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Research Article

Macaca sylvanus Linnaeus 1758 from the Middle Pleistocene of Quecchia quarry (Brescia, Northern Italy)

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Abstract

During the Plio-Pleistocene the Barbary macaque, *Macaca sylvanus* Linnaeus, 1758 was widely distributed throughout Europe and North Africa (Szalay and Delson, 1979; Delson, 1980; Rook et al., 2001), and it became extinct in Europe during the Late Pleistocene (Elton and O'Regan, 2014). Nowadays this primate is still present in North Africa and a small population has been reintroduced at Gibraltar (Modolo et al., 2005). The taxonomy of the Plio-Pleistocene European macaques is still debated but many authors agree in considering all the fossils as belonging to the *M. sylvanus* lineage, while the Pleistocene endemic *M. majori* Azzaroli, 1946 from Sardinia (Italy) has been considered a distinct valid species (Rook and O'Higgins, 2005). The occurrence of this species is documented from Late Pliocene to Late Pleistocene sites located in Northern and Central Italy. Here we describe unpublished dentognathic remains of *Macaca sylvanus* from the Middle Pleistocene site of Quecchia Quarry (Botticino, Brescia, North Italy).

Introduction

Fossil catarrhines of Italian peninsula provide important information for the study of primate populations in Europe during the Neogene. During the Pleistocene, the genus *Macaca* is the only cercopithecoïd which occurred in the Italian fossil record.

Nowadays the Barbary macaque, *Macaca sylvanus*, inhabits North Africa and Gibraltar, but it was widely distributed throughout Europe during the Plio-Pleistocene (Szalay and Delson, 1979; Delson, 1980; Ardito and Mottura, 1987; Fladerer, 1987; Alba et al., 2008). This primate expanded its range up to Northern Europe, in particular it was found in the large mammal assemblages of Untermassfeld (Germany; Zapfe, 2001) and Hoxne (UK; Singer et al., 1982).

European fossil macaques are usually considered as belonging to the *M. sylvanus* lineage, but there is some uncertainty regarding their specific taxonomic status. According to the literature three subspecies are 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 and Delson, 1979; Delson, 1980). No operational diagnoses for the different 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. In most cases, the specific or subspecific designation of the fossil remains is only tentative until the taxonomic distinction among European Pleistocene macaques (*M. s. florentina* and *M. s. pliocena*) is clarified (Alba et al., 2008). The only clear extinct species within the European fossil record of the genus is the latest Pliocene to Early Pleistocene endemic dwarf macaque from Sardinia,

Macaca majori (Azzaroli, 1946; Rook and O'Higgins, 2005). *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.

Fossil remains attributable to the genus *Macaca* from the Italian continental Pliocene and Pleistocene deposits have long been known (Cocchi, 1872; Forsyth Major, 1872; Ristori, 1890; Portis, 1917). Until recently, fossil remains were fragmentary and included only cranio-

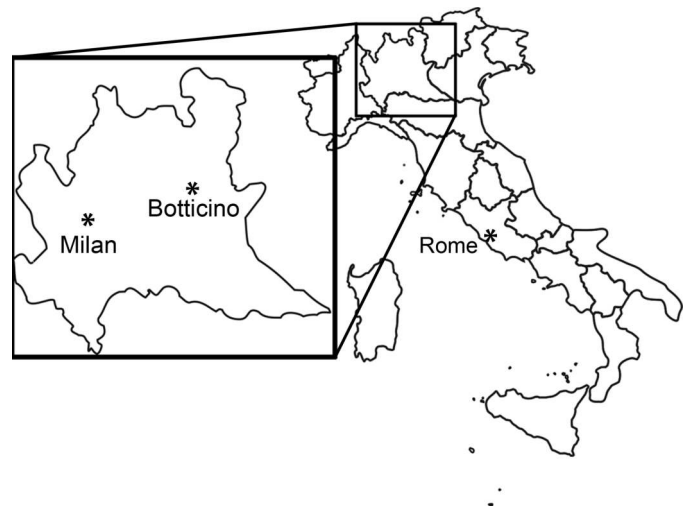


Figure 1 – Location map of the Botticino village located in the Eastern part of Lombardy (North Italy).

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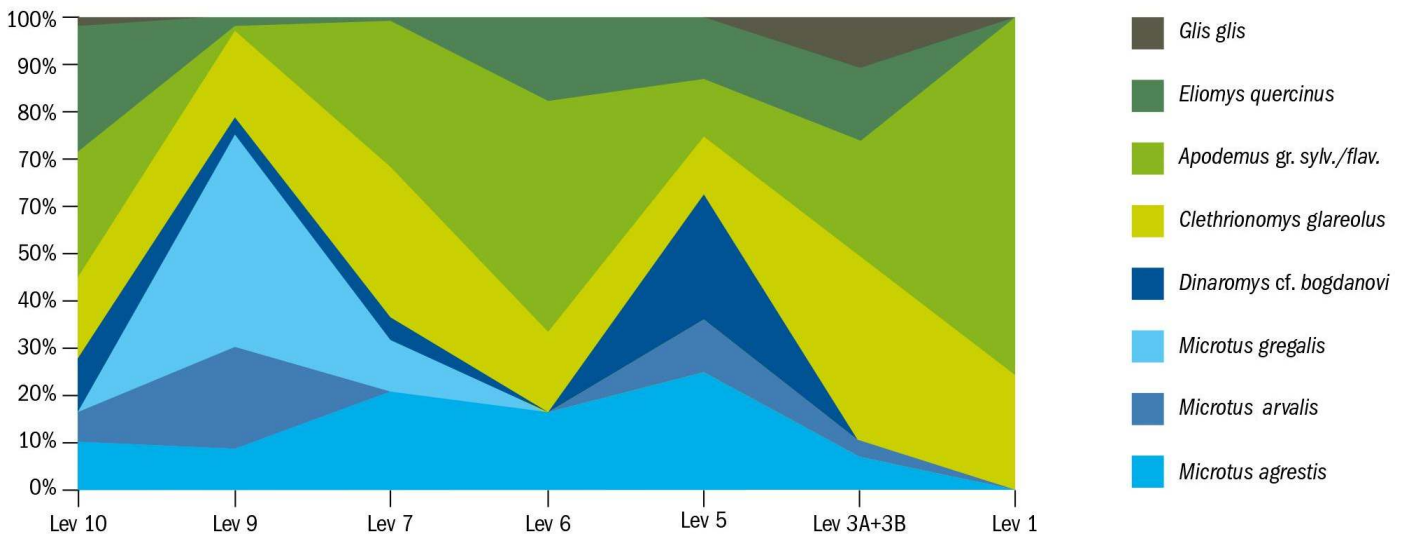


Figure 2 – Paleoecological and paleoclimatic implication of small mammal distribution along the stratigraphical sequences, with small mammals adapted to temperate and wooded environments in green and cold and open environments in blue.

mandibular fragments, isolated teeth or fragmentary postcranial bones (Gentili et al., 1998; Rook et al., 2001; Mazza et al., 2005). This situation and the extremely conservative characters of the specimens made it difficult to resolve the above-mentioned taxonomic assessment. An exception to this general picture of a “patchy” and fragmentary Plio-Pleistocene macaque record is the outstanding sample from Early Pleistocene lignite deposits of Pietrafitta (Perugia, Umbria, Central Italy) that, up to now, has been only partially described (Gentili et al., 1998).

In the Italian Late Pliocene/Early Pleistocene large mammal assemblages with *Macaca* remains have been found in the following sites: Villafranca d’Asti RDB (Rook et al., 2001); Orciano di Pisa (Ardito and Mottura, 1987); Casa Sgherri (Zanchetta et al., 1995); Upper Valdarno, Lower Valdarno and Barberino di Mugello (see Cocchi, 1872; Ristori, 1890; Szalay and Delson, 1979; Delson, 1980; Rook et al., 1997); Pietrafitta (Gentili et al., 1998); Monte Peglia (Basilici et al., 1991); Coste San Giacomo (Bellucci et al., 2012) and Zoppega II (Bon et al., 1991).

In the Italian Middle Pleistocene record, Sanso and Sardella (2008) recently reported *Macaca sylvanus* remains from two sites in Central Italy: several isolated teeth and postcranial bones at Casal Selce (Rome; dated to 0.6 Ma) and on fragmentary ulna at Fontana Ranuccio (Frosinone; dated approximately to 0.45 Ma). In addition an almost complete mandible from the Middle Pleistocene deposits of Monte Sacro (Roma) was discussed by Portis (1917). The author did not provide detailed stratigraphical information but in the area widely outcrop Middle Pleistocene deposits to be referred probably to MIS9 with early Aurelian faunal assemblages (see Kotsakis and Barisone, 2008, who indicates the locality with the term Casale Fiscale).

Here we describe the Barbary macaque fossil remains from Quecchia quarry (Botticino, Brescia, Lombardy). As pointed out before, due to the fragmentary nature of the *Macaca sylvanus* fossils in Italy, any new discovery is of great interest to increase the database related to this monkey. Moreover the fossils from Quecchia quarry were found in association with a diversified micromammal assemblage, which is of crucial importance to define the site’s biochronology and to reconstruct the paleoenvironmental changes in Northern Italy during the Middle Pleistocene. Only a few sites with a similar Toringian fauna, but without *Macaca* remains, are known: Grotta sopra Fontana Marella (Lombardy), dated more than 350000 years old (Bon et al., 2008); Boscochiesanuova (Veneto) (Bartolomei and Pasa, 1969) and San Giovanni di Duino (Friuli Venezia-Giulia) (Sala and Masini, 2007). At San Vito di Leguzzano (Bartolomei, 1965) was found a *Macaca* tooth with few small mammals of probably Toringian age.

Material and methods

The Barbary macaque fossil remains from Quecchia quarry consist of nine specimens reported in Tab. 2 and illustrated in Fig. 3. The material is stored in the Museo Civico di Scienze Naturali di Brescia (MC-SNBS). The main measurements are reported in Tab. 3, all the measures are taken following Alba et al. (2008). All the remains display the typical features of *Macaca sylvanus* (Szalay and Delson, 1979). The description of the dentognathic remains is illustrated below.

Geology and chronology

The *Macaca* remains were discovered in the karts fissure-fill deposits exposed at the Quecchia quarry (QQ) that is located near the village of Botticino (Brescia, Northern Italy) (Fig. 1). This area is well known for the exploitation of the renowned “Botticino Classico”, which is not a true marble but rather a Lower Jurassic limestone belonging to the “Corna” formation. This limestone is partially interested by the karstification (Schirrolli, 1997a,b).

In 2003 quarrymen unearthed at 233 m a.s.l. a karst fissure with a width of 14 m and filled by a stratified deposit including 11 levels. The complete stratigraphic sequence is referable to the Middle Pleistocene, according to the biochronological data of the small mammal assemblage (see Tab. 1). This is characterized by the occurrence of *Arvicola mosbachensis*, *Microtus (Terricola) gr. Multiplex-subterraneus*, *Pliomys coronensis* and *Microtus gregalis* (Tab. 1) (Sala and Masini, 2007). In addition, the analysis of the small mammals clarified the climatic fluctuations that occurred during the deposition of the sedimentary sequence. In particular an alternation of small mammals living in temperate and humid environments (levels 10, 6–7 and 1–3) with those more adapted to cold and open environments (levels 9 and 5) has been observed (Fig. 2). According to Masini and Sala (2011) and to the palaeoenvironmental figure (Fig. 2) the presence of *Pliomys coronensis* and *Arvicola mosbachensis* permits to interpret the level 9 as correlated to MIS 9, levels 6–7 to MIS 7e and levels 3A–3B to MIS 7a. The *Macaca* remains were unearthed in the levels 3A and 3B together with many large mammal remains that are still unpublished.

Description

Upper dentition

The upper dentition remains consist of a fragment of a left maxilla with P3/, P4/ and M1/ (MCSNBS PA11137); three canines (MCSNBS PA11138–39–40), and four M2/ (MCSNBS PA11141–42–43–44).

The crown of the upper canines is bucco-lingually compressed and displays a convex and bilobate mesial profile.

Table 1 – List of small mammals remains from Quecchia quarry along the stratigraphical sequence.

	Lev 1			Lev 3A+3B			Lev 5			Lev 6			Lev 7			Lev 9			Lev 10		
	n	MNI	MNI%	n	MNI	MNI%	n	MNI	MNI%	n	MNI	MNI%	n	MNI	MNI%	n	MNI	MNI%	n	MNI	MNI%
<i>Microtus (T.) gr. multiplex/subterraneus</i>				2	1	2.6	3	3	27.3	5	4	40.0	35	20	48.8	354	189	61.8	31	17	21.0
<i>Microtus agrestis</i>				4	2	5.3	2	2	18.2	1	1	10.0	8	4	9.8	12	6	2.0	8	5	6.2
<i>Microtus arvalis</i>				1	1	2.6	1	1	9.1							26	16	5.2	5	3	3.7
<i>Microtus gregalis</i>													4	2	4.9	58	32	10.5			
<i>Microtus sp.</i>	5	1	12.5	1	1	2.6									22	12	3.9	4	4	2.5	
<i>Arvicola mosbachensis</i>	14	3	37.5	10	3	7.9							1	1	2.4	11	4	1.3	16	6	7.4
<i>Clethrionomys glareolus</i>	1	1	12.5	35	12	31.6	2	1	9.1	2	1	10.0	10	6	14.6	68	13	4.2	17	9	11.1
<i>Pliomys coronensis</i>																14	3	1.0			
<i>Dinaromys cf. bogdanovi</i>							4	2	18.2							14	3	1.0			
<i>Apodemus gr. sylv./flav.</i>	4	3	37.5	13	6	15.8	1	1	9.1	3	3	30.0	8	6	14.6	2	1	0.3	36	14	17.3
<i>Eliomys quercinus</i>				14	4	10.5	1	1	9.1	1	1	10.0				2	1	0.3	21	13	16.0
<i>Glis glis</i>				9	3	7.9													1	1	1.2
<i>Talpa cf. caeca</i>				1	1	2.6													1	1	1.2
<i>Talpa cf. europaea</i>																			1	1	1.2
<i>Sorex cf. minutus</i>				2	2	5.3										16	10	3.3	5	5	3.7
<i>Sorex sp.</i>				2	2	5.3							1	1	2.4	23	12	3.9			
<i>Cf. Neomys</i>																1	1	0.3			
<i>Cricetus cricetus</i>																7	3	1.0			

The P3/ displays a sub-rounded shape whereas the P4/ has a sub-quadrangular shape. The M1/ has a bilophodont occlusal pattern and a sub-quadrangular shape, the mesial lobe becomes broader in the distal part and the buccal side is wider than the lingual one.

The M2/ show the same characteristics underlined for the M1/, but they are larger.

Lower dentition

The lower dentition is represented by the horizontal ramus of a right hemimandible MCSNBS PA11136. It is broken near the symphyseal midline; the half alveolus of the canine and the complete jugal dentition are present. The very low wear stage of the teeth suggests a young-adult individual.

The P/3 shows the typical development of the anterior and mesial side, the occlusal surface is sub-triangular and unicuspidate with the occlusal convex shape where the convex side is directed towards the buccal side. The P/4 is sub-rectangular, with a two cusped trigonid and a flat talonid.

The M/1 and M/2 display a more rectangular outline with the four cusps arranged, two by two, into two lophids. The two lobes are approximately equally wide, and the buccal cleft is much more conspicuous

than the lingual one. The lingual cusps are less rounded than the buccal ones. The mesial inter-cusps area is narrower than the distal one. The M/3 is a five cusped tooth with the typical bilophodont shape and shows a well-developed talonid.

Discussion

As outlined above, the taxonomic status of the *Macaca sylvanus* subspecies in the European Pleistocene record is still debated, and no operational diagnoses are now available (Alba et al., 2008); thus many scientists prefer to refer them to *Macaca sylvanus* with no subspecific designation.

We compared the upper and lower molars from Quecchia quarry with metrical data from selected European localities. In particular the upper M2/ mesiodistal length (MD) and buccolingual breadth (BL) has been compared with specimens from Early Pleistocene and Middle Pleistocene sites and with extant *M. sylvanus* individuals (both males and females average values from Mottura and Gentili, 2006). The lower M/2 has been compared with specimens from the Italian localities of Grotta degli Orsi Volanti (Late Pleistocene) and Upper Valdarno (Early Pleistocene) and from the Spanish site of Lezetxiki II (Middle/Late Pleistocene). According to our results (Fig. 4) the molars from Quecchia

Table 2 – List of *Macaca sylvanus* fossil remains from Quecchia quarry (Botticino, Lombardy, Italy).

Record no.	Description	Level	Pl./Fig.
MCSNBS PA11136	Right hemimandibular fragment with P ₃ -M ₃ (M ₁ crown slightly damaged)	3A	1/A-B-C
MCSNBS PA11137	Left maxillary fragment with P ³ -M ¹	3A	1/D-E
MCSNBS PA11138	Right Upper C	3B	1/S-T
MCSNBS PA11139	Right Upper C (crown apex broken)	3A	1/O-P
MCSNBS PA11140	Right Upper C	3A	1/Q-R
MCSNBS PA11141	Left M ²	3A	1/G-H
MCSNBS PA11142	Left M ²	3A	1/I-J
MCSNBS PA11143	Right M ²	3A	1/K-L
MCSNBS PA11144	Right M ²	3A	1/M-N

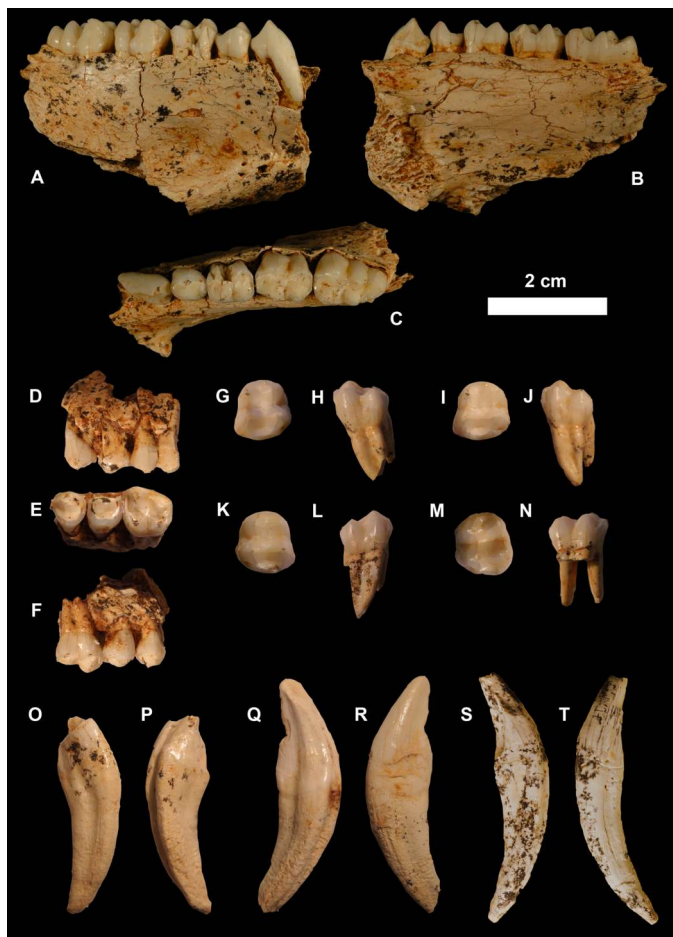


Figure 3 – *Macaca sylvanus* fossil remains from Quecchia quarry (Botticino, Lombardy, Italy). (A-C) right hemi-mandible fragment (MCSNBS PA11136) in (A) buccal, (B) lingual and (C) occlusal views. (D-F) left maxillary fragment (MCSNBS PA11136) in (D) buccal, (E) occlusal and (F) lingual views. (G-H) M² left (MCSNBS PA11141) in (G) occlusal and (H) lingual views. (I-J) M² left (MCSNBS PA11142) in (I) occlusal and (J) lingual views. (K-L) M² right (MCSNBS PA11143) in (K) occlusal and (L) lingual views. (M-N) M² right (MCSNBS PA11144) in (M) occlusal and (N) lingual views. (O-P) C^{sup} right (MCSNBS PA11139) in (O) mesial and (P) distal views. (Q-R) C^{sup} right (MCSNBS PA11140) in (Q) mesial and (R) distal views. (S-T) C^{sup} right (MCSNBS PA11138) in (S) mesial and (T) distal views.

Table 3 – Dental measurements (in mm) and breadth/length index (%) of *Macaca sylvanus* from Quecchia quarry (Botticino, Lombardy, Italy). MD=mesiodistal length; BL=buccolingual breadth; m=mesial lobe; d=distal lobe; BLI=breadth/length index: BL/MD×100; L=occlusal length of series of teeth. For all teeth BL is taken on maximum lobe length.

Record no.	Tooth	MD	BL(m)	BL(d)	BLI
MCSNBS PA11136	P ₃	6.9	5.3		76.8
MCSNBS PA11136	P ₄	6.1	5.6		91.8
MCSNBS PA11136	M ₁	7.7	6.5*	6.4	
MCSNBS PA11136	M ₂	9.5	7.8	7.0	82.1
MCSNBS PA11136	M ₃	12.1	8.2		67.8
MCSNBS PA11137	P ³	5.0	6.1		122.0
MCSNBS PA11137	P ⁴	5.3	5.3		100.0
MCSNBS PA11137	M ¹	7.8	7.7	/	98.7
MCSNBS PA11141	M ²	9.7	8.8	8.4	90.7
MCSNBS PA11142	M ²	9.3	8.6	8.0	92.5
MCSNBS PA11143	M ²	9.5	8.8	7.6	92.6
MCSNBS PA11144	M ²	9.6	8.6	8.4	89.6
MCSNBS PA11139	C ^{sup}	10.6	7.8		
MCSNBS PA11140	C ^{sup}	11.5	7.5		
MCSNBS PA11138	C ^{sup}	10.2	7.0		
MCSNBS PA11136	L _{P3-M3}	42.9			
MCSNBS PA11136	L _{P3-P4}	12.6			
MCSNBS PA11136	L _{M1-M3}	29.8			
MCSNBS PA11137	L _{P3-M1}	18.2			

* taken on mesial lobe.

quarry do not significantly differ from remains of macaques from Upper Valdarno (Mazza et al., 2005), Terrassa (Alba et al., 2008), Lezetxiki II cave (Castaños et al., 2011) and Grotta degli Orsi Volanti (Mazza et al., 2005).

On the basis of the lack of clear-cut taxonomic criteria defining the subspecies of *Macaca sylvanus* we prefer to refrain from attributing the remains from Quecchia quarry at the subspecies level, according to Montoya et al. (1999) and Zapfe (2001).

The occurrence at Quecchia quarry of rodents such as *Arvicola mosbachensis*, *Microtus (Terricola) gr. Multiplex-subterraneus*, *Pliomys coronensis* and *Microtus gregalis* suggest a Middle Pleistocene age for the assemblage (approximately between 0.5 to 0.3 Ma according to Sala and Masini, 2007). In addition, the co-occurrence of the Barbary macaque with these rodents in the 3A-3B levels is suggestive of mild-temperate palaeoclimate conditions and the occurrence of woodland in the region.

Macaca sylvanus remains have been recorded in northern and central Italian Middle Pleistocene sites, and the latest occurrence of the taxon is documented in the Late Pleistocene cave deposit at Grotta degli Orsi Volanti (Rapino, Pescara) (Mazza et al., 2005). The extinction of the Barbary macaque in Europe has to be considered in the framework of the large mammal turnover which occurred at the end of the Pleistocene with the loss of other large-bodied woodland-adapted mammals such as the straight-tusked elephant, *Palaeoloxodon antiquus*, and narrow-nosed rhinoceros, *Stephanorhinus hemitoechus* (Elton and O'Regan, 2014). As pointed out by Elton and O'Regan (2014) although *Macaca sylvanus* is now extinct, the climate in parts of present-day Europe may still be suitable for its survival, and the causes of its extinction need to be investigated in detail in further studies. The extinction of *Macaca sylvanus* in Europe might be related to: a) climate-induced vegetational changes; b) stochastic factors occurring as a result of small population sizes; c) and/or increased interaction and/or predation from *Homo*. ☞

References

- Alba D.M., Moyà-Solà S., Madurell J., Aurell P., 2008. Dentognathic remains of *Macaca* (Primates, Cercopithecidae) from the late Early Pleistocene of Terrassa (Catalonia, Spain). *J. Hum. Evol.* 55: 1160–1163.
- Ardito G., Mottura A., 1987. An overview of the geographic and chronologic distribution of west European cercopithecoids. *Hum. Evol.* 2: 29–45.
- Azzaroli A., 1946. La scimmia fossile della Sardegna. *Riv. Sci. Prehistor.* 1: 68–76. [in Italian]
- Bartolomei G., 1965. Primo rinvenimento di una scimmia pleistocenica nell'Italia Settentrionale e considerazioni sul significato ecologico. *Acc. Naz. Lincei* 38:533–536. [in Italian]
- Bartolomei G., Pasa A., 1969. La breccia ossifera di Boscochiesanuova nei monti Lessini (Verona): I depositi e la fauna. *Mem. Mus. Civ. St. Nat. Vr.* 17: 475–494. [in Italian]
- Basilici G., Farone A.G., Gentili S., 1991. Un nuovo reperto di *Macaca* nelle breccie ossifere pleistoceniche di Monte Peglia (Terni, Italia centrale) *Boll. Soc. Paleont.* 1. 30(2): 251–254. [in Italian]
- Bellucci L., Mazzini I., Scardia G., Bruni L., Parenti F., Segre A.G., Segre Naldini E., Sardella R., 2012. The site of Coste San Giacomo (Early Pleistocene, central Italy): Palaeoenvironmental analysis biochronological overview. *Quat. Int.* 267: 30–39.
- Bon M., Piccoli G., Sala B., 1991. I giacimenti quarternari di vertebrati fossili nell'Italia Nord-Occidentale. *Mem. Sc. Geol. Mem. Ist. Geol. Min. Univ. Pd.* 43: 185–231. [in Italian]
- Bona F., Sala B., Tintori A., 2008. Early Toringian small mammals fauna from Fontana Marella Cave (Varese, Lombardy, North Italy). *R. It. Pal. Strat.* 114: 133–144.
- Castaños P., Murelaga X., Arrizabalaga A., Iriarte M.-J., 2011. First evidence of *Macaca sylvanus* (Primates, Cercopithecidae) from the Late Pleistocene of Lezetxiki II cave (Basque Country, Spain). *J. Hum. Evol.* 60: 816–820.
- Cocchi I., 1872. Su di due scimmie fossili italiane. *Boll. Comitato Geol. Italia* 3: 59–71. [in Italian]
- Delson E., 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: Lindburg, D.E. (Ed.), *The Macaques. Studies in Ecology, Behavior and Evolution*. Van Nostrand, New York. 10–30.
- Elton S., O'Regan H., 2014. Macaques at the margins: the biogeography and extinction of *Macaca sylvanus* in Europe. *Quaternary Science Reviews*, 96: 117–130.
- Fladerer F.A., 1987. *Macaca* (Cercopithecidae, Primates) in the lower Pleistocene from Deutsch-Altenburg, Lower Austria. *Beitr. Paläot. Österr.* 13: 1–24.
- Forsyth Major C.L., 1872. Notes sur des singes fossiles trouvés en Italie, précédées d'un aperçu sur les quadrumanes fossiles en général. *Atti della Società Italiana di Scienze Naturali* 15: 79–95. [in French]
- Gentili S., Mottura A., Rook L., 1998. The Italian fossil primate record: recent finds and their geological context. *Geobios* 31: 675–686.
- Gervais P., 1859. *Zoologie et Paléontologie Françaises*. Bertrand, Paris. II, 2 vols. [in French]
- Kotsakis T., Barisone G., 2008. I vertebrati fossili continentali del Plio-Pleistocene dell'area romana. In: Funicello R., Praturon A., Giordano G., (Eds.), *La Geologia di Roma. Memorie Descrittive della Carta Geologica d'Italia*, 80: 115–143. [in Italian]

- Linnaeus C., 1758. Systema Naturæ. Laurentii Salvii, Holmiae. [in Latin]
- Masini F., Sala B., 2011. Considerations on an integrated biochronological scale of Italian Quaternary Mammals. *Il Quaternario* 24(2): 193–198.
- Mazza P., Rustioni M., Agostini S., Rossi A., 2005. An unexpected Late Pleistocene macaque remain from Grotta degli Orsi Volanti (Rapino, Chieti, central Italy). *Geobios* 38: 211–217.
- Modolo L., Salzburger W., Martin R.D., 2005. Phylogeography of Barbary macaques (*Macaca sylvanus*) and the origin of the Gibraltar colony. *PNAS* 102(20): 7392–7397.
- Montoya P., Alberdi M.T., Blázquez A.M., Barbadillo L.J., Fumanal M.P., van der Made J., Marin J.M., Molina A., Morales J., Murelaga X., Peñalver E., Robles F., Ruiz Bustos A., Sánchez A., Sanchiz B., Soria D., Szyndlar Z., 1999. La fauna del Pleistoceno Inferior de la Sierra de Quibas (Abanilla, Murcia). *Est. Geol.* 55: 127–161. [in Spanish]
- Mottura A., Gentili S., 2006. Cranio-mandibular biometrics and skull maturation of *Macaca sylvanus* L., 1758. *Hum. Evol.* 21: 223–239.
- Owen R., 1846. A History of British Fossil Mammals and Birds. John Van Voorst, London.
- Portis A., 1917. I primi avanzi di quadrumani del suolo di Roma. *Boll. Soc. Geol. It.* 35: 239–278. [in Italian]
- Ristori G., 1890. Le scimmie fossili italiane. *Boll. Regio Com. Geol. It.* 1: 178–196. [in Italian]
- Rook L., 1997. *Macaca sylvanus florentina* (Cocchi, 1872) from the Pleistocene Mugello basin (Northern Apennines, Italy). *Boll. Soc. Paleontol. Ital.* 35: 357–359.
- Rook L., Mottura A., Gentili S., 2001. Fossil *Macaca* remains from RDB quarry (Villafranca d'Asti, Italy): new data and overview. *J. Hum. Evol.* 40: 187–202.
- Rook L., O'Higgins P., 2005. A comparative study of adult facial morphology and its ontogeny in the fossil macaque *Macaca majori* from Capo Figari, Sardinia, Italy. *Folia Primatol.* 76: 151–171.

- Sala B., Masini F., 2007. Late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. *Quat. Int.* 160: 4–16.
- Sanso I., Sardella, R., 2008. *Macaca sylvanus* from the early Middle Pleistocene site of Cava di Breccia di Casal Selce (Roma). *Giornate di Paleontologia VIII edizione, Abstracts volume.* 144–146.
- Schirolli P., 1997a. La successione liassica nelle Prealpi cretacee centro-occidentali (Alpi Meridionali, Italia): stratigrafia, evoluzione paleogeografico-strutturale ed eventi connessi al *rifting*. *Atti Tic. Sc. Terra 6 (serie speciale):* 5–137. [in Italian]
- Schirolli P., 1997b. Il passato geologico della "terra dei marmi". L'evoluzione del paesaggio e l'assetto attuale. In: Porteri A., Simoni C. (Eds.) *Il marmo bresciano. Territorio, vicende, economia.* 13–44. [in Italian]
- Singer R., Wilff R.G., Gladfelter B.G., Wymer J.J., 1982. Pleistocene *Macaca* from Hoxne, Suffolk, England. *Folia primatol.* 37: 141–152.
- Szalay F., Delson E., 1979. *Evolutionary History of the Primates.* Academic Press, New York.
- Zapfe H., 2001. Zähne von *Macaca* aus dem Unterpleistozän von Untermassfeld. Teil 3. In: Kahlke, R.-D. (Ed.), *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen).* Dr. Rudolf Habelt GMBH, Bonn. 889–895. [in German]
- Zanchetta G., Petrucci S., Mazza P., Rustioni M., 1995. New Villafranchian finds from the lower Valdarno (Tuscany, central Italy). *Il Quaternario.* 8(2): 449–456.

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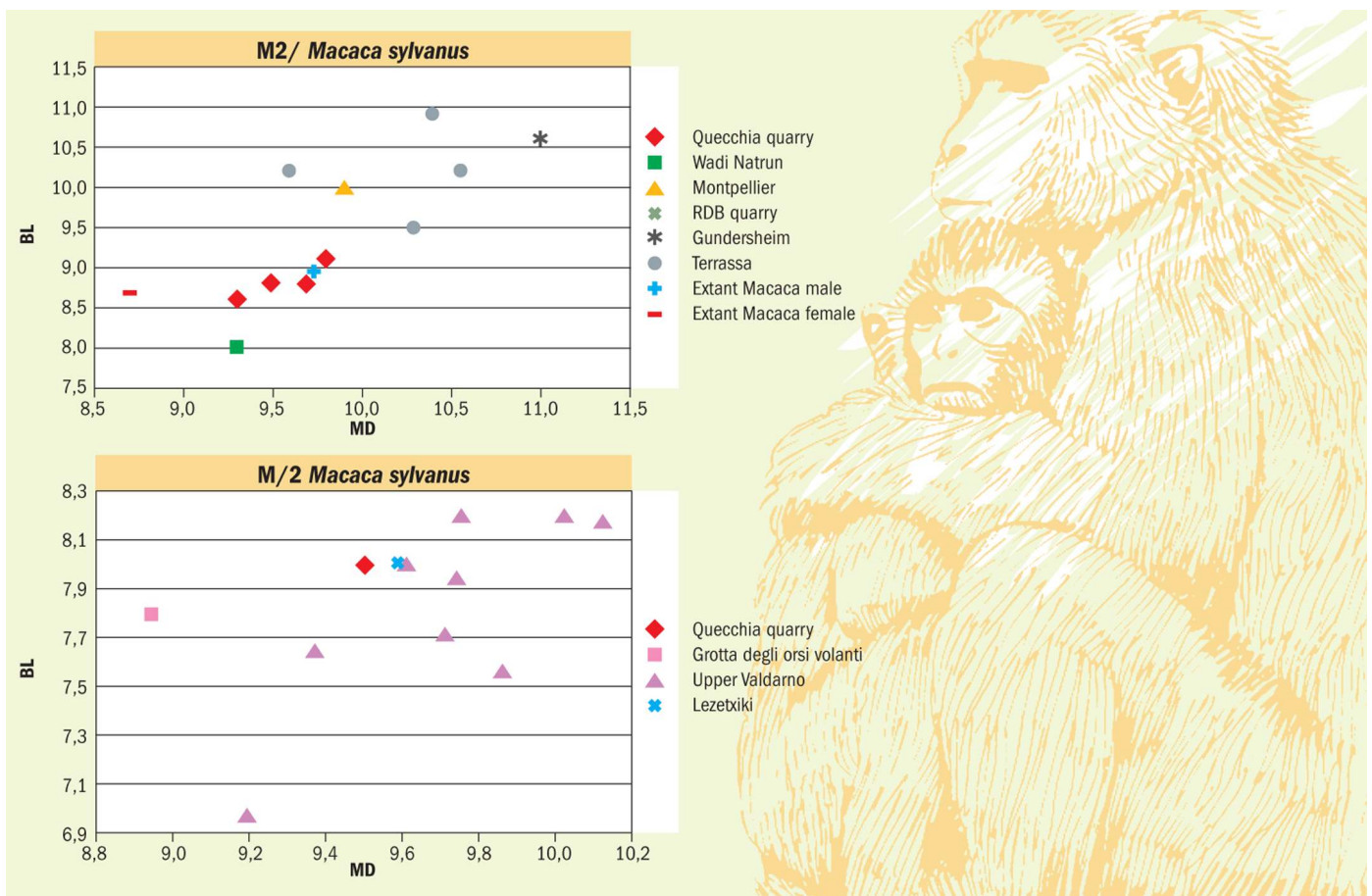


Figure 4 – Buccolingual breadth (mesial) vs. mesiodistal length scatter plot of M2/ of *M. sylvanus* from, in the upper graph, Lower Pleistocene localities with extant male and female (average values from Mottura and Gentili, 2006) and Quecchia quarry. In the lower graph M/2 of *M. sylvanus* from Valdarno (Mazza et al., 2005), Orsi Volanti (Mazza et al., 2005), Lezetxiki II (Castaños et al., 2011) and Quecchia quarry are plotted.