majori* teeth from Capo Figari indicate that the diet of these specimens was dominated by C₃ plants (MANTA et al. 2007).

Theropithecus

The genus *Theropithecus*, a typical African large-bodied baboon, is the latest primate to be identified in the Italian fossil record and its report has been object of a still open debate.

Theropithecus was widely distributed in Africa over the course of the Plio-Pleistocene (DELSON et al. 1993). The species *T. oswaldi* was one of the most abundant and widely distributed monkey species in Plio-Pleistocene Africa, identified from several localities from North (Algeria) to East (Ethiopia, Eritrea, Kenya) and South Africa (DELSON et al. 1993; MARTINEZ et al. 2004). Before the identification of a large cercopithecoid attributed to *Theropithecus* sp. indet. in Italy (ROOK et al. 2004b), fossils argued to be best attributed to *T. oswaldi*, *T. cf. oswaldi* or *Theropithecus* sp. had also been recovered outside Africa, from India (GUPTA & SAHNI 1981; DELSON 1993; PICKFORD 1993), Spain (GIBERT et al. 1995; MARTÍNEZ-NAVARRO et al. 2005, 2008) and the Middle East (BELMAKER 2002).

ROOK et al. (2004b) reported the discovery of three large primate cervical vertebrae from Pirro Nord, Italy (Early Pleistocene, late Villafranchian; ABBAZZI et al. 1996). On the basis of size comparisons with extant cercopithecoid primates, the authors concluded that the Pirro Nord cervical vertebrae represent a large cercopithecoid similar to, but substantially larger than extant *Theropithecus gelada*. These remains were attributed to *Theropithecus* sp. indet. (ROOK et al. 2004b: 272) on the basis of a discussion of the mammal fauna distribution and known biochronology of European faunal assemblages (GLIOZZI et al. 1997). As a consequence of ROOK et al. (2004b) reasoning, these fossils could be interpreted as evidence of an early dispersal of this genus out of Africa around 1.6–1.3 Ma, possibly coincident with an Early Pleistocene dispersal event of genus *Homo*. PATEL et al. (2007) question whether it is feasible to use primate cervical vertebrae to identify fossil *Theropithecus*, and criticise all the conclusions by ROOK et al. (2004b). PATEL et al. (2007) state that ROOK et al. (2004b) did not take into consideration the possibility that these specimens might belong to other large cercopithecoids present in the European penecontemporary fossil record: *Macaca*, *Dolichopithecus*, and *Paradolichopithecus*. While it is true that *Macaca* is widely spread in the European fossil record, from the latest Miocene to the Late Pleistocene (see previous section), its smaller dimensions make it an unsuitable candidate for the taxon represented by the Pirro Nord vertebrae. Conversely *Dolichopithecus* and *Paradolichopithecus* are potential candidates for these fossil vertebrae, but only in terms of their size. In fact, both genera had been excluded a priori from the analysis as they disappeared in Europe before the Plio-Pleistocene transition and there is no record of their persistence into the late Villafranchian (ROOK & MARTÍNEZ-NAVARRO in press). A further criticism of PATEL et al. (2007) is that “The biogeographic origin of the Pirro Nord vertebrae is further clouded by the fact that the rest of the Pirro Nord fauna are typical of Early Pleistocene Europe” (PATEL et al. 2007: 121). This statement, however, is not granted. In fact, while it is the case that Plio-Pleistocene

Eurasian large mammal assemblages are largely composed of taxa of Palaearctic origin (especially bovids and cervids) with some influence of Nearctic groups (such the single-toed equids of the genus *Equus*), the arrival of a very few rare species of Ethiopian origin is their most significant component. These rare species have, until recent times, been under-evaluated and hence under-appreciated. The Plio-Pleistocene transition (i.e., the middle to late Villafranchian transition of the European biochronology) marks a great change in mammalian assemblages of Eurasia, with some of the major taxa characterizing this faunal turnover being African in origin (MARTÍNEZ-NAVARRO 2004; MARTÍNEZ-NAVARRO & PALMQVIST 1995, 1996; MARTÍNEZ-NAVARRO et al. in press; PALMQVIST et al. 2007).

Finally PATEL et al. (2007) question whether *Theropithecus* remains can be used as possible faunal markers for the dispersal of hominins outside the African continent and, more specifically, whether *Theropithecus* was associated with the first hominins dispersing out of Africa around 1.8 Ma. In addition to a number of recent contribution on this matter available in the literature (TURNER & O'REGAN 2005; O'REGAN et al. 2006; HUGUES et al. 2008), the discovery of stone tools associated with the Pirro Nord faunal assemblage (ARZARELLO et al. 2006) is a strong argument supporting ROOK et al.'s (2004b) anticipation of this pattern of early *Homo* dispersal on the basis of faunistic considerations. The occurrence of *Theropithecus* associated with evidence of Early Pleistocene human presence at Pirro Nord, make this genus a fossil taxon relevant both as a faunal marker for fossil hominins outside of Africa, as well as in understanding the nature of out of Africa dispersal events at the Plio-Pleistocene transition that involved the genus *Homo*.

CONCLUSIVE REMARKS

Fossil catarrhines of Italy provide important documentation for the study of primate populations in Europe during the Neogene. The Late Miocene Italian record lacks most of the hominoids well represented in other parts of Europe (because of a peculiar palaeogeographic history; ROOK et al. 2006) and accounts only the endemic taxon, *Oreopithecus bambolii*. This "enigmatic" hominoid has been object in the recent years of a number of studies and of intense debate. Ongoing research on the anatomy of this species as well as on the palaeoecological, geological and chronological context will continue to provide new data on this endemic Italian primate. From the very Late Miocene (late Turolian, MN 13) onwards, in Italy cercopithecoids take the place of hominoids with no overlap in the fossil record. The Messinian record of the genus *Mesopithecus* seems to be consistent with the pattern of population fragmentation described in the much more exhaustive record of Greece. The last occurrence of the genus *Mesopithecus* is in the mid Pliocene (early Villafranchian) in the fauna of Villafranca d'Asti. The study of this material has been recently published with a palaeoecological analysis defining the extinction pattern of the genus. During Plio-Pleistocene times, the typical cercopithecoid present in the Italian fossil record is the genus *Macaca*. The continental record of this taxon (several subspecies of *M. sylvanus*) is currently included in the phylogenetic line that gave rise to the extant Barbary macaque. The most important sample of the late Villafranchian Italian record (Pietrafitta) has not yet been described in detail. The full study of this extremely rich sample is actually urgent since will provide crucial taxonomic and palaeobiological data of European Pleistocene fossil macaques. Conversely, the Sardinian endemic species *Macaca majori* has been object of a number of studies in the recent years, both because of the recovery of the new sample from Monte Tuttavista and because of the use of new analytical approaches to the study of its cranial anatomy. The latter has allowed to define unique ontogenetic and life-history characteristics for the Sardinian species. Further investigation on *M. majori* palaeobiology will likely continue to provide new evidence on this peculiar species.

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