



ALMA MATER STUDIORUM
UNIVERSITÀ DI BOLOGNA

ARCHIVIO ISTITUZIONALE
DELLA RICERCA

Alma Mater Studiorum Università di Bologna Archivio istituzionale della ricerca

Macaca ulna from new excavations at the Notarchirico Acheulean site (Middle Pleistocene, Venosa, southern Italy)

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Beniamino Mecozzi, A.I. (2021). Macaca ulna from new excavations at the Notarchirico Acheulean site (Middle Pleistocene, Venosa, southern Italy). JOURNAL OF HUMAN EVOLUTION, 153, 1-7 [10.1016/j.jhevol.2020.102946].

Availability:

This version is available at: <https://hdl.handle.net/11585/806956> since: 2021-02-25

Published:

DOI: <http://doi.org/10.1016/j.jhevol.2020.102946>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).
When citing, please refer to the published version.

(Article begins on next page)

Macaca ulna from new excavations at the Notarchirico Acheulean site (Middle Pleistocene, Venosa, southern Italy)

Beniamino B. Mecozzi^{a,*}, Alessio Iannucci^a, Raffaele Sardella^a, Antonio Curci^b, Camille Daujeard^c and Marie-Hel  n  Moncel^c

^aDipartimento di Scienze della Terra, Sapienza Universit  di Roma, Italy, p.le Aldo Moro 5, 00185, Rome, Italy

^bDipartimento di Storia Culture Civilt , Universit  di Bologna, P.za S. Giovanni in Monte, 2, 40124

^cUMR 7194 HNHP (MNHN-CNRS-UPVD), D partement Homme et Environnement, Mus um National d'Histoire Naturelle, 1 rue Ren  Panhard, F-75013 Paris, France.

*Corresponding author.

Email address: Beniamino.mecozzi@uniroma1.it (B. Mecozzi)

Short Communications

Macaca ulna from new excavations at the Notarchirico Acheulean site (Middle Pleistocene, Venosa, southern Italy)

Keywords: Barbary macaque, anatomy; Cercopithecoidea; Mediterranean area

1. Introduction

1.1. *The taxonomy of European macaques*

The first records of macaques in Eurasia are from the latest Miocene fossiliferous sites of Almenara-Casablanca-M (Spain; Köhler et al., 2000) and Moncucco Torinese (Italy; Alba et al., 2014), yielding remains assigned to cf. *Macaca* sp. (Supplementary Online Material [SOM] Table S1). These data suggest that macaques likely dispersed out of Africa between 5.9 and 5.3 Ma, when the sea level dropped during the Messinian Salinity Crisis (Agustí et al., 2006; Alba et al., 2014, 2015; Colombero et al., 2017). Although there is consensus that the European fossil macaques belong to the *Macaca sylvanus* lineage (e.g., Alba et al., 2014, 2015; Bona et al., 2016), uncertainty persists regarding their specific taxonomic status.

European fossil remains of macaques are usually grouped in chronologically successive subspecies of *Macaca sylvanus*: the Pliocene *M. sylvanus prisca* Gervais, 1859; the late Pliocene to Early Pleistocene *M. sylvanus florentina* Cocchi, 1872; and the Middle-to-Late Pleistocene *M. sylvanus pliocena* Owen, 1846 (Szalay and Delson, 1979; Delson, 1980; Alba et al., 2008, 2011, 2016; Marigó et al., 2014; SOM Table S1). However, most of the taxonomic attributions are based on the chronology of the specimens, with only subtle differences recognized between *M. sylvanus* subspecies (Szalay & Delson, 1979; Delson, 1980; Alba et al., 2019). Indeed, fossil remains of *M. s. florentina* are considered larger than those of *M. s. prisca*, but close to extant specimens of *M. s. sylvanus* (Rook et al., 2001); whereas specimens of *M. s. pliocena* are nearly identical to those of *M. s. florentina*, except for slightly wider cheek teeth in the latter (Delson, 1980). Given the lack of adequate diagnostic characters, several attributions do not go beyond the species level (Montoya et

al. 1999; Zapfe, 2001). A second macaque lineage in Europe is represented by the extinct *Macaca majori*, an endemic primate from the Plio-Pleistocene of Sardinia (Italy; Rook & O'Higgins, 2005; Rook, 2009; Alba et al., 2014; Zoboli et al., 2016; SOM Table S1). The rich sample collected from Capo Figari, Monte Tuttavista and Is Oleris allows a clear diagnosis for this taxon (e.g., a short anteroposterior palatal length, reduced body size; see Zoboli et al. 2016).

1.2. Fossil macaques from the Italian record

Most of the Italian fossil primates were described from the 1870s to the beginning of the 1900s (Gervais, 1872; Cocchi, 1872; Forsyth Major, 1872a, b, 1875, 1914; Ottolenghi, 1898; Seguenza, 1902, 1907; Merciai, 1907; Portis, 1917). Nevertheless, this mammalian group was almost forgotten by Italian paleontologists during the last century, and as recently as in the last decades only a few studies have been published (Tozzi, 1969; Basilici et al., 1991; Rook et al., 2001; Mazza et al., 2005; Rook & O'Higgins, 2005; Rook, 2009; Zoboli et al., 2016; Bona et al., 2016).

Notably, one of the earliest occurrences of macaques in Europe is from Moncucco Torinese (dated approximately 5.41–5.33 Ma), where *Mesopithecus pentelicus pentelicus* is also documented (Alba et al., 2014; Colombero et al., 2017). Except for *M. majori*, the Italian Plio-Pleistocene record of macaques has been poorly investigated (Gentili et al., 1998; Rook, 2009). The Pliocene macaque from Villafranca d'Asti has been tentatively assigned to *M. s. prisca* (Rook et al., 2001), whereas the fossil remains from the Early Pleistocene are generally ascribed to *M. s. florentina*, from Italian sites including Barberino del Mugello, Monte Peglia, Pietrafitta, and Valdarno Superiore (Rook, 1997; Gentili et al., 1998; SOM Table S1). Many fossils recorded from the Middle Pleistocene sites of the Italian Peninsula are commonly referred to *Macaca sylvanus* ssp., but seldom described in detail (SOM Table S1). The latest occurrence of Barbary macaques from the Italian Peninsula is currently affirmed by the early Late Pleistocene of Grotta degli Orsi Volanti (Mazza et al., 2005; SOM Table S1).

Here, a fossil macaque from recent fieldwork at Notarchirico (Venosa basin, southern Italy), which represents the southernmost and easternmost occurrence of *Macaca* in the Italian fossil record, is described for the first time (Fig. 1).

1.3. Geological and paleontological context

The Notarchirico site, discovered in 1979, has yielded a 7 m-thick sequence of fluvial sediments within eleven archaeological levels (Figs. 1b–c). The early excavations yielded a rich fossil sample, including a hominin femur fragment in the upper part of the sequence (level α , Belli et al., 1991). The faunal assemblage, mainly collected from the upper part of the sedimentary succession, was attributed to the Isernia faunal unit (Sala et al., 1999). $^{40}\text{Ar}/^{39}\text{Ar}$ ages and electron spin resonance dates have revised the chronology of the entire sedimentary sequence and constrained between ca. 610 and 675 ka all the archaeological levels from the upper part of the sequence (levels A–F; Fig. 1b), excavated by M. Piperno in the 1980's (Pereira et al., 2015).

Since 2016, a new excavation campaign was initiated at Notarchirico (Moncel et al., 2019). New fieldwork focusing on the unknown base of the sequence permitted the team to recognize four additional units (G, H, I and J), all older than 668 ± 6 ka (Pereira et al., 2015; Moncel et al., 2019, 2020; Figs. 1b–c). The $^{40}\text{Ar}/^{39}\text{Ar}$ ages calculated for levels I and J (695.2 ± 6.2 ka and 690.3 ± 5.8 ka, respectively) are indistinguishable, suggesting a rapid deposition of the mainly fluvial sediments during MIS 17 and the transition to MIS 16 (Moncel et al., 2020). Among large mammals, the main faunal association includes *Palaeoloxodon antiquus*, *Hippopotamus antiquus*, *Dama* cf. *clactoniana* and *Bison schoetensacki*, among others. Cervids are dominant among the large mammals, whereas equids, rhinocerotids and carnivorans are absent. The mammal association indicates the presence of humid zones in a varied landscape and a relatively warm climate. Biochronologically, the mammal assemblage also permits the attribution of levels A and α , as well as the newly excavated levels G to I, to the Galerian period, consistent with the recent chronometric dating and lithic artefacts (Moncel et al., 2020). Levels G, H and I yield evidence of hominin occupations with artifacts including

bifaces in level G, pushing back the age of the earliest biface production (and the Acheulean) in Southern Europe (Moncel et al., 2020; but see also Walker et al., 2020).

2. Materials and methods

The macaque specimen from Notarchirico is a proximal fragment of a right ulna. The B24GNC specimen was recovered from the level G and will be accessioned at the laboratory of the Soprintendenza of Basilicata (it is temporarily stored at the laboratory of Museo Nazionale Archeologico di Venosa, Potenza, Basilicata; Figs. 1b–c).

To build our comparative dataset, we used measurements available from the literature on extant specimens of *M. s. sylvanus* (Table 1; Gentili et al., 1998; Rook et al., 2001). We also used morphological and biometric data on extant specimens of *M. s. sylvanus* housed at the Civic Zoology Museum of Rome and the Royal Belgian Institute of Natural Sciences, Brussels. In addition, we considered the fossil remains of *M. sylvanus* from Villafranca d’Asti (RDB quarry; Rook et al., 2001) and Pietrafitta (Gentili et al., 1998). We also collected measurements and included in the morphological analysis the Middle Pleistocene specimens of Barbary macaques from Fontana Ranuccio (FR; specimen 85, housed in the Italian Institute of Human Paleontology) and Cava di Breccia di Casal Selce-upper level (CS; specimen 520, housed in the PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome). As comparative taxa, we also considered fossil specimens of *Mesopithecus pentelicus pentelicus* from Moncucco Torinese (Alba et al., 2014) and Pikermi (Delson, 1973) and *Dolichopithecus ruscinensis* from Perpignan and Pestzentlorinc (Delson, 1973).

Measurements of greatest breadth of the olecranon (OB), greatest breadth across the anconeal process (APB), greatest breadth across the coronoid process (CPB), greatest height of olecranon fossa (HOF) and greatest depth across the anconeal process (APD), were taken with a digital caliper to the nearest 0.1mm (Table 1; Fig. 2; SOM Table S2).

3. Description and comparisons

MNAV B24GNC is the proximal portion of a well-preserved right ulna, including about one-fourth of the shaft (Fig. 1d–f). Medially, the olecranon is relatively high, with the anterior border higher than the posterior one; its rough surface delineates the insertion area of the triceps brachii, brachialis and flexor carpi ulnaris muscles (Fig. 1d). In anterior view, the olecranon is mediolaterally compressed and its medial and lateral crests are similarly developed, separated by a shallow groove (Fig. 1e). Laterally, the inner spongy bone of the olecranon is visible due to weathering, which obscures the attachment area of the flexor carpi ulnaris muscle, in the proximal portion, and the epitrochleo-anconeus muscle, along the distal border (Fig. 1f). In medial view, at the level of the trochlear notch, the shaft surface is rough, which indicates the attachment area of the flexor carpi ulnaris and extensor pollicis longus muscles. The anconeal process ends in a marked crest anteroposteriorly directed in medial view; its anterior border is distolaterally inclined in anterior view; its process is robust and anteriorly projecting in lateral view. The trochlear notch is quite reduced and its opening is semicircular in shape in medial and lateral views, whereas it is medio-laterally wide in anterior view with a straight medial and a curved lateral outline. The coronoid process is robust and projects anteriorly in medial and lateral views. The radial notch is well developed, and its posterior border extends to half the shaft width in medial view. Anteriorly, the radial notch is strongly concave, the border is inclined medially, and the facet is butterfly-shaped (according to Harrison, 1989).

Despite the fragmentary nature of the specimen, its taxonomic identity as *Macaca* can be inferred from the morphology of the proximal epiphysis of the ulna is highly diagnostic. The overall morphology of the ulna from Notarchirico resembles the fossil remains of *M. s. cf. prisca* from Villafranca d’Asti (NMB V.J. 130; Rook et al., 2001), *M. s. florentina* from Pietrafitta (IR-1703; Gentili et al., 1998), *M. sylvanus* ssp. from Casal Selce (CS 520) and Fontana Ranuccio (FR 85), and extant specimens of *M. sylvanus* (Harrison, 1989) in several features, including a relatively long and straight olecranon with the anterior border higher than the posterior one in lateral and medial

views; wide surface of articulation with the radius in lateral view; anteriorly-protruding anconeal process and coronoid process in lateral and medial views. The Notarchirico specimen differs from *Me. pentelicus* in the shape of the olecranon (i.e., a straight proximal outline in lateral and medial views), and in the profile of the trochlear and radial notches (i.e., less anteriorly-directed anconeal and coronoid processes in lateral and medial views and less developed articular surface with the radius in lateral view; Delson, 1973; Alba et al, 2014). Compared to *Dolichopithecus rusciniensis* from Perpignan and Pestzentlorinc (Delson, 1973), the Notarchirico ulna differs in having an anteriorly-protruding coronoid process in lateral and medial views, the anterior border of the olecranon higher than the posterior one in lateral and medial views and a larger radial notch in lateral view. The ulnae of the extant colobines differ from that of Notarchirico since those possess an anterior concavity of the proximal shaft and a retroflected olecranon in lateral and medial views (Rose 1998; Egi et al., 2007). The ulnar morphology of *M. sylvanus* is strongly related to that of the distal epiphysis of the humerus (with which it forms the humeroulnar joint), and is linked to its quadrupedal locomotion, with the close-pack position of the elbow providing high stability during parasagittal movements (Rose, 1988).

The absolute and relative size of the macaque ulna from Notarchirico (Table 1) was compared with those of other extinct and extant macaques and *Me. pentelicus* in Figure 3. The values of the CPB of the fossil specimens fell within the range of variation of the extant Barbary macaque, with the exception of the Notarchirico fossil, which displayed the absolutely largest CPB among the analyzed sample (Fig. 3a). Figure 3b shows HOF relative to CPB for the fossil specimens of *M. sylvanus*, with the ulna from Notarchirico occupying the extreme right of the plot (with the largest CPB) and that from RDB quarry with the lowest HOF value. Furthermore, the fossil of *Me. pentelicus pentelicus* from Moncucco Torinese shows different proportions of the ulna, with a similar CPB value, but a higher HOF compared with those of the fossil *M. sylvanus* (Fig. 3b). However, given the range of variation and the limited sample available for extinct *M. sylvanus* and *Me. pentelicus pentelicus*, more data are needed to confirm this relative size separation.

4. Discussion and conclusion

4.1. Taxonomy

In the last several decades, studies have focused on the description of fossil macaques, involving both new finds and revisions of earlier collections. Most of the available material of *M. sylvanus* consists of mandibular and maxillary remains, which are very similar to the extant North African subspecies. Following the proposal by Szalay and Delson (1979) and Delson (1980), fossil European macaques are often grouped in three temporal-geographic subspecies of *M. sylvanus*, but the reliability of this division is debated (e.g., Rook et al., 2001; Alba et al., 2008, 2018, 2019; Bona et al. 2016). Indeed, due to the lack of clear-cut morphological criteria, identifications are often either based on chronology (e.g., Alba et al., 2016, 2018, 2019) or limited to *M. sylvanus* ssp. (e.g., Montoya et al., 1999; Zapfe, 2001).

Moreover, the unresolved taxonomy is based solely on craniodental remains. Indeed, postcranial remains are limited to a few finds across Europe, such as those from Untermassfeld (Zapfe, 2001), Deutsch-Altenburg (Fladerer, 1987) and Sierra de Quibas (Alba et al., 2011). Apart from the Italian specimens, other macaque ulnae have been recorded from Swanscombe and Senèze (Singer et al., 1982), but the material was not described or figured. The morphological analysis conducted in the current study, although limited in scope, reveals a strong affinity between the studied material and the fossil and extant specimens of *M. sylvanus* (Harrison, 1989; Gentili et al., 1998; Rook et al., 2001), while at the same time emphasizing the differences with *Me. pentelicus pentelicus* (Delson, 1973; Alba et al, 2014), *Dolichopithecus ruscinensis* (Delson, 1973) and extant colobines (Rose, 1988). Biometrically, the specimens from the Middle Pleistocene sites of the Italian Peninsula fall within the range of variation of the extant Barbary macaque. The ulna from Notarchirico is slightly larger than the other analyzed specimens, but considering the restricted sample, these differences may not be significant. Nevertheless, the studied ulna of *Me. pentelicus pentelicus* has different proportions, especially in the relatively higher olecranon fossa, compared

with that of extant and extinct Barbary Macaques. Thus, considering the lack of diagnostic features for macaque subspecies, and the paucity of primate fossil postcranial material, we ascribe the ulna from Notarchirico to *Macaca* sp., avoiding the taxonomical attribution based on chronological grounds. A more comprehensive analysis is needed to clarify the alpha-taxonomy of extinct *M. sylvanus* subspecies (e.g., Bona et al., 2016; Alba et al., 2018, 2019).

4.2. *Paleoenvironment*

The macaque from Notarchirico was recovered from level G, associated with fossil remains of *Palaeoloxodon antiquus*, *Hippopotamus antiquus* and *Bison schoetensacki* (Moncel et al., 2020). Although only a few mammalian species were identified, these taxa indicate the presence of open forest, bodies of water, and warm climatic conditions. Considering the revised chronology of the site, this very likely indicates the end of MIS 17 (Moncel et al., 2019, 2020). The extant Barbary macaque inhabits a variety of environments from shrublands to evergreen forests, and even herbaceous-dominated rocky ridges (Fooden, 2007, and references therein). The presence of arboreal vegetation is nonetheless a limiting factor, since the Barbary macaque requires trees for sleeping, feeding, and escaping from predators (Delson, 2004; Fooden, 2007). In addition, it needs to be near water (Masseti and Bruner, 2009). Thus, the ecological preferences of the Barbary macaque are compatible with the presence at Notarchirico of wooded and wet areas previously suggested by Moncel et al. (2020).

4.3. *Paleobiogeographic and taphonomic implications*

During the Pleistocene, European representatives of macaque subspecies mainly occurred in the Mediterranean area, being probably bound by both climatic and latitudinal factors (Ardito and Mottura, 1987; Elton and O'Regan, 2008; Fig. 4). Indeed, a Mediterranean climate, with warm dry summers and relatively wet winters, also characterizes the current distribution range of the extant Barbary macaque populations, even though the species can tolerate winter snow at high elevations

(Delson, 2004; Fooden, 2007). Considering the known ecological tolerance, a strong relationship between the areal expansion and Plio-Pleistocene climatic fluctuations for the extinct *M. sylvanus* subspecies has been hypothesized (Fooden, 2007; Elton and O'Regan, 2008). According to this idea, the European fossil macaques extended their geographical ranges to much higher latitudes during the interglacials, whereas they retreated into Mediterranean glacial refugia during cold episodes (Fooden, 2007; Elton and O'Regan, 2008). The past distribution of the Barbary macaque indicates that this primate was widespread along the Mediterranean coasts of Europe, especially in the Italian and Iberian peninsulas (Fig. 4). By contrast, the presence of Barbary macaques in central Europe, as well as in Britain, has only been documented from deposits chronologically referred to as an interglacial stage (Fig. 4). An exception is the Late Pleistocene site of Hunas (Germany; Rosendahl et al., 2011), where Barbary macaque remains were found in levels K–H (MIS 4), therefore representing the only occurrence in central Europe during a glacial episode. As shown in Figure 4, the presence of the macaque at Notarchirico is the southernmost and easternmost known in Italy.

At Notarchirico, the co-occurrence of macaques and hominins is documented (Moncel et al., 2020), as in some other fossiliferous deposits (e.g., Gruta da Aroeira, Lezetxiki II and Grotta degli Orsi Volanti). Faunal remains from levels F to I of the recent fieldwork are generally highly affected by abrasion (trampling and hydraulic transport), and bone surfaces are poorly preserved. Therefore, even though neither cut marks nor other anthropic percussion marks have been observed, this could be a mere lack of documentation. However, despite a relatively good state of surface preservation (moderate abrasion), the macaque ulna shows no cut marks. Similarly, the ulna from Fontana Ranuccio was found associated with lithic artifacts (Segre & Ascenzi, 1984; Strani et al., 2018), but there is no indication of human exploitation.

Despite the widespread distribution of the Barbary macaque in Europe throughout the Pliocene and Pleistocene, the fossil record of this taxon is limited. The majority of the documented specimens in Europe are isolated teeth, and there are relatively few postcranial elements. Plio-

Pleistocene *Macaca sylvanus* likely could have inhabited both deciduous and coniferous forest, but could also have been adapted to transitional environments.

The European macaque became locally extinct in the early Late Pleistocene. Elton and O'Regan (2014) pointed out that its extinction may be related to vegetation change or increased predation from *Homo*, but also to stochastic factors occurring as a result of small population sizes. The early Late Pleistocene extinctions also included some megafauna (*Palaeoloxodon antiquus*, *Hippopotamus amphibius*, and *Stephanorhinus hemitoechus*), which can be related to the lowering of global and regional temperatures in the Last Glacial period that caused reduction in forest cover. Another plausible factor is the influence of hominins. Clearly the potential *Homo-Macaca* interactions during the Pleistocene deserve more attention from both paleoecological and archaeozoological viewpoints. During the Pleistocene in Europe, *Macaca sylvanus* co-existed alongside earlier *Homo* species for over one million years, but the Barbary macaques became extinct before the earliest occurrence of *Homo sapiens* in Europe (Elton and O'Regan, 2014). Modern *Macaca sylvanus* distribution is negatively affected by human occupation (e.g., Ménard et al., 2014). In many Middle and Late Pleistocene sites, hominins and macaques were found together, especially in resource-limited environments. Although there is currently no evidence in the paleontological literature, a possible scenario where *Homo* included primates in its diet cannot be ruled out (Meloro and Elton, 2012). The environmental context given by this find of macaque provides informative data on the climatic conditions of the hominin occupations and the vegetational environments where hominins able to produce the earliest bifaces in southern Italy lived.

Acknowledgments

This work was made possible thanks to the financial and scientific support of the Leakey Foundation ('Early Evidence of Acheulean bifacial technology in Europe' grant, 2015–2016) and the National Museum of Natural History, Paris, France (ATM Action Transversale du Muséum,

2016–2018). We are indebted to the Soprintendenza of Basilicata (Italy) for the agreement to study fossil collections of the site of Notarchirico, especially T.E. Cinquantaquattro, F. Canestrini, R. Pirraglia, and S. Mutino. We thank the Venosa Museum and A. Mantrisi for their assistance. We are grateful to R. Carlini (Civic Zoology Museum of Rome) and O. Pauwels (Royal Belgian Institute of Natural Sciences, Brussels) for their support of the study of the comparative material. The authors thank L. Bellucci, J. Conti, D.A. Iurino and F. Strani for their useful suggestions and support. We are indebted to Eric Delson for the English revision of the submitted work. We thank Eric Delson and two anonymous reviewers, the Associate Editor and Editor-in-Chief Andrea B. Taylor for their helpful comments and suggestions, which were crucial to substantially improving our manuscript.

References

- Abbazzi, L., Angelone, C., Arca, M., Barisone, G., Bedetti, C., Delfino, M., Kotsakis, T., Marcolini, F., Palombo, M.R., Pavia, M., Piras, P., Rook L., Torre, D., Tuveri C., Valli A.M.F., Wilkens B., 2004. Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, E. Sardinia, Italy), an overview. *Rivista Italiana di Paleontologia e Stratigrafia* 110(3), 681–706
- Adam, K.D., 1963. *Mittelpleistozane Säugetier Fauna aus dem Heppenloch bei Gutenberg (Württemberg)*. Stuttg. Beitr. Naturk. Set B 3, 1–247.
- Agustí, J., Garcès, M., Krijgsman, W., 2006. Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 5–14.
- Alba, D.M., Moyà-Solà, S., Madurell, J., Aurell, J., 2008. Dentognathic remains of *Macaca* (Primates, Cercopithecidae) from the late early Pleistocene of Terrassa (Catalonia, Spain). *J. Hum. Evol.* 55, 1160–1163.
- Alba, D.M., Carlos Calero, J.A., Manchēno, M._A., Montoya, P., Morales, J., Rook, L., 2011. Fossil remains of *Macaca sylvanus florentina* (Cocchi, 1872) (Primates, Cercopithecidae) from the Early Pleistocene of Quibas (Murcia, Spain). *J. Hum. Evol.* 61, 703–718.

- Alba, D.M., Delson, E., Carnevale, G., Colombero, S., Delfino, M., Giuntelli, P., Pavia, M., Pavia, G., 2014. First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. *J. Hum. Evol.* 67, 1–18.
- Alba, D.M., Montoya, P., Pina, M., Rook, L., Abella, J., Morales, J., Delson, E., 2015. First record of *Mesopithecus* (Cercopithecidae, Colobinae) from the Miocene of the Iberian Peninsula. *J. Hum. Evol.* 88, 1–14.
- Alba, D.M., Madurell-Malapeira, J., Delson, E., Vinuesa, V., Susanna, I., Espigares, M.P., Ros-Montoya, S., Martínez-Navarro, B., 2016. First record of macaques from the early Pleistocene of Incarcal (NE Iberian Peninsula). *J. Hum. Evol.* 96, 139–144.
- Alba, D.M., Delson, E., Morales, J., Montoya, P., Romero, G., 2018. Macaque remains from the early Pliocene of the Iberian Peninsula. *J. Hum. Evol.* 123, 141–147.
- Alba, D.M., Daura, J., Sanz, M., Santos, E., Yagüe, A.S., Delson, E., Zilhao, J., 2019. New macaque remains from the Middle Pleistocene of Gruta da Aroeira (Almonda karst system, Portugal). *J. Hum. Evol.* 131, 40–47. doi.org/10.1016/j.jhevol.2019.02.003
- Anzidei, A.P., Bulgarelli, G.M., Catalano, P., Cerilli, E., Gallotti, R., Lemorini, C., Milli, S., Palombo, M.R., Pantano W., Santucci, E., 2012. Ongoing research at the late Middle Pleistocene site of La Polledrara di Cecanibbio (central Italy), with emphasis on human–elephant relationships. *Quat. Int.* 255, 171–187.
- Ardito, G., Mottura, A., 1987. An overview of the geographic and chronologic distribution of west European cercopithecoids. *Hum. Evol.* 2, 29–45.
- Belli, G., Belluomini, G., Cassoli, P.F., Cecchi, S., Cucarzi, M., Delitala, L., Fornaciari, G., Mallegni, F., Piperno, M., Segre, A.G., 1991. Découverte d'un fémur acheuléen à Notarchirico (Venosa, Basilicate). *L'Anthropologie* 95(1), 47–88.

- 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.
- Blasco, R., Peris F., Rosell J., 2008. Human consumption of tortoises at Level IV of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 2839-2848
- Bon, M., Piccoli, G., Sala, B., 1991. I giacimenti quaternari di vertebrati fossili nell'Italia Nord Occidentale. *Mem. Sc. Geol. Mem. Ist. Geol. Min. Univ. Pd.* 43, 185–231.
- Bona, F., Bellucci, L., Casali, D., Schirolli, P., Sardella, R., 2016. *Macaca sylvanus* Linnaeus 1758 from the Middle Pleistocene of Quecchia quarry (Brescia, Northern Italy). *Hystrix* 27. doi.org/10.4404/hystrix-27.2-11503.
- 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. R. Comit. Geol. Ital.* 3, 59-71.
- Colombero, S., Alba, D.M., D'Amico, C., Delfino, M., Esu, D., Giuntelli, P., Harzhauser, M., Mazza, P., Mosca, M., Neubauer, T.A., Pavia, G., Pavia, M., Villa, A., Carnevale, G., 2017. Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleocological and paleoclimatological implications. *Palaeontol. Electron.* 20, 10A.
- Delson, E., 1973. Fossil colobine monkeys of the Circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia). Ph.D. Dissertation, Columbia University.
- Delson, E., 1974. Preliminary review of cercopithecoid distribution in the circum Mediterranean region. *Mémoires du Bureau de Recherches Géologiques et Minières (France)* 78, 131-135.
- 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, pp. 10–30

- Delson, E. (2004). Cercopithecidae from the Pliocene of Saint-Vallier. *Geobios* 37, S318–S322.
- Di Nucci, A., 2006. Studio arche-zoologico e tafonomico delle faune a grandi mammiferi di Isernia La Pineta (Molise, Italia). Tesi di dottorato in Sistemi Biologici. Università degli Studi di Ferrara.
- Egi, N., Nakatsukasa, M., Kalmykov, N.P., Maschenko, E.N., Takai, M., 2007. Distal humerus and ulna of *Parapresbytis* (Colobinae) from the Pliocene of Russia and Mongolia: Phylogenetic and ecological implications based on elbow morphology. *Anthropol. Sci.* 155, 107–117.
- Elton, S., O'Regan, H.J., 2014. Macaques at the margins: The biogeography and extinction of *Macaca sylvanus* in Europe. *Quat. Sci. Rev.* 96, 117–130.
- Fistani, A.B., 1996. *Sus scrofa* (Goldfuss, De Serres) (Mammalia, Artiodactyla, Suidae) from the Middle Pleistocene layers of Gajtan 1 site, southeast of Shköder (North Albania). *Ann. de Paléontol.* 82(3), 177-229.
- Fladerer, F.A., 1987. *Macaca* (Cercopithecidae, Primates) im Altpleistozän von Deutsch-Altenburg, Niederösterreich. *Beitr. Paläont. Österr.* 13, 1-24.
- Fooden, J., 2007. Systematic review of the Barbary macaque, *Macaca Sylvanus* (Linnaeus, 1758). *Fieldiana Zool.* 113, 1–60.
- Forsyth Major, C.J., 1872a. Note sur des singes fossiles trouves en Italie, précédée d'un aperçu sur les quadrumanes fossils en général. *Atti Soc. Ital. Sci. Nat.* 15, 1–17.
- Forsyth Major, C.J., 1872b. La faune des vertébrés de Monte Bamboli (Maremmes de la Toscane). *Atti Soc. Ital. Sci. Nat.* 15, 290–303.
- Forsyth Major, C.J., 1875. Considerazioni sulla fauna a mammiferi pliocenici e post-pliocenici della Toscana. *Atti Soc. Tosc. Sci. Nat.* 2, 223–242.
- Forsyth Major, C.J., 1914. Observations sur la Faune des Mammifères quaternaires de Corse et Sardaigne. *IX Congres International de Zoologie, Sec. IV*, 594.

- 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*, 2nd ed. Bertrand, Paris.
- Guillén Castejón, J., 2010. Canal Negre 1, un jaciment càrstic de vertebrats del Miocè, Pliocè i Pleistocè de Catalunya. *Exploracions* 19, 7–87.
- Harrison, T., 1989. New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. *J. hum. Evol.* 18, 3–54
- Heintz, E., Delson, E., Crusafont, M., 1971. Note sur la Macaque de la Puebla de Valverde (Teruel, Espana). *Boll. R. Soc. Espan. Hist. Nat. (Geol.)* 69, 299–302.
- Kalhke, H.D., 1961. Revision der Säugetierfaunen der Klassischen deutschen Pleistozan-Fundstellen von Sussenborn, Mosbach und Tobach. *Geologie*, 10, 493–518.
- Köhler, M., Moyà-Solà, S., Alba, D.M., 2000. *Macaca* (Primates, Cercopithecidae) from the Late Miocene of Spain. *J. Hum. Evol.* 38, 447–452.
- Marigò, J., Susanna, I., Minwer-Barakat, R., Madurell-Malapeira, J., Moyà-Solà, S., Casanovas-Vilar, I., Robles, J.M., Alba, D.M., 2014. The primate fossil record in the Iberian Peninsula. *J. Iber. Geol.* 40, 179–211.
- Martin Penela, A., 1983. Presencia del género *Macaca* en el yacimiento Pleistoceno de la Solana del Zamborino, Fonelas, Granada, España. Estudio preliminar. *Bol. R. Soc. Esp. His. Nat. (Geol.)*, 81(3–4), 187–195.
- Mashchenko, E.N., 2005. Cenozoic primates of eastern Eurasia (Russia and adjacent areas). *Anthropol. Sci.* 113, 103–115.
- Masseti, M., Bruner, E., 2009. The primates of the western Palaeartic: A biogeographical, historical, and archaeozoological review. *J. Anthropol. Sci.* 87, 33–91.

- Mazza, P., Rustioni, M., Agostani, S., Rossi, A., 2005. An unexpected Late Pleistocene macaque remain from Grotta degli Orsi Volanti (Rapino, Chieti, central Italy). *Géobios* 38, 211–217.
- Meloro, C., Elton, S., 2012. The evolutionary history and palaeo-ecology of primate predation: *Macaca sylvanus* from Plio-Pleistocene Europe as a case study. *Folia Primatol.* 83, 216–235.
- Ménard, N., Rantier, Y., Foulquier, A., Qarro, M., Chillasse, L., Vallet, D., Pierre, J.-S., Butet, A., 2014. Impact of human pressure and forest fragmentation on the endangered Barbary macaque *Macaca sylvanus* in the Middle Atlas of Morocco. *Oryx* 48(2), 276-284.
- Merciai, G., 1907. Sopra alcuni resti di vertebrati miocenici delle ligniti di Ribolla. *Atti Soc. Tosc. Sci. Nat. Mem. Serie A.* 23, 79–86.
- Moigne, A.M., Palonbo M.R., Belda, V., Heriech-Briki, D., Kacimi, S., Lacombat, F., De Lumley, M.A., Mountoussamy, J., Rivals, F., Quilès, J., Testu, A., 2006. An interpretation of large mammal fauna from la Caune de l'Arago (France) in comparison to a Middle Pleistocene biochronological fram from Italy. *L'Anthropologie* 110(5), 788–831.
- Moncel M.-H., Santagata C., Pereira A., Nomade S., Bahain J.-J., Voinchet P., Piperno, M., 2019. A biface production older than 600 ka ago at Notarchirico (Southern Italy) contribution to understanding early Acheulean cognition and skills in Europe. *PLoS One* 14(9), e0218591. doi.org/10.1371/journal.pone.0218591
- Moncel, M.-H., Santagata, C., Pereira, A., Nomade, S., Voinchet, P., Bahain, J.-J., Daujeard, C., Curci, A., Lemorini, C., Hardy, B., Eramo, G., Berto, C., Raynal, J.P., Arzarello, M., Mecozi, B., Iannucci, A., Sardella, R., Allegretta, I., Delluniversità, E., Terzano, R., Dugas, P., Jouanic, G., Queffelec, A., D'andrea, A., Valentini, R., Minucci, E., Carpentiero, L., Piperno, M., 2020. The origin of early Acheulean expansion in Europe 700 ka ago: New findings at Notarchirico (Italy). *Sci. Rep.* doi.org/10.1038/s41598-020-68617-8
- Montoya, P., Alberdi, M.T., Blázquez, A.M., Barbadillo, L.J., Fumanal, M.P., van der Made, J., Marín, J.M., Molina, A., Morales, J., Murelaga, X., Penalver, 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.

- Nocchi, G., Sala, B., 1997. The fossil rabbit from Valdemino cave (Borgio Verezzi, Savona) in the context of western Europe Oryctolagini of Quaternary. *Palaeovertebrata* 26(1–4), 167–187.
- Ottolenghi, F., 1898. Nota sopra una scimmia fossile italiana. *Atti Soc. Ligustica Sci. Nat. Geog.* 9, 399-403.
- Pereira, A., Nomade, S., Voinchet, P., Bahain, J.-J., Falguères, C., Garon, H., Lefèvre, D., Raynal J.P., Scao, V., Piperno, M., 2015. The earliest securely dated hominin fossil in Italy and evidence of Acheulian occupation during glacial MIS 16 at Notarchirico (Venosa, Basilicata, Italy). *J. Quat. Sci.* 30(7), 639–650.
- Portis, A., 1917. Primi avanzi di Quadrumani del suolo di Roma. *Boll. Soc. Geol. Ital.* 35, 239–278.
- Reumer J.W.F., Mol D., Kahlke R.D., 2017. First finds of Pleistocene *Macaca sylvanus* (Cercopithecidae, Primates) from the North Sea. *Rev. de Paléobiologie* 37(2), 555–560.
- Ristori, G., 1890. Le scimmie fossili italiane. *Boll. Regio Com. Geol. It.* 1, 178–196.
- 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., 2009. The Italian fossil primate record: An update and perspectives for future research. *Boll. Soc. Paleontol. Ital.* 48(2), 67–77.
- 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.
- 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.
- Rose, M.D., 1988. Another look at the anthropoid elbow. *J. Hum. Evol.* 17, 193-224.

- Rosendahl, W., Ambros, D., Hilpert, B., Hambach, U., Alt, K.W., Knipping, M., Reisch, L., Kaulich, B., 2011. Neanderthals and monkeys in the Würmian of Central Europe: the Middle Paleolithic site of Hunas, Southern Germany. In Conard, N.J., Richter, J. (Eds.), Neanderthal Lifeways, Subsistence and Technology: One Hundred Fifty Years of Neanderthal Study, Springer, Dordrecht, pp. 15-23 DOI:10.1007/978-94-007-0415-2-3
- Sala, B. 1999. Nuovi dati sulla microteriofauna di Notarchirico. In: Piperno, M. (Ed.), Notarchirico un sito del Pleistocene medio iniziale nel bacino di Venosa. Ediz. Osanna per Soprint. speciale al Museo Nazionale Preistorico Etnografico "L. Pigorini", Roma, pp. 439-441.
- Schrebe, H.D., Loscher, M., 2011. The second find of a primate from the early Middle Pleistocene locality of Mauer (SW Germany): A molar of *Macaca* (Mammalia, Cercopithecidae). N. Jb. Geol. Paläont. Abh. 260(3), 297–304.
- Schreve, D.C., 2001. Mammalian evidence from Middle Pleistocene fluvial sequences for complex environmental change at the oxygen isotope substage level. Quat. Int. 79, 65–74.
- Schreve, D.C., Bridgland, D.R., Allen, P., Blackford, J.J., Gleed-Owen C.P., Griffiths, H.I., Keen, D.H., White, M.J., 2002. Sedimentology, palaeontology and archaeology of late Middle Pleistocene River Thames terrace deposits at Purfleet, Essex, UK. Quat. Sci. Rev. 21, 1423–1464.
- Segre, A.G., Ascenzi, A., 1984. Fontana Ranuccio: Italy's earliest Middle Pleistocene hominid site. Curr. Anthropol. 25 (2), 230–233.
- Seguenza, L., 1902. I vertebrati fossili della provincia di Messina. Parte II: mammiferi e geologia del piano Pontico. Bollettino della Società Geologica Italiana 21, 115-172.
- Seguenza, L., 1907. Nuovi resti di mammiferi fossili di Gravitelli presso Messina. Bollettino della Società Geologica Italiana 26, 7-119.
- Singer, R., Wilff, R.G., Gladfelter, B.G., Wymer, J.J., 1982. Pleistocene *Macaca* from Hoxne, Suffolk, England. Folia Primatol. 37, 141–152.

- Springer, M.S., Meredith, R.W., Gatesy, J., Emerling, C.A., Park, J., Rabosky, D.L., Stadler, T., Steiner, C., Ryder, O.A., Janecka, J.E., Fisher, C.A., Murphy, W.J., 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS One* 7, e49521.
- Strani, F., DeMiguel, D., Bona, F., Sardella, R., Biddittu, I., Bruni, L., De Castro A., Guadagnoli F., Bellucci, L., 2018. Ungulate dietary adaptations and palaeoecology of the Middle Pleistocene site of Fontana Ranuccio (Anagni, Central Italy). *Palaeogeogr., Palaeoclimatol. Palaeoecol.* 496, 238-247.
- Symenoidis, N., Zapfe, H., 1976. Primatenzahne (Cercopithecidae) aus einer Pleistozänen Spaltenfüllung im Steinbruch Tourkobounja, Athen. *Ann. Geol. Pays. Hellen.* 28, 207-214.
- Szalay, F., Delson, E., 1979. *Evolutionary History of the Primates*. Academic Press, New York.
- Terzea E., 1984. Mammifères rares du Pléistocène inférieur de Beftia XIII (Bihor, Roumanie). *Travaux de l'institut de Spéologie "E. Racovitza"* 23, 49-56.
- Terzea E., 1996. Biochronology of the Pleistocene deposits at Beftia (Bihor, Romania). *Acta Zool. Cracov.* 39(1), 531-540.
- Tesakov, A.N., Mashchenko, E.N., 1992. The first reliably identified Macaque (Cercopithecidae, Primates) from the Pliocene of the Ukraine. *Paleontol. Journal* 26(4), 55-61.
- Walker, M.J., Uriarte, M.H., Jiménez, A.L., Martínez, M.L., Lerma, I. M., van der Made, J., Duval M., Grün, R. 2020. Cueva Negra del Estrecho del Río Quípar: A dated late Early Pleistocene Palaeolithic site in Southeastern Spain. *J. Paleolith. Archaeol.* <https://doi.org/10.1007/s41982-020-00062-5>
- Zapfe, H., 2001. Zähne von Macaca aus dem Unterpleistozän von Untermassfeld. In: Kahlke R.-D. (Ed.), *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*, Teil 2, Habelt Verlag, Bonn, pp. 889-895

Zoboli, D., Pillola, G.L., Lorenzo, R., 2016. New remains of *Macaca majori* Azzaroli, 1946 (Primates, Cercopithecidae) from Is Oleris (Fluminimaggiore, southwestern Sardinia). *Bollettino della Società Paleontologica Italiana* 55(3), 227-230.

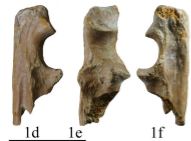
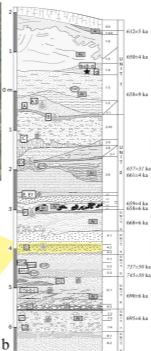
Figure legends

Figure 1. a) Map of the location of the Notarchirico site (southern Italy). The monkey outline indicates the geographic position of the site. Composite section of the stratigraphic succession of Notarchirico (southern Italy) showing dates and position of the macaque ulna (b); view of partial trench through lower levels of Notarchirico site (c). B24GNC, proximal right ulna from Notarchirico in (d) medial (e), anterior and (f) lateral views. Scale bar = 3 cm.

Figure 2. Ulnar measurements used in the current study. Measurement abbreviations: OB: greatest breadth of the olecranon; APB: greatest breadth across the anconeal process; CPB: greatest breadth across the coronoid process; HOF: greatest height of olecranon fossa; APD: greatest depth across the anconeal process. See SOM Table S2 for more details.

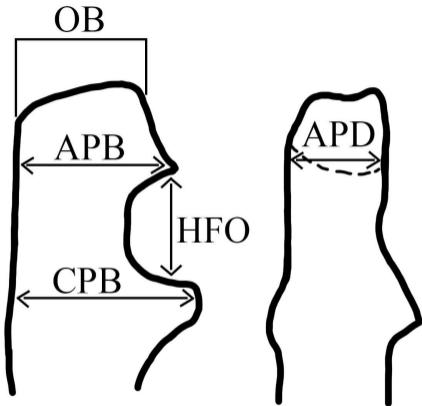
Figure 3. Boxplots of (a) greatest breadth across the coronoid process (CBP) and (b) greatest height of olecranon fossa (HOF) vs. CBP, of the ulna of *Macaca* sp. from Notarchirico, compared to extinct and extant specimens of Barbary macaque and *Mesopithecus pentelicus pentelicus*. See Table 1 for additional details of specimens.

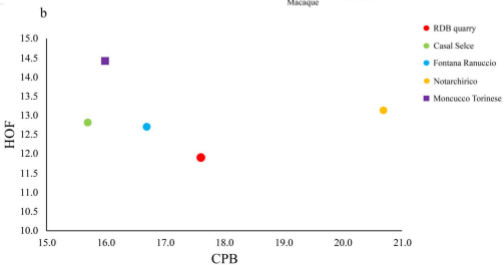
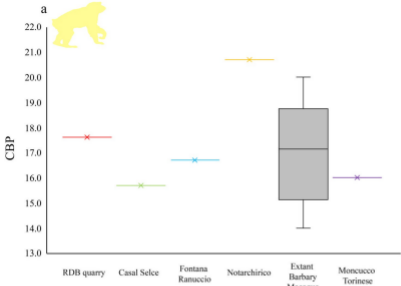
Figure 4. *Macaca* remains from the late Miocene to Late Pleistocene of Europe (details are provided in SOM Table S1). Question mark denotes uncertain age. Map produced with QGIS v. 3.12.



Legend

- ★ Human femur
- ⊕ Presence of lithic artefacts
- ⊞ Presence of hand-axes
- ⊞ Levels dated with $^{40}\text{Ar}/^{39}\text{Ar}$ method
- ⊞ Level dated with ESR method
- Archaeological levels





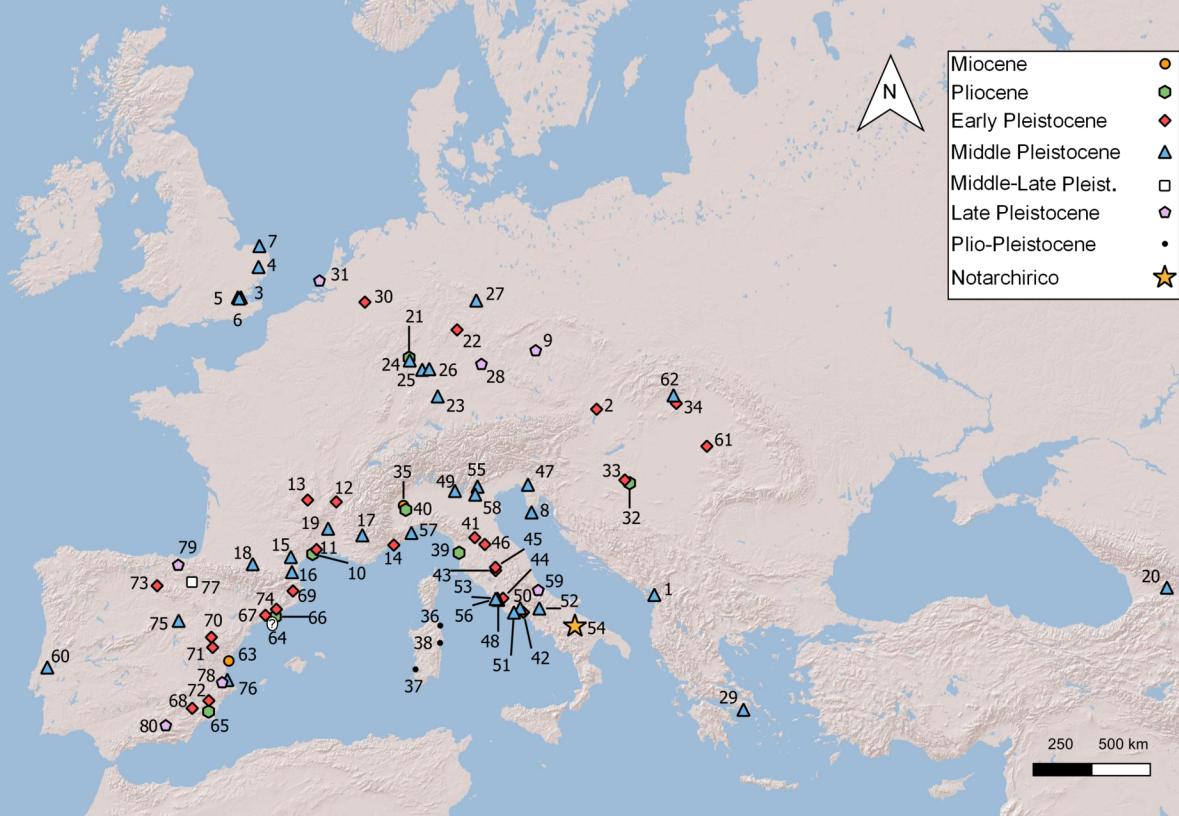


Table 1

Measurements of ulna of extinct and extant specimens of Barbary macaque and extinct *Mesopithecus pentelicus pentelicus*.^{a-b}

Species	Catalogue number	Site	Age	Reference	OB	APB	CPB	HOF	APD
<i>Macaca sylvanus</i> cf. <i>prisca</i>	NMB VJ 130	RDB quarry	Late Pliocene	Rook et al. (2001)			17.6	11.9*	8.3*
<i>Macaca sylvanus</i>	PF - CS520	Cava di Breccia di Casal Selce - upper level	Middle Pleistocene	This work			15.7	12.9	7.8
<i>Macaca</i> cf. <i>sylvanus</i>	IsIPU - FR85	Fontana Ranuccio	Middle Pleistocene	This work	13.5	14.4	16.7	13.3	8.3
<i>Macaca</i> sp.	MNAV - B24GNC	Notarchirico	Middle Pleistocene	This work	14.1	18.0	20.7	13.1	9.3
	CAM-1637			Rook et al. (2001)			15.0		
	CAM-283/4			Rook et al. (2001)			18.0		
	NHMW-34222			Rook et al. (2001)			14.0		
Extant <i>Macaca sylvanus sylvanus</i>	NHMW-32990			Rook et al. (2001)			19.0		
	MHNG-3383			Rook et al. (2001)			20.0		
	MHNG-446-36			Rook et al. (2001)			18.0		
	CZMR - MP 128			This work			16.0		
cf. <i>Mesopithecus pentelicus pentelicus</i>	MGPT-PU 130507	Moncucco Torinese	Late Miocene	Alba et al. (2013)	14.1		16.0	14.4	

*Estimated measurements from Rook et al. (2001).

^aInstitutional abbreviations: CAM: Comparative Anatomy Museum, University of Modena; CZMR: Civic Zoology Museum of Rome; IsIPU: Italian Institute of Human Paleontology; MGPT: Museum of Geology and Paleontology, Turin University; MHNG: Muséum d'Histoire Naturelle de Genève; MNAV: Museo Nazionale Archeologico di Venosa; NMB: Naturhistorisches Museum Basel; NHMW: Naturhistorisches Museum Wien; PF: PaleoFactory laboratory, Department of Earth Sciences, Sapienza University of Rome.

^bMeasurement abbreviations: OB: greatest breadth of the olecranon; APB: greatest breadth across the anconeal process; CPB: greatest breadth across the coronoid process; HOF: greatest height of olecranon fossa; APD: greatest depth across the anconeal process.