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Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/142319> since 2017-05-16T10:28:38Z

Published version:

DOI:10.1016/j.jhevol.2013.11.001

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**First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene
of Europe**

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Keywords: Colobinae, Cercopithecinae, Fossil monkeys, Miocene, Moncucco Torinese, Tertiary Piedmont Basin, Italy

Abstract

Cercopithecoid fossil remains from the post-evaporitic Messinian (5.40-5.33 Ma, MN13, latest Turolian, latest Miocene) locality of Moncucco Torinese (Tertiary Piedmont Basin, NW Italy) are described. A talus is assigned to the fossil colobine *Mesopithecus pentelicus*, while a proximal fragment of ulna and a male lower canine are attributed to cf. *Me. pentelicus*. An isolated I2 and M3 are assigned to the papionin cf. *Macaca* sp., and two cercopithecoid phalanges are left unassigned even to the subfamily level. The record of *Mesopithecus* at Moncucco Torinese agrees well with the previously-known range of this species in Italy and elsewhere in Europe, whereas that of cf. *Macaca* constitutes only the second occurrence of macaques in the Miocene of Eurasia. Although the co-occurrence of these two genera in a single locality had been previously reported in the Pliocene, this is the first instance in which macaques are associated with the Late Miocene *M. pentelicus* instead of *Mesopithecus monspessulanus*. The record of cf. *Macaca* and *Mesopithecus* and especially the latter's talar morphology, similar to that of extant arboreal colobines fits well with paleoenvironmental reconstructions of Moncucco Torinese based on the associated fauna, which indicate a humid and densely-forested environment, probably with more open and drier habitats nearby. From a paleobiogeographic viewpoint, the record of *Macaca* at Moncucco Torinese, together with the previously reported occurrence at Almenara-Casablanca M (Spain), supports the contention that macaques dispersed from Africa into Europe during the latest Miocene (ca. 5.9e5.3 Ma) at the same time as the sea level drop associated with the Messinian Salinity Crisis.

Introduction

Cercopithecine and colobine Old World monkeys coexisted in Europe throughout the Pliocene and into the earliest Pleistocene (e.g., Delson, 1974; Eronen and Rook, 2004), with the former having dispersed there from Africa by the latest Miocene (Köhler et al., 2000). Here we report new fossil cercopithecoid remains from the post-evaporitic Messinian (MN13, late Turolian) locality of Moncucco Torinese (5.40e5.33 Ma), which has produced diverse fossil assemblages of aquatic and

terrestrial invertebrates and vertebrates (Angelone et al., 2011; Colombero, 2012). The presence of a cercopithecoid primate in this locality was first noted by Angelone et al. (2011) on the basis of an isolated talus, which they preliminarily attributed to *Mesopithecus* sp. Since then, additional postcranial and dental remains have been discovered during fieldwork and the preparation of previously-recovered fossil specimens. Here we provide photographs and describe in detail most of the currently available primate remains from Moncucco Torinese (Alba et al., 2013a) and conclude that both *Mesopithecus* and cf. *Macaca* are recorded at this site. Although the extinct colobine *Mesopithecus* had been found associated with *Macaca* in some Pliocene localities, this is the first time that both genera are reported together from a Miocene site. In fact, the cf. *Macaca* from Moncucco Torinese represents only the second record of macaques from the Late Miocene of Europe. The paleobiogeographic, biochronologic and paleoenvironmental implications of these finds are discussed below.

Age and geological background

The site of Moncucco Torinese is located in the Moncucco gypsum quarry, along the southern flank of Torino Hill within the Tertiary Piedmont Basin (NW Italy; Fig. 1; Rossi et al., 2009; Dela Pierre et al., 2011). The Moncucco quarry exposes a Messinian lithostratigraphic succession that ranges from the pre-evaporitic Messinian up to the Miocene-Pliocene boundary (Trenkwalder et al., 2008; Angelone et al., 2011). In the SE part of the quarry, the outcropping post-evaporitic horizons overlie the chaotic sediments that were deposited during the Messinian Salinity Crisis (MSC) (Dela Pierre et al., 2007). These sedimentary layers record the transition from shallow brackish waters ('Lago-Mare' facies) to freshwater/terrestrial environments (Angelone et al., 2011). The fossil assemblages from Moncucco Torinese (including ostracods, brackish-water mollusks and micromammals) indicate a Late Miocene age (MN13, late Turolian; Angelone et al., 2011; Colombero, 2012), in agreement with the stratigraphic data. An ostracod assemblage pertaining to the so-called *Loxocorniculina djafarovi* Zone (5.40e5.33 Ma; Grossi et al., 2011) was reported by Angelone et al.

(2011) from a single layer underlying those containing the fossil vertebrate remains. For this reason, the Messinian fossiliferous deposits of the Moncuoco quarry can be assigned to the upper post-evaporitic unit (p-ev2), which has been cyclostratigraphically constrained to the time interval between 5.42 and 5.33 Ma (e.g., Roveri et al., 2008). Therefore, the age of the vertebrate remains from Moncuoco Torinese is bracketed between 5.40 and 5.33 Ma. The outcrop consists of more than 3 m of mostly sandy and argillaceous marls, in which nine sedimentary units have been defined (Angelone et al., 2011; Colombero, 2012). Most of the fossil remains described in this paper (Table 1) come from unit 3, which is a 0.30 m-thick layer composed of slightly sandy clays with scattered pebbles, abundant mollusk shells, and some small- to medium-sized vertebrate remains. These sediments most likely correspond to a debris-flow deposited in a water-dominated environment (Angelone et al., 2011). Another of the described fossils might also come from unit 3 or alternatively from the overlying unit 4, a layer of 0.30–0.50 m in thickness, mainly composed by sandy clays with microconglomeratic lenses, and also a clast-supported conglomerate on top. Finally, an intermediate phalanx comes from unit 7, a layer up to 110 cm thick. This layer consists of laminated dark sandy clays with small calcareous pebbles in the lower portion and greenish homogenized sandy clays in the upper portion, with some microconglomeratic horizons containing mollusk shells and vertebrate remains.

Material and methods

Studied material

The fossil remains described in this paper (see Table 1) are housed at the collections of the Museum of Geology and Paleontology of Torino University (Italy), whose catalogue numbers are preceded by the acronym ‘MGPT-PU’. Specimens of extant cercopithecids were examined in the collections of various institutions, but especially at the American Museum of Natural History, Department of Mammalogy (AMNH).

Measurements and statistical comparisons

Measurements of the dental and postcranial remains were taken with digital calipers to the nearest 0.1 mm. Statistical comparisons were made using the SPSS v. 16.0 and PAST (Hammer et al., 2001) statistical packages. Further methodological details are provided below when necessary.

Systematic paleontology

Order Primates Linnaeus, 1758

Infraorder Catarrhini Geoffroy Saint-Hilaire, 1812

Superfamily Cercopithecoidea Gray, 1821

Family Cercopithecidae Gray, 1821

Cercopithecidae indet.

(Fig. 2aek)

Description and comparisons

Phalanges The distal fragment of a proximal phalanx MGPT-PU 130509 (Fig. 2gek; Table 2) is broken close to midshaft level. The preserved portion is symmetrical in dorsal/volar views. The shaft is quite compressed (wider than high), with a convex transverse dorsal contour and a flattened volar contour. Conspicuous but narrow flexor ridges extend on both sides of the volar side of the shaft until about 3 mm before reaching the trochlea, which protrudes volarly and slightly mediolaterally with respect to the shaft. The latter displays a minimal degree of curvature along most of its length, except for its distal-most portion, so that the trochlea is somewhat bent volarly. The trochlea is slightly broader than high (broadest on its basal-most portion) and displays large pits for the insertion of the collateral ligaments. The articular surface is biconvex, slightly extending onto the dorsal side, but much longer proximodistally on the volar side. The middle phalanx MGPT-PU 130504 (Fig. 2aef; Table 2) is completely preserved. This phalanx is short and has a relatively stout appearance. It is quite symmetrical in dorsal/ventral views, and only moderately curved (the ventral concavity being more pronounced than the dorsal convexity). The base is much stouter than the trochlea and especially the shaft. The former displays an elliptical shape (shorter

than broad), being mostly occupied by two symmetrical articular surfaces, and further displays two moderately-developed basal tubercles. The shaft becomes slightly narrower and markedly flattened distally, and on its volar side it displays a slightly convex mediolateral cross-section. The shaft further displays faint insertions for the flexors that extend over the distal two-thirds of the shaft length, without reaching the trochlear region. The trochlea protrudes somewhat mediolaterally and volarly relative to the distal shaft portion. The size and articular dimensions of the proximal and intermediate phalanges described above are consistent with belonging to the same cercopithecoid taxon, although not the same individual since they come from different stratigraphic levels. The proximal phalangeal specimen has a flattened shaft with a volarly-bent trochlea, which suggests that it belongs to the hand, but this cannot be conclusively ascertained given the similarities between manual and pedal phalanges among cercopithecoids (e.g., Alba et al., 2011). This issue hinders the anatomical identification as well as taxonomic attribution of isolated phalangeal specimens.

To further explore the morphological affinities of the Moncucco Torinese intermediate phalanx, we used a Principal Components Analysis (PCA). The PCA was based on log-transformed Mosimann shape variables (Mosimann, 1970; Jungers et al., 1995), i.e., we divided each measurement by the geometric mean of all measurements and then used the natural logarithm (ln). Mean-species data, separately for the hand and the foot, were taken from Nakatsukasa et al. (2003) or derived from measurements taken by E.D. et al. [being prepared for posting on NYCEP's PRIMO (PRimate Morphometrics Online) database (<http://primo.nycep.org>)] or kindly provided by Sergio Almécija (Personal communication to DMA; Table S1). The first principal component (PC1) of the PCA (Fig. 3 and Table S2) explains most of the variance, being driven by relative length (the longer the phalanx, the more positive the PC1 scores, as shown by most extant colobines). In this sense, the relative length of the Moncucco Torinese specimen is quite short (only those of baboons are considerably shorter in relative terms), thus differing from all extant colobines and *Mesopithecus monspessulanus*, but most closely resembling the foot phalanx of *Me. pentelicus* included in the analysis (Fig. 3). As noted previously, *Mesopithecus* displays stouter phalanges than usual among

extant colobines (Delson, 1973; Szalay and Delson, 1979), being in this regard more similar to *Macaca* (Fig. 4). We therefore conclude that the Moncucco Torinese cercopithecoid phalanges are best left unassigned to genus.

Subfamily Cercopithecinae Gray, 1821

Tribe Papionini Burnett, 1828

Subtribe Macacina Owen, 1843

Genus *Macaca* Lacépède, 1799

cf. *Macaca* sp.

(Fig. 5a-e, k-o)

Description and comparisons

Third lower molar The left M3 MGPT-PU 130506 (Fig. 5keo; Table 2) is almost completely preserved (except for the apical-most portion of the distal root). The crown shows a slight degree of wear, with only minimal dentine exposure at the apex of the buccal cuspids, as well as a small contact facet against the M2. This molar has two roots: a vertical root corresponding to the metalophid, and a distally-inclined root of triangular contour that, as is typical of M3, corresponds to the hypolophid plus the hypoconulid. The crown displays the typical papionin bilophodont pattern with a moderate degree of buccal flare (see e.g., Delson, 1973). It has an ovoid (distally-tapering) occlusal profile with a distinct third lobe, which are characteristic features of M3. The third lobe bears a well-developed hypoconulid (located close to the crown midline) but no tuberculum sextum. There is a marked median buccal cleft with no ectostylid, and shallower and narrower mesial and distal buccal clefts, all of which end well before the cervix. The lingual median and distal notches are quite shallow (their depth being much less than the distance from notch base to cervix), as well as featureless at their bases (except for a short and faint vertical groove that does not reach the cervix on the median notch). The mesial fovea (trigonid basin) is extensive and

subquadrangular. It is bordered mesially by a distinct mesial shelf and displays a buccal groove that joins the mesial buccal cleft, thus delimiting a cusplike enamel thickening at the mesiobuccal corner of the crown. The subquadrangular central fovea (talonid basin) is somewhat more extensive and deeper than the mesial fovea. The subtriangular distal fovea is also well-developed, although somewhat more restricted than the central fovea and, unlike the latter, clearly longer than broad. There are no cingulids. The occlusal morphology of the M3 from Moncucco Torinese fits the typical papionin pattern of macaques (Delson, 1973, 1975; Szalay and Delson, 1979), rather than that of colobines including *Mesopithecus*. The M3s of the latter differ from those of *Macaca* by displaying a more marked crown relief with more buccolingually compressed cusps, a smaller mesial fovea without a mesiobuccal enamel thickening, deeper median and distal lingual notches, and less buccal flare. Given that the tooth is from a papionin, can it be assigned to a genus? Its size and especially its geographical context suggest attribution to *Macaca* rather than to any of several sub-Saharan African papionins with similar teeth. The only other European papionin is *Paradolichopithecus*, known from the later Pliocene through Early Pleistocene, but even the smallest known specimens are much larger than the Moncucco Torinese M3. However, it is still possible that this tooth might derive from an as yet unknown species of one of these other extinct papionins, or even from an as yet unknown genus, as all papionin molars are so similar. We therefore attribute the specimen to cf. *Macaca* sp. (the taxon is not employed here as a ‘form-genus’, i.e., ?*Macaca*).¹ Although other authors might prefer to leave the specimen unassigned to genus (i.e., *Papionini* indet.; e.g., Benefit et al., 2008), in our opinion its attribution to cf. *Macaca* is preferable and most informative. The same situation might also be argued for other (sub)species referred to *Macaca*, namely *Macaca libyca* (Stromer, 1920) from the Late Miocene of Africa, *Macaca sylvanus prisca* Gervais, 1859 from the Pliocene of Europe, or *Macaca* sp. from the latest Miocene of Spain (e.g., Szalay and Delson, 1979; Köhler et al., 2000), all of which lack diagnostic facial morphology and are allocated on biogeography as much as morphology. In the present case, the size and proportions of the Moncucco Torinese specimen agree with those of extant and extinct

subspecies of *M. sylvanus* (Linnaeus, 1758) (Fig. 6c), being larger than those of *Mesopithecus* spp. (Table 3). On the other hand, given that the teeth of *M. libyca* are in the size range of extant *M. sylvanus*, and that all of the extinct subspecies of *M. sylvanus* overlap in size to a large extent (Rook et al., 2001; Alba et al., 2011; Fig. 6c and Table 3), a species attribution based on the single available papionin molar from Moncucco Torinese is not warranted. Lateral upper incisor The right I2 MGTP PU130501 (Fig. 5aee; Table 2) is completely preserved, but in addition to some apical wear, it is polished all over its surface, thus indicating some degree of transport before burial. The root is mesiodistally compressed and higher than the crown, and both are somewhat asymmetrical (the crown being tilted mesially). The cervix is V-shaped on the distal and, especially, the mesial sides. The crown displays a subtrapezoidal occlusal profile, being slightly longer than wide. The labial crown wall is markedly convex in all directions, whereas the lingual surface displays a slightly concave to straight contour in mesial/distal views. The lingual surface is quite worn and hence the original lingual features (if any) can no longer be discerned, except for a faint cingulum that is still present close to the somewhat bulging lingual crown base. Whereas the lower incisors of colobines and cercopithecines can be easily distinguished based on the lack of lingual enamel in the latter (e.g., Delson, 1973), the distinction of the upper incisors is less straightforward. The morphology of the Moncucco Torinese I2 fits better with a papionin, given the poor development of the lingual cingulum and the lack of a mesial bulge at the base of the crown above the cervix (Delson, 1973). However, dental dimensions of the I2 (Fig. 6a) extensively overlap between *M. sylvanus* and *Me. pentelicus*, with the Moncucco Torinese specimen falling in the overlap zone of the two taxa (see also Table 3). Given the papionin-like morphology of the Moncucco Torinese specimen, but further taking into account the overlap in size and the impossibility to evaluate the variability in incisor lingual features in the single available specimen, we provisionally attribute this specimen to cf. *Macaca*.

Subfamily Colobinae Blyth, 1863

Tribe incertae sedis

Genus *Mesopithecus* Wagner, 1839

Mesopithecus pentelicus Wagner, 1839

Mesopithecus pentelicus pentelicus Wagner, 1839

(Figs. 21-q and 8a)

Description and comparisons

Talus The right talus MGPT-PU 127000 (Fig. 21eq) is completely preserved, except for the lateral tubercle and some minimal cortical damage (especially on the head). Eleven linear measurements (Youlatos, 1991, 1999; Fig. 7) were taken (Table 4). The Moncucco Torinese specimen displays a broad and moderately-high talar body. The neck is relatively stout and not markedly elongated, and the talar head is quite torsioned (24°) and clearly longer than high. The talar trochlea is moderately asymmetrical (somewhat higher laterally than medially) and moderately wedged (it tapers slightly posteriorly). The medial tubercle is swollen and protruding, but the groove for the flexor tibialis muscle is poorly developed and inconspicuous. The sustentacular facet (median talar facet) does not extend much laterally, thus not contacting the distal facet for the calcaneus, from which it is separated by a large non-articular invagination for the ligament cervicis tali. The facet for the plantar calcaneonavicular ligament is well-developed dorsomedially but similarly restricted laterally. The proximal talar facet for the calcaneus is relatively elongated and shapes a considerable concavity. In plantar view, this facet displays a roughly subquadrangular outline, with its lateral side being straight and about as long as the medial side (so that the tapering of the articular area is minimal). The comma-shaped medial malleolar facet is dorsomedially oriented, and quite concave and extensive. Along its distal ventral border this facet displays a marked edge that approaches the sustentacular facet, to the point at which it begins to taper proximally. The facet for the lateral tibial malleolus is proximodistally longer than dorsoventrally high, and rather flat except for the distal ventral portion corresponding to the lateral process, which slightly protrudes laterally from the level defined by the lateral trochlear edge.

The Moncucco Torinese talus overall displays a colobine-like morphology (Strasser, 1988; see also Strasser and Delson, 1987; Zapfe, 1991; Youlatos, 1999; Youlatos and Koufos, 2010; Fig. 8), as reflected in the distally-wide and only slightly-wedged trochlea, the quite torsioned talar head, the swollen medial tubercle, the lack of contact between the malleolar cup and the sustentacular facet, the long proximal talar facet, and the laterally-restricted facet for the plantar calcaneonavicular ligament. At the same time, the specimen displays a few cercopithecine-like features, such as the poorly-developed channel for the flexor tibialis muscle, the well-developed medial malleolar facet, the relatively short and robust neck, and the somewhat curved proximal talar facet. In the abovementioned features, the morphology of the Moncucco Torinese talus resembles *Me. pentelicus* (Gaudry, 1862; Delson, 1973; Zapfe, 1991; Youlatos, 1991; Youlatos and Koufos, 2010), which displays a combination of arboreal, colobine-like features coupled with some other characteristics more closely resembling those of semiterrestrial colobines (i.e., *Semnopithecus*) and cercopithecines (Szalay and Delson, 1979; Gebo, 1989; Youlatos, 1991, 1999; Zapfe, 1991; Youlatos and Koufos, 2010). In contrast, the Moncucco Torinese specimen differs from the tali of *Macaca* (and more closely resembles *Mesopithecus*) in several features, such as the broader and less wedged trochlea, the longer head, the larger proximal talar facet, and the more dorsally-directed malleolar cup. The Moncucco Torinese talus is slightly larger in size than those from *Me. Pentelicus* at Pikermi (reported by Youlatos, 1991; Table 4) and displays a slightly lower degree of talar head torsion (24°) compared with the values from those specimens (mean 29.7°, range 26.0–32.0, $N = 3$; Youlatos, 1999). However, the overall morphology of the Moncucco Torinese talus fits well with that of *Me. pentelicus* and, together with its Miocene age, justifies an attribution to this species.

To evaluate the closer morphologic affinities of the Moncucco Torinese talus and further confirm its taxonomic attribution to *Mesopithecus*, we performed a multivariate analysis based on the above-mentioned 11 linear measurements of the talus. The comparative sample includes 391 tali of 71 extant species from 23 anthropoid genera, plus three tali of *Me. pentelicus* from Pikermi (data taken

from Youlatos, 1991 and by DMA; Table 4, Table S3). The Moncucco Torinese talus is compared with extant cercopithecoid genera and *Mesopithecus* in Fig. 8. A canonical variate analysis (CVA) was performed with SPSS at the genus level, based on logtransformed Mosimann variables. The three tali of *Me. Pentelicus* from Pikermi were defined a priori (like the extant genera), whereas the Moncucco Torinese talus was left unassigned.

Given the aim of this study, instead of analyzing *M. sylvanus* together with other species of the same genus, the former was defined a priori as a different group from the remaining macaques (*Macaca* spp.).

On the basis of the canonical axes scores for the group centroids and the Moncucco Torinese specimen (Table 5), a cluster analysis (Ward's method) was performed with PAST. When only the first six canonical axes (explaining 95% variance) are employed (Fig. 9A), three different clusters are obtained: one including apes and atelids; another including terrestrial quadrupeds (the cercopithecines *Erythrocebus*, *Mandrillus*, *Papio* and *Theropithecus*), which clusters with the former despite a large morphometric distance; and a third, larger group, including all colobines and the remaining cercopithecines (with several subclusters). Among the latter, the Moncucco Torinese talus clusters with *Me. pentelicus* from Pikermi, with both being most similar to the arboreal colobines *Nasalis*, *Presbytis* and *Colobus* (which are arboreal quadrupeds practicing some climbing and suspensory behaviors, depending on the taxon; Youlatos et al., 2012). When all of the canonical axes (100% variance) are employed in the cluster analysis (Fig. 9b), however, subtle differences emerge between the Moncucco Torinese talus and other *Mesopithecus* specimens. The cluster analysis distinguishes two main groups: hominoids þ atelids versus cercopithecoids. Among the latter, terrestrial quadrupeds are clustered separately from the rest, whereas the remaining monkeys are distributed in three different subclusters. The Moncucco Torinese specimen clusters again with the arboreal colobines *Nasalis*, *Presbytis* and *Colobus*, whereas *Me. pentelicus* from Pikermi clusters with the semi-terrestrial *Semnopithecus*, within the subcluster that unites the remaining colobines (*Procolobus*, *Trachypithecus*, *Rhinopithecus* and *Pygathrix*). With the exception of

Pygathrix and some Trachypithecus, these colobines differ from those clustering with the Moncucco Torinese specimen by intermittently moving on the ground, although to a lesser extent than Semnopithecus (Youlatos et al., 2012). Macaques are grouped in a third subcluster with the remaining (semi-terrestrial to arboreal) cercopithecines. Our multivariate analyses therefore support strongly the colobine affinities of the Moncucco Torinese talus and further reflect its similarities with *Me. pentelicus* from Pikerimi. At the same time, our analyses also indicate that the Moncucco Torinese specimen displays some subtle morphological differences that more closely approach the condition of arboreal (i.e., *Colobus*) rather than semi-terrestrial (*Semnopithecus*) colobines. Such subtle differences might merely reflect intraspecific (or even individual) variation, and given the small sample of *Mesopithecus* analyzed, we do not think it is warranted to give these differences taxonomic value.

cf. *Mesopithecus pentelicus pentelicus* Wagner, 1839

Description and comparisons (Figs. 5fej and 7rew)

Lower canine The right lower canine PU 130502 (Fig. 5fej; Table 2) is preserved in five main pieces glued together, which overall preserve most of the root and crown, except for mesial and lingual portions of the cervix and the basal portion of the root. The mesial basal-most portion of the crown is also damaged and slightly displaced mesially from its original position, although mesiodistal length can be readily estimated. The crown shows only a very slight degree of wear, which is restricted to the lingual and distal apical-most portions, with no dentine exposure. Accordingly, the preserved crown height must be very close to the original (unworn) value. The root is about as high as the crown. Both are buccolingually compressed and display an oval contour, being somewhat longer than broad, and slightly broader mesially than distally. In labial/lingual views, the root and crown display a convex mesial profile (more marked in the crown), whereas the distal profile is concave in the crown and rather straight in the root. From cervix to apex, the root progressively tapers, further

displaying a uniformly curved, convex lingual profile, and a much flatter buccal contour. The crown is somewhat tilted distally, with the pointed apex slightly behind the distal-most portion of the crown base. The mesial and buccal aspects of the crown are uniformly curved and quite smooth, with only very subtle vertical enamel crenulations on the buccal wall. The distolingual portion of the crown is convex, whereas the distolabial aspect is concave. The latter progressively becomes wider from apex to base, where it terminates in a moderately-developed, distal basal bulge that only protrudes slightly from the cervix. The lingual aspect of the crown is separated from the mesial portion by a slightly-curved, sharp cristid that descends from the apex to slightly beyond mid-crown height, where it joins the pointed apical end of the lingual cervix, which forms a very marked inverted 'V'. Just distal to the above-mentioned cristid, there is a broad but shallow vertical lingual sulcus, which apically becomes inconspicuous before reaching the crown apex. Basally, this sulcus is interrupted by a very narrow but marked lingual cingulid, which originates at the end of the above-mentioned cristid and terminates at the distal bulge. Except for a small lingual depression on the root just below the cervix, no distinct sulcus can be discerned on the preserved apical two-thirds of the root. The large crown (comparable in height with the root), with a suboval occlusal outline, a marked inverted-V lingual cervix morphology, and a moderately-developed lingual sulcus, indicate that this specimen corresponds to a cercopithecoid lower male canine. Upper male canines display a triangular (instead of suboval) occlusal crown profile and a deeper mesial (instead of lingual) sulcus that is not interrupted by the lingual cingulum. Female cercopithecoid canines, in turn, generally display a shorter crown (both absolutely and relative to root height) with a more stout (sometimes more incisiform) morphology (e.g., Delson, 1973). Distinguishing between cercopithecoid subfamilies on the basis of the canines is generally not possible (Delson, 1973; Hill and Gundling, 1999; Delson et al., 2005), which complicates their taxonomic attribution when a colobine and a similarly-sized cercopithecine are recorded within the same site, as in this case.

Dental size and proportions (Fig. 6b) are of little help in this regard. Thus, although *M. sylvanus*, especially *Macaca sylvanus florentina* (Cocchi, 1872), displays on average larger male lower

canines than *Mesopithecus pentelicus*, both species overlap to some degree, with the Moncucco Torinese specimen being slightly above the maximum known size range of *Me. pentelicus* (Table 3). Moreover, although macaques tend to display more buccolingually-compressed lower canines, similar size and proportions to those displayed by the Moncucco Torinese specimen can be found in *Macaca sylvanus pliocena* Owen, 1846 (Fig. 6b). However, several morphological features of the Moncucco Torinese specimen support an attribution to *Mesopithecus* instead of *Macaca* (Delson, 1973; Bonis et al., 1990; Kullmer, 1991; Zapfe, 1991; Alba et al., 2011), including the poorly-developed (little protruding) distal bulge on the basal portion of the crown (instead of a well-developed, heel-like projection in cercopithecines), the convex (instead of flatter) distolingual crown profile, and the moderately-developed lingual sulcus that is interrupted by the lingual cingulid (more conspicuous and non-interrupted in macaques). We therefore assign the Moncucco Torinese lower canine to cf. *Me. pentelicus pentelicus*, given that an attribution to either *Mesopithecus pentelicus delsoni* or *Me. monspessulanus* can be discounted on the basis of its larger dimensions (Fig. 6b; see Discussion below). The slightly larger size of the Moncucco Torinese specimen compared with lower canines of *Me. pentelicus pentelicus* from other localities is in agreement with the slightly larger size of the talus described above. An attribution to *Dolichopithecus ruscinensis* (not recorded until the Pliocene) can be discounted on the basis of its much larger male lower canine dimensions (Delson et al., 2005). Although we favor the colobine affinities of the described specimen, given the impossibility of evaluating the variability of the above-mentioned features in the single specimen from Moncucco Torinese, we consider the attribution to *Mesopithecus* as provisional.

Ulna The proximal fragment of left ulna MGPT-PU 130507 (Fig. 2rew; Table 2) preserves the most proximal portion of the diaphysis as well as most of the articular region. The olecranon process is slightly abraded on the medial side and partly broken on the lateral side, but the proximal end of the process is preserved, so that its length can be adequately assessed. The trochlear notch is well preserved, except for some erosion along the medial side of the coronoid process as well as on the

proximal end of the notch. The proximal diaphysis of the ulna is mediolaterally compressed, with straight anterior and posterior contours. It progressively decreases in height distally due to the sloping of the anterior contour. On the medial side, a faint crest for insertion of the brachialis muscle extends distally from the lower-most medial side of the coronoid process. On the lateral side of the proximal shaft, there is a much more marked supinator crest, which extends from the radial notch to the most distal preserved portion of the shaft. The radial notch is shallow, oval and anteriorly oriented. Proximally, between the radial notch, the trochlear notch and the anteriormost portion of the coronoid process, there is an ill-defined articular depression for the radial head. Unlike the radial notch, this articular area does not constitute a distinct facet as it is not separated from the radial notch, thereby suggesting the presence of a single radio-ulnar articulation. The coronoid process protrudes anteriorly slightly beyond the anterior-most level of the olecranon process. The trochlear notch is narrow, displays no median keel (indicating the presence of a conical humeral trochlea) and is somewhat obliquely oriented with regard to the main proximodistal axis of the bone (as defined by the olecranon process and the proximal diaphysis). The distal portion of the trochlear notch, next to the coronoid process, is proximomedially oriented for articulation with the medial keel of the humerus. On its most proximal portion, the articular surface extends onto the lateral side of the shaft for articulation with the lateral portion of the humeral trochlea. The olecranon process is moderately long and aligned with the rest of the shaft, with its proximal margin forming an approximate right angle with the posterior margin of the shaft. The proximal ulnar morphology described above (e.g., narrow trochlear notch with no median keel, anteriorly-oriented radial notch, relatively long olecranon process) is typically cercopithecoidlike, indicating a close-packing position of the elbow joint in fully pronated postures, which provides stability during parasagittal movements as an adaptation to quadrupedalism (e.g., Rose, 1988). The Moncucco Torinese ulna further resembles in size and morphology specimens of *Me. pentelicus* (Gaudry, 1862; Delson, 1973; Zapfe, 1991), which differ from those of most extant colobines in lacking the anterior concavity of the proximal shaft and by displaying a moderately retroflected

olecranon. This morphology presumably indicates a lesser degree of arboreality in this taxon (Delson, 1973). Unlike cercopithecines and most *Semnopithecus* (Delson, 1973), this specimen displays a shallow and single articulation with the radius, which together with the shorter olecranon process and less anteriorly-protruding coronoid process, tends to reject an alternative taxonomic attribution to *Macaca*. However, given the variability of some of these features and the impossibility to evaluate such variation from the single specimen available from Moncucco Torinese, we consider this taxonomic attribution merely provisional.

Discussion

Taxonomy

Mesopithecus The genus *Mesopithecus* is widely recorded from the Late Miocene and Pliocene of Eurasia (Delson, 1973, 1974, 1975; Szalay and Delson, 1979; Jablonski, 2002; Jablonski et al., 2011; Alba et al., 2013b). Two or three European species are distinguished (Delson, 1973, 1975, 1994; Szalay and Delson, 1979; Andrews et al., 1996; Rook, 1999; Jablonski, 2002; Pradella and Rook, 2007; Rook and Alba, 2012): *Me. pentelicus*, perhaps from the Vallesian (MN9 or MN10 of Wissberg)² and especially from the Turolian (MN11eMN13) of Europe, Iran and Afghanistan; *Me. monspessulanus* (Gervais, 1849) from the Pliocene (MN14eMN17) and maybe the late Turolian (MN13) of Europe; and *Me. delsoni* Bonis et al., 1990 from the early Turolian (MN11) of Greece (Bonis et al., 1990, 1997; Koufos et al., 2003, 2004; Koufos, 2009a,b; Rook and Alba, 2012). The latter is purportedly distinguished on the basis of mandibular and lower cheektooth morphological details (Bonis et al., 1990; Koufos et al., 2003, 2004). However, *Me. delsoni* has been considered a junior subjective synonym of *Me. pentelicus* by several authors (Zapfe, 1991; Delson, 1994; Andrews et al., 1996; Pradella and Rook, 2007), and several presumably intermediate forms between the two species have been reported (Koufos et al., 2003, 2004; Koufos, 2009a,b). Therefore, until the taxonomic status of this taxon is further clarified, we prefer to merely recognize it here at the subspecies rank (i.e., *Me. pentelicus delsoni*).

The three taxa mentioned above mainly differ in dental size, *Me. pentelicus pentelicus* being larger than *Me. monspessulanus*, but generally smaller than *Me. pentelicus delsoni*, except for the canines (Koufos et al., 2003; Koufos, 2006). *Mesopithecus pentelicus pentelicus* further differs from *Me. monspessulanus* by the relatively wider lower molars, the more marked molar flare, and the more posteriorly-reflected medial epicondyle of the humerus (Delson, 1973, 1975; Szalay and Delson, 1979; Bonis et al., 1990; Ciochon, 1993; Andrews et al., 1996; Delson et al., 2000). None of these features can be ascertained on the Moncucco Torinese sample, but the large size of the male lower canine enables us to discount an attribution to either *Me. monspessulanus* or *Me. pentelicus delsoni*, instead implying attribution to the nominotypical subspecies. No taxonomic significance is given to the slight differences in talar morphology revealed by our analysis, given that only a single specimen is available from Moncucco Torinese and in light of the intraspecific variability displayed by the Pikermi sample. cf. *Macaca* There is consensus that all European fossil macaques (probably including *Macaca majori* Azzaroli, 1946) have an African origin and belong to the same lineage as the extant Barbary macaque (*M. sylvanus sylvanus*) from North Africa (Delson, 1974, 1980; Szalay and Delson, 1979; Alba et al., 2008, 2011). It is possible that the North African *M. libyca* might also be included in this *M. sylvanus* species group, but that requires further analysis (see Szalay and Delson, 1979). The previously-known record of *Macaca* from the European Miocene was left unassigned to the species level (Köhler et al., 2000), but the Plio-Pleistocene macaques from Europe identified to the species level are considered to belong to the lineage of *M. sylvanus*. Within the latter, the remains from Sardinia are included into a distinct, endemic insular species *M. majori* (Rook and O'Higgins, 2005), whereas other remains are customarily divided into several subspecies of *M. sylvanus* (Szalay and Delson, 1979; Delson, 1980; Alba et al., 2011). All of these subspecies overlap extensively in dental dimensions with the extant subspecies, which coupled with the lack of complete cranial material hinders their differential diagnosis (Delson, 1973, 1975, 1980; Szalay and Delson, 1979; Jablonski, 2002; Alba et al., 2011). As noted by Alba et al. (2011), there are some morphometric criteria that substantiate the distinction of the *M. sylvanus florentina* (Late Pliocene

to Early Pleistocene) at the subspecies level, whereas in contrast the taxonomic status of both *M. sylvanus prisca* (Middle to Late Pleistocene) and *M. sylvanus pliocena* (earlier Pliocene) should be subject to further scrutiny. Regardless, the scarce dental remains of cf. *Macaca* from Moncucco Torinese do not allow us to provide an attribution to the species level, since these teeth do not distinguish among *M. libyca* and the several putative Plio-Pleistocene subspecies of *M. sylvanus* (other than *M. sylvanus florentina*). More complete craniodental remains would therefore be required to provide a species attribution. Locomotor inferences for *Mesopithecus* from Moncucco Torinese Together with the morphology of the distal humerus (Delson, 1973; Youlatos et al., 2012) and the calcaneus (Youlatos, 1991, 1999, 2003), talar morphology has previously played a significant role in the reconstruction of the locomotor behavior of *Mesopithecus* (Youlatos, 1991, 1999; Youlatos and Koufos, 2010). Cercopithecids have a distinctive talar morphology characterized by adaptations for securing the foot during cursorial quadrupedalism (asymmetric and moderately-wedged talar trochlea; subrectangular proximal talar facet; separate sustentacular and distal talar facets; Strasser, 1988). Colobines further display subtle differences in talar morphology compared with cercopithecines (more torsioned talar head; medial malleolar cup more restricted, not contacting the sustentacular facet; longer and more curved proximal talar facet; laterally-restricted facet for the plantar calcaneonavicular ligament; better-developed groove for channeling the flexor tibialis muscle). These differences relate to the greater terrestriality of cercopithecines and the presumed re-adaptation to arboreality in colobines (Strasser, 1988). Although *Mesopithecus monspessulanus* displays several colobine talar features related to arboreality (e.g., distally-wide and only slightly-wedged trochlea; malleolar cup not contacting the sustentacular facet; long proximal talar facet; torsioned talar head; Strasser, 1988; Zapfe, 1991; Youlatos, 1999; Youlatos and Koufos, 2010), it also shows other characteristics (e.g., relatively short and robust neck; moderately-curved proximal talar facet) suggesting more quadrupedal locomotor behaviors (Gebo, 1989; Youlatos, 1999; Youlatos and Koufos, 2010). The slightly lower degree of talar head torsion in the Moncucco Torinese specimen might suggest a less arboreal locomotor repertoire, since the

higher angle of extant colobines compared with cercopithecines is functionally related to habitual foot inversion during arboreal behaviors, by enabling opposition of the hallux to the remaining toes (Strasser, 1988; Youlatos, 1991; Youlatos and Koufos, 2010). However, the semi-terrestrial colobine *Semnopithecus* displays similar angles to those of more arboreal colobines (Youlatos, 1999). Moreover, this feature is quite variable in the Pikermi sample (Youlatos, 1991). Therefore, the slightly less-rotated head of the Moncucco Torinese talus does not necessarily bear any functional significance. Larger samples would be required to be able to perform more meaningful comparisons in this regard. The cercopithecine-like, poorly-developed groove for the m. flexor tibialis (m. flexor hallucis longus) in *Mesopithecus* might also be significant from a functional viewpoint. In extant colobines, the larger development of this groove (in some taxa associated with a swollen medial tubercle) compared with cercopithecines reflects the tendency of the m. flexor tibialis to operate the hallux without assistance from the flexor fibularis muscle (m. flexor digitorum longus) in the former (Strasser and Delson, 1987; Strasser, 1988; Youlatos, 1991). This is probably related not only to the reduction of hallucal phalanges in extant colobines, perhaps in part an epigenetic consequence of pollex reduction (Strasser, 1988), but also functionally related to the lateral shift of the main axis of the foot in these taxa (Strasser and Delson, 1987). In this regard, the Moncucco Torinese talus resembles the Pikermi specimens in displaying a poorly-developed groove, whereas the medial tubercle (large in the former) is variably developed among the latter (Youlatos, 1991). The condition of *Mesopithecus* in this regard apparently reflects an earlier stage, less adapted to arboreality, in colobine locomotor evolution with no significant differences between the Moncucco Torinese talus and those from Pikermi. In agreement with the poor development of the m. flexor tibialis groove, the well-developed medial malleolar facet of the Moncucco Torinese talus and other *Me. pentelicus* specimens most closely resembles the condition of the semi-terrestrial colobine *Semnopithecus* (Youlatos, 1991). The latter's condition is intermediate between that of arboreal extant colobines (more restricted facet) and that of cercopithecines (a greater degree of tibiotalar contact even during foot plantarflexion being functionally related to greater

terrestriality; Strasser, 1988). Both *Mesopithecus* and *Semnopithecus*, however, display a more colobine than cercopithecine-like condition, in the sense that the facet is more dorsomedially (not medially) oriented and does not contact the sustentacular facet (Strasser, 1988; Youlatos, 1991). This morphology suggests a semi-terrestrial locomotor repertoire for the fossil form. Within an overall semi-terrestrial locomotor repertoire, however, other features of the *Mesopithecus* talus are more indicative of arboreal than terrestrial or semi-terrestrial locomotion. Thus, the large and distally-wide (i.e., only slightly-wedged) talar trochlea in this genus more closely approaches the morphology of extant arboreal colobines (Youlatos and Koufos, 2010), which favors an increased degree of abduction/adduction in the upper ankle joint, being thus functionally related to locomotion on uneven arboreal supports (Strasser, 1988; Youlatos and Koufos, 2010). Moreover, the proximal talar facet of *Me. pentelicus* from Pikermi is long (similar to that of extant arboreal colobines), although less markedly curved than in arboreal colobines, and thus more similar to *Semnopithecus*. This has been interpreted as indicating a partially restricted range of astragalocalcaneal mobility in *Mesopithecus*, although less so than in cercopithecines (Youlatos and Koufos, 2010). The Moncucco Torinese specimen, however, differs in this regard from those from Pikermi by displaying a relatively long and markedly curved proximal talar facet, which is more comparable with that of *Colobus* (Youlatos, 1991). This morphology implies a higher degree of foot inversion/eversion, and suggests a higher degree of arboreality in the Moncucco Torinese population. A more arboreal locomotor repertoire for the Moncucco Torinese specimen is further supported by the results of our multivariate analysis. This analysis points to subtle differences in talar morphology, since the Moncucco Torinese specimen appears most similar to some extant arboreal colobines (such as *Nasalis* and *Colobus*), whereas the Pikermi specimens, as previously concluded by the multivariate analyses of the talus and calcaneus (Youlatos, 1991, 1999), are more similar to the semi-terrestrial *Semnopithecus*. Interestingly, in a recent analysis based on functionally relevant features of the talus, Youlatos and Koufos (2010) found a prevalence of arboreal over semi-terrestrial features in *Me. Pentelicus* from Pikermi. In fact, the three Pikermian

tali analyzed here (Youlatos, 1991, 1999) display some variability regarding the development of colobine features. This is further reflected by our analysis, according to which PIK-236 is closest to the *Semnopithecus* centroid (squared Mahalanobis distance $\frac{1}{4}$ 5.4), whereas PIK-238 is closest to that of *Colobus* (4.7), although less so than the Moncucco Torinese specimen is to the latter (3.6). In light of the variability in the Pikermi sample, and given that only a single specimen is available from Moncucco Torinese, it seems preliminary to conclude on the basis of the talus alone that *Mesopithecus* from Moncucco Torinese was more arboreally-adapted than those from the type locality. This remains a possibility that should be tested using larger samples and other postcranial elements. Thus, our study suggests that *Me. pentelicus* in general was no more (maybe even less) terrestrial than extant langurs (see also Youlatos and Koufos, 2010), and certainly more arboreally-adapted than semiterrestrial cercopithecines such as *M. sylvanus*. Biochronological and paleobiogeographic implications From a biochronological viewpoint, the association of the murids *Paraethomys meini* and *Apodemus gudrunae* in the small mammal assemblage from Moncucco Torinese is most significant (Colombero, 2012). In Europe, the former species is first recorded ca. 6.2e6.1 Ma (MN13) in the Iberian Peninsula (Garcés et al., 1998; Agustí et al., 2006), and subsequently from the Pliocene (MN14) (e.g., Minwer-Barakat et al., 2012). *Apodemus gudrunae*, however, is a typical species of MN13 faunas, and its association with *P. meini* has led to the definition of the *A. gudrunae* Assemblage Zone (ca. 6.2e 5.3 Ma) in the Guadix Basin (Granada, southern Spain) (Minwer- Barakat et al., 2012). Overall, the micromammal assemblage from Moncucco Torinese enables correlation of this locality to MN13 and excludes a later, Pliocene (MN14) age (Colombero, 2012). The age of Moncucco Torinese is further constrained to 5.40e5.33 Ma by its Messinian post-evaporitic (p-ev2) stratigraphic context (Roveri et al., 2008; Grossi et al., 2011). Although the genera *Mesopithecus* and *Macaca* have been previously recorded together at the Pliocene localities of Montpellier (MN14, France) and Fornace RDB (MN16, Italy) (e.g., Delson, 1974; Szalay and Delson, 1979; Eronen and Rook, 2004; Delson et al., 2005), the former is represented there by *Me. monspessulanus* instead of *Me. pentelicus*. The vertebrate assemblage

from Moncucco Torinese therefore not only represents the first co-occurrence of *Mesopithecus* and *Macaca* in the Late Miocene, but also the first instance in which the latter genus is recorded together with the Late Miocene species *Me. pentelicus*. The paleobiogeographic and biochronological implications of these genera are discussed separately below in greater detail. *Mesopithecus* In Italy, *Mesopithecus* has been previously recorded from several MN13 localities (Gentili et al., 1998; Rook, 1999, 2009; Rook and Alba, 2012). In the Casino Basin and Monticino gypsum quarry (Brisighella), specimens were attributed to *Me. pentelicus*, while the more fragmentary or lost material from Bacinello V3 and Gravitelli was attributed to *Mesopithecus* sp. The record of *Me. pentelicus* at Moncucco Torinese therefore agrees well with the record of this species in Italy, since its presence has already been recorded from Brisighella, which, like Moncucco Torinese, is correlated to the *A. gudrunae* Assemblage Zone (Minwer-Barakat et al., 2012). It has been tentatively suggested that *Me. Pentelicus* and *Me. monspessulanus* might have coexisted at the MN13 locality of Dytiko-2 in Greece (Bonis et al., 1990, 1997; Andrews et al., 1996; Koufos et al., 2004; Delson et al., 2005; Koufos, 2009a,b). The few *Mesopithecus* specimens from the MN13 of Baccinello V3 in Italy are metrically similar to both species (Rook, 1999) and might indicate the presence of either or both (Rook, 2009). The fact is, however, that *Me. pentelicus* has not been reported from any locality in the European Pliocene. As such, from a biochronologic viewpoint, the identification of *Me. pentelicus* from Moncucco Torinese supports the contention, based on small mammals (Colombero, 2012), that this locality is MN13 (and not MN14) in age. *Macaca* The occurrence of cf. *Macaca* at Moncucco Torinese is interesting from both biochronologic and paleobiogeographic viewpoints, since it represents only the second Miocene citation of this genus in Eurasia. The other Miocene occurrence is [cf.] *Macaca* sp. from the karstic locality of AlmenaraeCasablanca M in Spain (Köhler et al., 2000). Delson (1996) reported the presence of two teeth of cf. *Macaca* sp. from the Mahui Formation (Yushe Basin, ca. 5.5 Ma) in China (on the basis of information received from Chinese colleagues). However, these specimens had been purchased rather than collected in situ and it now appears most likely that they derived from the Lower

Pliocene Gaozhuang Formation (see Tedford et al., 2013 for a review of Yushe geology). Moreover, their provisional attribution to the genus *Macaca* by Delson (1996) has not yet been justified by means of a morphological description and metrical comparisons of these remains (currently in preparation). Therefore, the Miocene record of *Macaca* in Eurasia is probably limited to Spain and Italy. In Africa, *Macaca* is also recorded during the Late Miocene by *M. libyca* (Stromer, 1920) from Wadi Natrun (Egypt) as well as by ?*Macaca* sp. from several other North African sites (Delson, 1973, 1975, 1980; Szalay and Delson, 1979; Thomas and Petter, 1986; Jablonski, 2002; Benefit et al., 2008). Based on the preliminary study of the Moncucco Torinese micromammal fossil assemblage, Angelone et al. (2011) concluded that this locality included a mixture of eastern and western European elements with Italian endemics, thus highlighting the role of NW Italy as a cross-road for faunal dispersal into the Italian Peninsula. The record of cf. *Macaca* further shows the presence of at least one taxon of African origin, which is consistent with the previous record of this genus in MN13 of Spain. On the basis of micromammal remains, Köhler et al. (2000) attributed an age of 6.1e5.3 Ma to the Late Miocene European macaque from AlmenaraeCasablanca M. These authors related the dispersal of *Macaca* from Africa into Europe by this time to the MSC (e.g., Krijgsman et al., 1999), but they were unable to discern whether such a dispersal event took place before the onset of the crisis or afterward. Subsequent biostratigraphic refinements in Iberia support the second possibility. Based on small and large mammals, three different Late Miocene dispersal events have been recognized for the Iberian Peninsula (Agustí et al., 2006): (1) the ‘muroid event’ at 7.2 Ma, which involved a significant turnover in muroid rodent associations; (2) the ‘Paraethomys event’ at 6.2 Ma, which is characterized by the dispersal of the murid *Paraethomys* as well as camelids and hippopotamids, indicating the occurrence of the earliest African-Iberian exchange at least 0.2 Ma before the onset of the evaporite deposition linked to the MSC; and (3), the ‘gerbil event’ at 5.9e5.3 Ma, which involved the dispersal of gerbil rodents from Africa, in association with the sea level drop that occurred during the MSC. According to Agustí et al. (2006), the presence of gerbils at AlmenaraeCasablanca M would indicate a maximum age of 5.9 Ma for

this locality, thereby suggesting that the macaque dispersal event was directly associated with the MSC. This is further supported by the post-evaporitic stage (5.40e5.33) of Moncucco Torinese, where the lack of African gerbils documented at Almenarae Casablanca M and other Iberian localities (Minwer-Barakat et al., 2009) is most likely attributable to paleoenvironmental reasons (see below). The presence of macaques in two roughly coeval southern European localities during and/or slightly after the evaporitic phase of the MSC reinforces the contention that these monkeys dispersed at the same time as the sea level drop associated with the crisis and further shows that, once dispersed into Europe, they extended their geographic distribution in a relatively short time.

Paleoenvironmental implications Most of the cercopithecoid remains from Moncucco Torinese come from unit 3, which corresponds to a debris-flow deposited in a water-dominated environment, although there is also one phalanx from unit 7, which was deposited in a freshwater environment (Angelone et al., 2011). The freshwater and terrestrial gastropods recovered from the latter horizon suggest the presence of permanent water at Moncucco Torinese surrounded by a wooded area with frequent rainfalls (Angelone et al., 2011). With regard to vertebrates, many of the recorded small mammals (including several dormice and flying squirrels) have inferred ecological affinities for humid, forested and warm environments, although some rarer taxa with preferences for more open and drier environments have also been recorded (Colombero, 2012). Among the large mammals (Angelone et al., 2011), the presence of *Tapirus* further agrees with the paleoenvironmental inferences based on the micromammals, being indicative of dense, warm and closed forest environments (Guérin and Eisenmann, 1994). Interestingly, the only other Italian record of *Tapirus* sp. is at the slightly older (6.7e6.4 Ma; Rook et al., 2011) MN13 locality of Baccinello V3 (Guérin and Eisenmann, 1994), where *Mesopithecus* sp. is also present (Rook, 1999, 2009). Overall, the fauna from Moncucco Torinese associated with primates is indicative of a relatively warm and humid environment, with densely-forested areas and water nearby, although more open and arid environments would probably have been present some distance away. Such a paleoenvironmental reconstruction is also in agreement with paleobotanical data, according to which broadleaved

evergreen and warm-temperate mixed forests would have persisted in northern and central Italy from 6.0 to 3.5 Ma, with moist warm-temperate conditions and subtropical humid forests even prevailing during the evaporitic Messinian ca. 5.9e5.6 Ma (Bertini and Martinetto, 2008, 2011). During the post-evaporitic Miocene (ca. 5.6e5.3), grasses and some associated tropical plants would have expanded in this area, especially ca. 5.5 Ma, coinciding with the peak of the MSC (Bertini and Martinetto, 2008, 2011). Forested environments would have persisted in this area, but in the form of less humid and more open subtropical forests, as indicated among others by the disappearance of beeches and the rarity of laurels, with some other plant taxa with marked humid affinities probably having become restricted to gallery forests (Kovar-Eder et al., 2006; Bertini and Martinetto, 2008, 2011). The extant North African populations of *M. sylvanus* occupy a varied suite of environments (including cedar, fir and evergreen and deciduous oak forests, scrub, grasslands and rocky ridges dominated by herbaceous vegetation), which are nevertheless characterized by a Mediterranean climate with warm dry summers and relatively wet winters (Fooden, 2007). The past distribution *M. sylvanus* in Europe during the Pleistocene was constrained by climatic and latitudinal factors, as shown by their more extensive distribution during the interglacials and their retreat toward the Mediterranean during the glacials (Fooden, 2007; Elton and O'Regan, 2008). In this sense, the presence of macaques at Moncucco Torinese fits relatively well with the warm and humid climate inferred for this locality on the basis of the associated fauna. Evergreen forests of cedar and oak appear to be the optimal biotope for extant Barbary macaques, whereas rocky slopes without arboreal vegetation are less favorable because these monkeys need to be near water (Masseti and Bruner, 2009) and require trees for sleeping, feeding and escaping from predators (Fooden, 2007). As such, the record of cf. *Macaca* at Moncucco Torinese is in agreement with the presence of forested areas and water bodies at this locality, although it is not incompatible with the existence of more arid and open environments nearby, as indicated by some of the associated micromammals. *Mesopithecus* was widely distributed in Europe during the Turolian, not only being recorded from relatively humid localities, but also from some drier ones (Eronen and Rook, 2004). Such ecological

versatility would have been possible due to an opportunistic diet as well as a semi-terrestrial mode of locomotion (less arboreal than in most extant colobines). Paleodietary analyses, in particular, indicate that *Mesopithecus* was less folivorous (Reitz and Benefit, 2001; Reitz, 2002) and relied more heavily on hard seeds (Merceron et al., 2009a,b) than its extant counterparts. Moreover, on the basis of several postcranial features, it has been previously argued that *Me. pentelicus* displayed a semi-terrestrial lifestyle more similar to that of macaques and the semi-terrestrial extant langur *Semnopithecus* (Gaudry, 1862; Delson, 1973, 1975, 1994; Szalay and Delson, 1979; Zapfe, 1991; Youlatos, 1999, 2003 [but see Escarguel, 2005, for an alternative interpretation]; Youlatos and Koufos, 2010; Youlatos et al., 2012).

The paleodietary and locomotor inferences summarized above would be in agreement with *Me. pentelicus* inhabiting relatively open, mosaic habitats, with patchily forested open savanna as well as bushy areas and gallery forests (Delson, 1994; Youlatos, 2003; Koufos et al., 2003; Koufos, 2009b). In some other localities, *Me. pentelicus* might have even inhabited more homogeneous, poorly wooded environments with a well-developed herbaceous layer of grasses (Clavel et al., 2012). In any case, it is generally assumed that *Me. monspessulanus*, given its more arboreal adaptations, would have inhabited more wooded and humid environments than *Me. pentelicus* (Delson, 1973, 1975; Szalay and Delson, 1979; Ciochon, 1993). This assumption is somewhat contradicted by the talar morphology of *Me. pentelicus* from Pikermi (Youlatos and Koufos, 2010) and especially Moncucco Torinese, which is most similar to that of extant arboreal colobines. This morphology agrees with the presence of densely-forested areas at Moncucco Torinese, as inferred from most of the associated mammalian taxa. Overall, the record of *Me. pentelicus* at this locality is consistent with the presence of densely-forested areas, but like the record of cf. *Macaca*, it does not reject the presence of more open and drier environments nearby.

Summary and conclusions The cercopithecoid dental and postcranial remains from the locality of Moncucco Torinese (Tertiary Piedmont Basin, NW Italy) are described. On the basis of its sedimentological context and biostratigraphy, this site is attributed to the post-evaporitic Messinian, with an estimated age

between 5.40 and 5.33 Ma (MN13, latest Turolian, Late Miocene). Most of the reported remains are attributed to the fossil colobine *Mesopithecus pentelicus pentelicus*. This attribution is more secure for the described talus, and merely provisional for the lower male canine and proximal ulnar fragment. The presence of *Me. pentelicus* at Moncucco Torinese is consistent with its previously-known chronostratigraphic range in Italy and elsewhere in Europe. In contrast, this species of *Mesopithecus* has never been recorded from Pliocene localities, thus further supporting a Late Miocene (MN13) age for Moncucco Torinese. Among the remaining cercopithecoid fossils from Moncucco Torinese, two phalanges (an intermediate and a partial proximal) are left unassigned, whereas a lateral upper incisor and third lower molar are identified as cf. *Macaca* on the basis of the typical papionin morphology of the molar, size and geographic location. No species assignment is possible based on so few remains. This is only the second record of *Macaca* from the Late Miocene of Europe (or all of Eurasia), as well as the first instance in which this genus is found with *Me. pentelicus* instead of *Me. monspessulanus*. Together with the previously reported Late Miocene [cf.] *Macaca* from the Iberian locality of Almenarae Casablanca M, the presence of cf. *Macaca* at Moncucco Torinese supports the contention that macaques dispersed from Africa into Europe sometime between 5.9 and 5.3 Ma, when the sea level dropped during the Messinian Salinity Crisis. From a paleoecological viewpoint, the presence of cf. *Macaca* and *Me. pentelicus* at Moncucco Torinese is consistent with the existence of a warm and humid densely-forested environment with standing water (as inferred from most of the associated fauna), but given the locomotor versatility and opportunistic diet of these taxa, the presence of more open and drier environments nearby cannot be discounted.

Acknowledgments

This work has been supported by the Italian MIUR PRIN 2009MSSS9L_002 ('Paleobiogeografia e dinamica di popolazione nel tardo Miocene: nuove evidenze dal Mediterraneo centrale', to G.P.), the Spanish Ministerio de Economía y Competitividad (CGL2011-28681, CGL2011-27343, and

RYC-2009-04533 to D.M.A.) and the Generalitat de Catalunya (2009 SGR 754 GRC, and 2011 BE-DGR 00310 to D.M.A.). We are grateful to the quarry agent, the Fassa Bortolo Agency, and to Igor Muller for facilities during fieldwork activities; the collaboration of the Soprintendenza ai Beni Archeologici del Piemonte in Torino, which helped us to obtain the excavation permit, is also acknowledged. We also thank Eileen Westwig for access to the extant comparative sample in the AMNH Mammalogy Department, Sergio Almécija for providing measurements and helpful discussion, Salvador Moyà-Solà and Joan Madurell for discussion of the fossil material, all those that participated in fieldwork for their enthusiasm, and three anonymous reviewers and the Associate Editor for helpful comments and suggestions on a previous version of this paper.

Appendix A. Supplementary data

Supplementary data related to this article can be found at [http://](http://.....)

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Table and figure captions

Table 1

List of fossil remains of Cercopithecidae from Moncucco Torinese described in this paper, indicating the geological unit of provenance as well as taxonomic attribution.

Catalogue No. Unit Taxon Description Figure

MGPT-PU 127000 3 Mesopithecus

pentelicus pentelicus

Right talus Fig. 2leq

MGPT-PU 130501 3 cf. *Macaca* sp. Right I2 Fig. 5aee

MGPT-PU 130502 3 cf. *Mesopithecus*

pentelicus pentelicus

Right _ lower

canine

Fig. 5fej

MGPT-PU 130504 7 Cercopithecidae

indet.

Intermediate

phalanx

Fig. 2aef

MGPT-PU 130506 3 cf. *Macaca* sp. Left M3 Fig. 5keo

MGPT-PU 130507 3 cf. *Mesopithecus*

pentelicus pentelicus

Proximal fragment

of left ulna

Fig. 2rew

MGPT-PU 130509 3/4 Cercopithecidae

indet.

Distal fragment of

proximal (manual?)

phalanx

Fig. 2gek

Abbreviations: MGPT-PU, Museum of Geology and Paleontology, Torino University.

Table 2

Measurements of the fossil remains of Cercopithecidae from Moncucco Torinese, other than the talus MGPT-PU 127000 (reported in Table 4).

Catalogue No.	Taxon	Ulnar measurements	HPS	WPS	WTN	LTN	DUC	DUN	DOP	APR	PDR	PDO
MGPT-PU 130507	cf. <i>Me. pentelicus pentelicus</i>	Proximal ulnar fragment	12.5	8.1	7.8	14.4	16.0	9.1	14.1	6.2	6.3	7.5

Catalogue No.	Taxon	Phalangeal measurements	L	WB	HB	WMS	HMS	WT	HT
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MGPT-PU 130509	Cercopithecidae	indet. Proximal phalanx	>17.9	e	e	(5.3)	(3.8)	5.9	4.4
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MGPT-PU 130504	Cercopithecidae	indet. Intermediate phalanx	16.2	6.3	4.9	4.2	3.1	4.7	3.1
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Catalogue No. Taxon Dental measurements MD_b BL_m BL_d BLI CH RH

MGPT-PU 130506 cf. *Macaca* sp. M3 11.0 7.9 6.8 71.8 e e

MGPT-PU 130501 cf. *Macaca* sp. I2 4.3 4.0 e 93.0 >6.0 8.6

MGPT-PU 130502 cf. *Me. pentelicus pentelicus* _ lower canine (8.7) 6.0 e (69.0) >19.8 19.9

Ulnar measurements abbreviations: APR, radial notch anteroposterior diameter; DOP, ulnar maximum anteroposterior depth at the olecranon process; DUC, ulnar maximum anteroposterior depth at the coronoid process; DUN, ulnar minimum anteroposterior depth at the trochlear notch; HPS, proximal shaft anteroposterior height (just distal to the radial notch); LTN, trochlear notch maximum proximodistal length; PDO, olecranon process maximum proximodistal length behind trochlear notch; PDR, radial notch proximodistal diameter; WPS, proximal shaft mediolateral width; WTN, trochlear notch maximum articular breadth.

Phalangeal measurements abbreviations: HB, base height; HMS, midshaft height (dorsovolar); HT, trochlea height; L, maximum length; WB, base width; WMS, midshaft width (mediolateral); WT, trochlea width.

Dental measurements abbreviations: BL_d, buccolingual crown width (on distal lobe of molars); BLI, breadth/length crown index, computed as (maximum BL/MD)*100; BL_m, buccolingual (or labiolingual) crown width (on mesial lobe of molars, or maximum for other teeth); CH, labial crown height; MD, mesiodistal crown length; RH, labial (or buccal) root height.

a All measurements in mm, except for indices (dimensionless, in %). Those between parentheses are estimates, whereas those preceded by '>' are maximum preserved values.

b In canines, MD corresponds to the maximum crown basal dimension (considered BL by some authors, e.g., Delson, 1973).

Table 3

Descriptive statistics for the dental measurements of the Moncucco Torinese specimens, compared to selected *Macaca* and *Mesopithecus* species.

I2 N MD BL BLI

Taxon Mean SD Range Mean SD Range Mean SD Range

cf. *Macaca* sp. (Moncucco) 1 4.30 e e e 4.00 e e e 93.02 e e e

M. s. sylvanus (extant) 13 4.44 0.54 3.7 5.5 4.75 0.45 4.1 5.5 107.64 9.87 95.5 126.3

M. s. prisca 1 5.60 e e e 5.70 e e e 101.79 e e e

M. s. florentina 1 5.30 e e e 3.60 e e e 67.92 e e e

Me. p. pentelicus 17 4.16 0.49 3.3 5.0 4.38 0.38 3.8 5.0 106.93 16.49 79.2 136.4

Me. p. delsoni 1 4.20 e e e 3.80 e e e 90.48 e e e

C1 _ N MD BL BLI

Taxon Mean SD Range Mean SD Range Mean SD Range

cf. *Me. p.*

pentelicus (Moncucco)

1 (8.70) e e e 6.00 e e e (68.97) e e e

M. s. sylvanus (extant) 5 9.00 0.51 8.3 9.7 5.24 0.26 4.9 5.6 58.28 2.39 55.1 61.4

M. s. prisca 1 8.20 e e e 5.80 e e e 70.73 e e e

M. s. pliocena 1 9.60 e e e 5.00 e e e 52.08 e e e

M. s. florentina 8 10.64 0.78 9.5 11.8 5.94 0.36 5.4 6.4 56.00 3.95 51.7 64.0

Me. p. pentelicus 26 7.47 0.47 6.5 8.5 5.07 0.41 4.2 5.9 68.13 6.23 56.3 79.4

Me. p. delsoni 2 7.35 0.95 6.7 8.0 4.55 0.23 4.4 4.7 62.25 4.98 58.7 65.8

Me. monspessulanus 4 6.65 0.24 6.3 6.8 4.33 0.26 4.1 4.6 65.19 6.14 60.3 73.0

M3 N MD BL BLI

Taxon Mean SD Range Mean SD Range Mean SD Range

cf. *Macaca* sp. (Moncucco) 1 10.80 e e e 6.90 e e e 63.89 e e e

M. libyca 2 12.45 1.06 11.7 13.2 8.75 0.64 8.3 9.2 70.32 0.88 69.7 70.9

M. s. sylvanus (extant) 45 11.61 1.04 9.3 14.6 8.04 0.73 6.4 9.5 69.39 4.65 59.7 79.7

M. s. prisca 1 10.80 e e e 6.90 e e e 63.89 e e e

M. s. pliocena 12 12.59 1.12 10.2 14.4 8.02 0.76 7.1 9.4 63.73 3.27 58.8 70.1

M. s. florentina 14 12.85 0.95 11.5 14.5 7.96 0.53 6.8 8.8 62.16 4.64 53.8 72.7

Me. p. pentelicus 61 9.19 0.47 7.9 10.5 6.52 0.33 5.9 7.3 71.02 3.59 64.0 81.6

Me. p. delsoni 3 10.01 1.14 8.7 10.9 6.81 0.11 6.7 6.9 68.67 8.29 61.8 77.9

Me. monspessulanus 8 8.99 0.52 8.3 9.6 5.79 0.29 5.4 6.2 64.46 2.33 60.6 67.4

Data sources as for Fig. 6. Except for the Moncucco specimen, those of *M. sylvanus* unassigned to subspecies and those of *Mesopithecus* unassigned to (sub)species are not included.

Abbreviations: N, sample size; SD, standard deviation.

Table 4

Talar measurements for the right talus (MGPT-PU 127000) of *Mesopithecus pentelicus pentelicus* from Moncucco Torinese (see Fig. 7 for the definition of the variables), compared to mean values for the comparative sample (see Table S3 for details on sample composition).

Taxon AS1 AS2 AS3 AS4 AS5 AS6 AS7 AS8 AS9 AS10 AS11

Alouatta

(N ¼ 31)

Mean 4.85 6.81 10.05 23.89 1.95 11.44 9.34 7.15 7.11 11.77 9.41

SD 0.53 0.66 0.67 1.43 0.26 0.88 0.70 0.66 0.66 0.87 0.92

Ateles

(N ¼ 6)

Mean 5.85 8.83 10.98 28.53 2.40 13.33 11.03 8.63 9.32 14.92 11.25

SD 0.84 0.80 1.14 2.22 0.31 0.99 0.54 0.51 0.75 1.33 0.78

Cercocebus

(N ¼ 10)

Mean 6.70 6.75 12.89 24.92 2.96 10.57 10.88 9.11 9.25 11.95 10.31

SD 1.45 0.81 1.91 1.86 0.52 0.94 1.14 0.91 0.92 1.04 0.96

Cercopithecus

(N ¼ 44)

Mean 5.02 5.71 10.54 21.90 2.75 9.52 8.92 7.42 7.27 10.05 8.68

SD 0.78 1.01 1.17 2.19 0.52 1.00 0.97 0.81 0.99 1.01 1.02

Chlorocebus

(N ¼ 11)

Mean 4.89 5.85 10.25 21.35 2.59 9.27 8.82 7.33 7.50 9.85 8.64

SD 0.60 0.73 1.53 1.82 0.30 0.77 0.78 0.79 1.06 0.98 0.79

Colobus

(N ¼ 16)

Mean 6.68 8.08 13.01 26.74 3.61 12.41 12.26 8.96 10.46 13.22 11.04

SD 0.73 1.28 1.11 2.13 0.39 1.44 0.87 0.67 0.93 1.15 0.97

Erythrocebus

(N ¼ 7)

Mean 5.00 8.60 12.64 26.39 3.20 11.89 12.10 10.07 9.47 13.43 10.70

SD 0.61 0.81 2.17 1.72 0.51 0.98 1.11 1.02 1.00 0.89 0.64

Gorilla

(N ¼ 24)

Mean 15.06 23.83 25.15 61.35 6.78 34.53 32.45 23.62 29.39 36.59 26.43

SD 2.37 3.05 3.03 5.38 2.15 4.24 3.61 2.88 3.91 3.77 3.76

Hylobates

(N ¼ 27)

Mean 5.38 7.21 10.01 22.17 2.10 11.60 9.92 8.02 7.98 10.62 8.59

SD 0.66 0.96 1.14 2.09 0.39 1.42 1.09 0.76 1.11 1.20 0.91

Lophocebus

(N ¼ 6)

Mean 6.78 7.27 12.35 25.68 3.02 11.22 11.17 9.37 9.27 12.60 10.70

SD 0.72 1.07 1.18 0.90 0.48 0.85 0.82 0.68 0.57 0.79 0.88

Macaca spp.

(N ¼ 39)

Mean 5.74 6.72 12.02 24.22 2.79 10.50 10.38 9.12 8.69 11.73 10.16

SD 1.24 1.55 1.62 3.48 0.54 1.51 1.64 1.44 1.54 1.83 1.63

M. sylvanus

(N ¼ 11)

Mean 6.26 7.23 13.48 27.18 3.35 11.56 11.15 9.42 9.91 12.97 11.05

SD 0.76 0.87 1.43 2.38 0.49 1.01 0.94 0.87 1.30 1.02 0.86

Mandrillus

(N ¼ 17)

Mean 8.32 9.67 14.43 29.69 3.52 12.90 13.92 11.71 12.61 14.79 12.22

SD 1.72 2.19 1.61 3.44 0.59 1.93 2.10 1.84 2.05 2.22 1.86

Nasalis

(N ¼ 9)

Mean 8.88 11.38 16.33 32.23 4.63 15.07 14.54 11.62 12.52 15.44 12.92

SD 0.95 2.68 1.84 2.99 0.82 1.59 1.37 0.99 1.14 1.72 1.24

Pan

(N ¼ 33)

Mean 12.09 15.59 18.76 48.21 5.32 25.28 22.80 18.18 19.34 24.02 19.19

SD 1.29 1.43 1.82 3.32 0.99 2.25 2.27 2.26 1.93 1.81 1.73

Papio

(N ¼ 26)

Mean 8.26 10.39 16.14 30.75 3.73 13.88 14.33 12.32 12.87 15.69 12.75

SD 1.36 1.71 1.71 2.28 0.56 1.58 1.89 1.46 1.49 1.88 1.66

Pongo

(N ¼ 7)

Mean 7.60 12.57 19.33 47.51 3.83 22.13 20.47 14.34 17.23 22.41 19.37

SD 1.25 1.65 3.22 4.60 0.77 1.42 2.12 1.66 1.89 2.46 1.57

Presbytis

(N ¼ 11)

Mean 5.90 6.75 11.66 23.81 2.95 10.86 11.07 8.07 8.81 11.43 10.05

SD 0.39 0.67 1.09 1.35 0.84 0.89 0.63 0.47 0.44 0.81 0.69

Procolobus

(N ¼ 10)

Mean 6.05 6.72 13.30 26.06 3.64 11.74 11.92 9.31 10.06 12.31 10.10

SD 1.15 1.21 0.61 2.24 0.26 1.42 0.78 0.65 0.67 1.31 0.60

Pygathrix

(N ¼ 6)

Mean 6.92 7.28 14.47 27.72 4.55 12.55 12.13 10.47 10.30 12.77 10.75

SD 0.51 1.22 1.93 2.22 1.14 1.29 1.18 1.21 0.92 0.81 0.93

Rhinopithecus

(N ¼ 12)

Mean 5.03 5.59 11.28 21.26 2.96 9.70 9.23 7.63 7.69 10.23 8.70

SD 0.96 2.05 0.70 3.39 0.45 1.69 1.76 1.68 1.39 1.92 1.73

Semnopithecus

(N ¼ 4)

Mean 7.13 7.58 14.98 27.08 3.88 11.83 11.80 10.08 10.28 13.60 10.93

SD 0.32 0.78 1.37 1.58 0.51 0.57 0.64 0.62 0.71 0.70 0.33

Theropithecus

(N ¼ 9)

Mean 7.22 9.40 15.16 29.28 3.53 13.13 13.51 11.31 12.24 14.44 12.04

SD 1.14 1.20 1.68 2.39 0.33 1.42 1.60 1.11 1.44 1.34 1.20

Trachypithecus

(N ¼ 14)

Mean 6.12 6.68 11.93 24.31 3.11 11.13 10.56 8.62 9.00 11.31 9.85

SD 0.92 1.32 1.63 1.84 0.59 1.28 1.15 1.05 1.20 1.09 1.00

Mesopithecus

(N ¼ 3)

Mean 6.23 6.90 14.50 25.07 3.17 11.67 11.37 8.93 9.57 12.97 10.57

SD 0.12 0.56 0.60 1.35 0.21 0.21 0.61 1.07 0.84 0.15 0.35

Moncucco

(N ¼ 1)

Mean 7.30 9.70 12.90 27.80 3.50 12.70 12.40 9.40 10.80 13.60 11.70

Abbreviations: N, sample size; SD, standard deviation. See abbreviations of variables in Fig. 7.

Table 5

Results of the Canonical Variate Analysis (CVA) based on log-transformed Mosimann shape variables of the talusa (reported in Fig. 7 and Table 4) performed at the genus level on a sample of extant anthropoids (Table S3) as well as Mesopithecus.

CA1 CA2 CA3 CA4 CA5 CA6 CA7 CA8 CA9 CA10

Canonical Variate Functions

Eigenvalue 4.147 2.567 0.776 0.570 0.546 0.272 0.197 0.162 0.107 0.043

% of Variance 44.175 27.344 8.268 6.069 5.814 2.902 2.103 1.723 1.144 0.457

Cumulative % 44.175 71.519 79.787 85.857 91.670 94.573 96.675 98.398 99.543 100

Canonical Correlation 0.898 0.848 0.661 0.602 0.594 0.463 0.406 0.373 0.311 0.203

Standardized Canonical Function Coeffilcients

AS1* 0.064 0.600 _0.084 0.917 0.303 0.738 0.170 _0.199 0.084 1.523

AS2* 0.394 0.595 0.545 1.223 0.473 _0.087 0.225 0.872 _0.055 1.266

AS3* _0.034 0.280 0.361 1.101 0.584 _0.444 0.517 _0.048 0.470 1.295

AS4* 0.257 _0.139 _0.127 0.009 _0.316 0.143 _0.242 0.525 0.084 1.142

AS5* 0.468 1.029 _0.257 0.781 0.408 0.518 1.081 0.824 0.153 1.978

AS6* 0.822 0.168 _0.439 0.686 0.113 0.004 0.399 0.011 0.475 0.454

AS7* 0.322 0.447 _0.308 0.094 0.278 _0.308 0.259 _0.233 _0.610 0.855

AS8* 0.008 0.603 0.067 0.563 _0.761 0.068 0.464 0.103 0.089 0.660

AS9* 0.359 0.891 0.078 0.034 _0.013 0.060 _0.128 0.264 0.726 0.773

AS10* 0.585 0.301 0.650 0.147 0.074 0.468 0.629 _0.101 0.066 0.857

Scores at Group Centroids and Moncucco

Alouatta 2.754 _3.292 0.788 0.346 0.258 0.179 _0.022 _0.161 _0.095 0.118

Ateles 3.253 _2.057 1.970 _0.462 _0.118 1.236 _0.298 0.724 0.351 0.212

Cercocebus _2.229 _0.053 0.282 _0.267 _0.108 0.300 _0.404 _0.751 _0.133 0.176

Cercopithecus _1.105 _1.384 _0.486 _0.216 _0.115 0.235 0.174 0.279 _0.042 0.036

Chlorocebus _1.137 _0.882 _0.223 _0.380 _0.101 0.023 _0.326 0.539 0.140 _0.251

Colobus _0.355 0.218 _0.374 _0.682 1.847 0.087 _0.191 0.172 _0.184 _0.079
 Erythrocebus 0.412 0.341 1.192 _0.052 _0.714 _1.358 1.377 1.158 _1.185 0.125
 Lophocebus _1.472 _0.240 0.325 _0.187 _0.274 0.760 _0.137 _0.559 _0.470 0.007
 Macaca spp. _1.485 _0.336 0.482 _0.193 _1.070 _0.073 0.206 _0.315 _0.101 _0.256
 M. sylvanus _1.334 _0.546 0.484 _0.732 _0.191 0.317 _0.123 0.300 0.643 _0.058
 Mandrillus _1.861 1.952 0.766 _0.080 _0.302 0.246 _0.803 _0.073 _0.246 0.376
 Mesopithecus _1.017 _0.373 0.613 0.127 1.515 _0.398 0.826 _1.198 0.512 _0.059
 Nasalis _1.675 0.469 _0.213 1.216 1.774 0.121 _0.315 0.989 _0.161 _0.314
 Papio _1.718 1.583 1.251 0.760 0.046 _0.237 _0.158 0.090 0.152 0.038
 Presbytis _0.623 _0.355 _0.780 _0.697 1.248 _0.491 _0.416 _0.713 _0.878 _0.147
 Procolobus _0.826 0.810 _1.216 _0.849 0.340 _0.568 0.567 _0.165 0.178 0.766
 Pygathrix _2.061 0.526 _1.456 0.188 _0.019 0.228 0.907 0.368 0.359 0.214
 Rhinopithecus _1.320 _0.523 _0.670 _0.223 0.437 _0.111 0.870 _0.367 0.479 _0.120
 Semnopithecus _2.274 0.274 0.695 0.265 0.654 0.585 0.770 _0.228 0.378 0.297
 Theropithecus _1.383 1.448 0.756 0.182 0.011 _0.718 _0.343 0.347 0.365 _0.029
 Trachypithecus _1.099 _0.203 _0.989 _0.133 0.184 0.131 _0.219 _0.094 0.285 _0.183
 Gorilla 4.010 3.077 0.837 _0.470 0.549 0.207 0.459 _0.214 0.101 _0.141
 Hylobates 1.548 _0.278 _0.753 1.849 _0.139 _0.650 _0.168 _0.215 0.147 0.024
 Pan 2.210 1.550 _1.366 0.078 _0.842 0.572 _0.147 0.149 _0.160 _0.007
 Pongo 3.778 _1.016 _0.291 _2.533 _0.698 _2.072 _1.059 0.266 0.514 _0.029
 Moncucco _0.816 0.022 0.403 0.084 1.843 0.339 _1.058 1.001 _0.416 _0.679

a The asterisk after the abbreviation of each variable as depicted in Fig. 7 denotes the log-transformed Mosimann shape variable, computed by dividing the original variable by the geometric mean of the eleven measured linear variables, and then applying natural logarithms. AS11* failed to pass the tolerance test, and hence was excluded from the analysis.

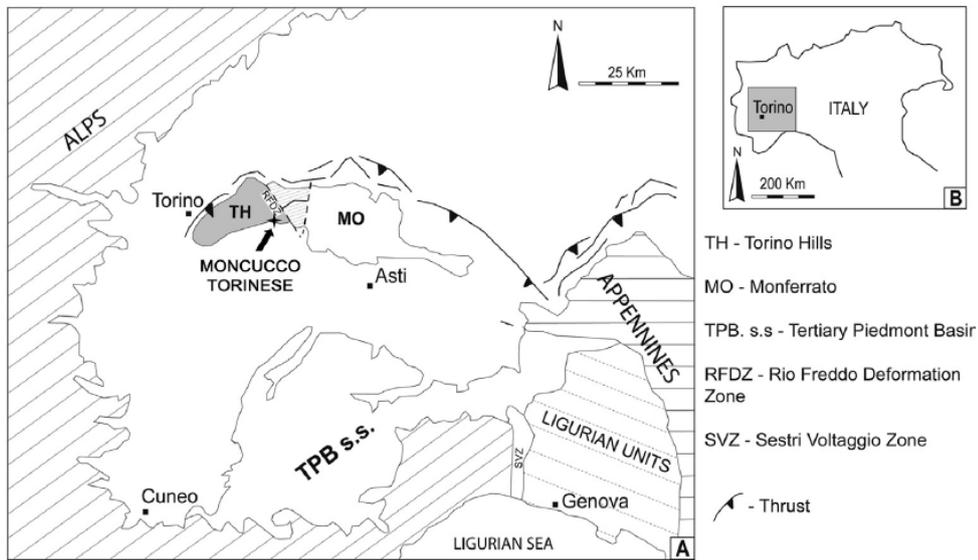


Figure 1. Schematic geological map showing the geographic location and geological setting of Moncucco Torinese. Modified from Zunino and Pavia (2009).

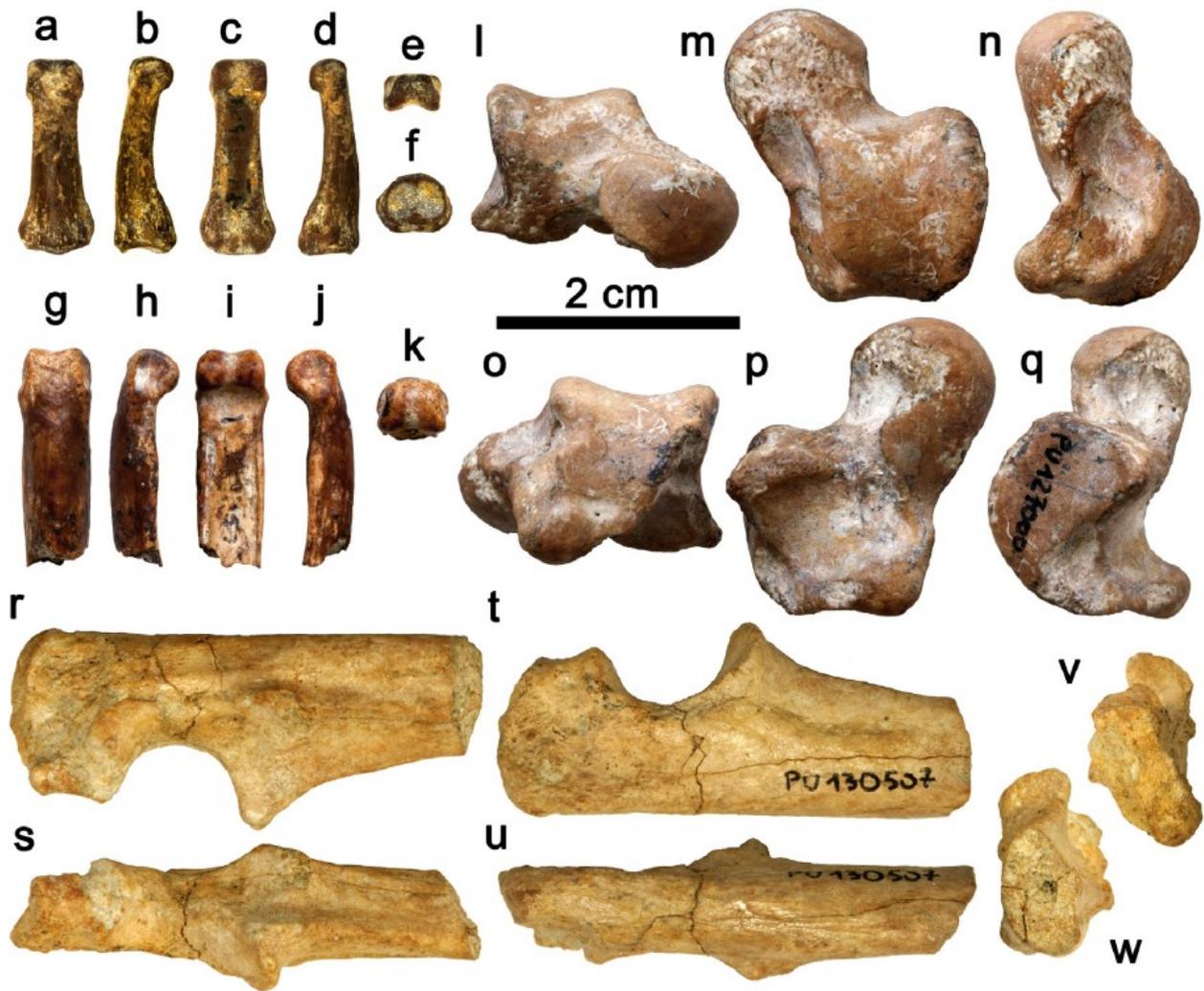


Figure 2. Cercopithecoid postcranial remains from Moncucco Torinese (see Table 1 for further details on geological unit provenance). aef, Intermediate phalanx MGPT-PU 130504 of Cercopithecidae indet., in dorsal (a), volar (c), medial/lateral (b, d), distal (e) and proximal (f) views; gek, Distal fragment of proximal phalanx MGPT-PU 130509 of Cercopithecidae indet., in dorsal (g), volar (i), medial/lateral (h, j) and proximal (k) views; leq, Right talus MGPT-PU 127000 of *Mesopithecus pentelicus*, in distal (l), dorsal (m), medial (n), proximal (o), plantar (p) and lateral (q) views; rew, Left partial (proximal) ulna MGPT-PU 130507 of cf. *M. pentelicus*, in lateral (r), anterior (s), medial (t), posterior (u), proximal (v) and distal (w) views.

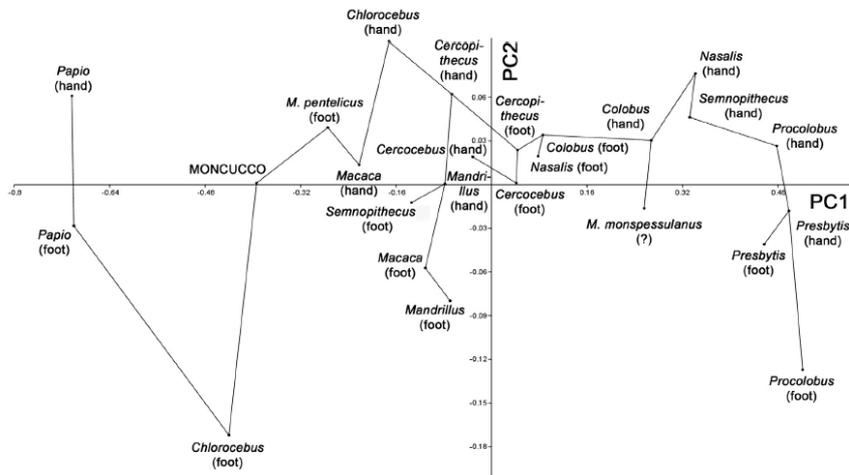


Figure 3. Results of the Principal Components Analysis (PCA) performed with the covariance matrix based on the Mosimann shape variables of intermediate phalanges reported in Table S1 (see also Table S2), depicted as a bivariate plot of PC2 versus PC1 and a minimum spanning tree.

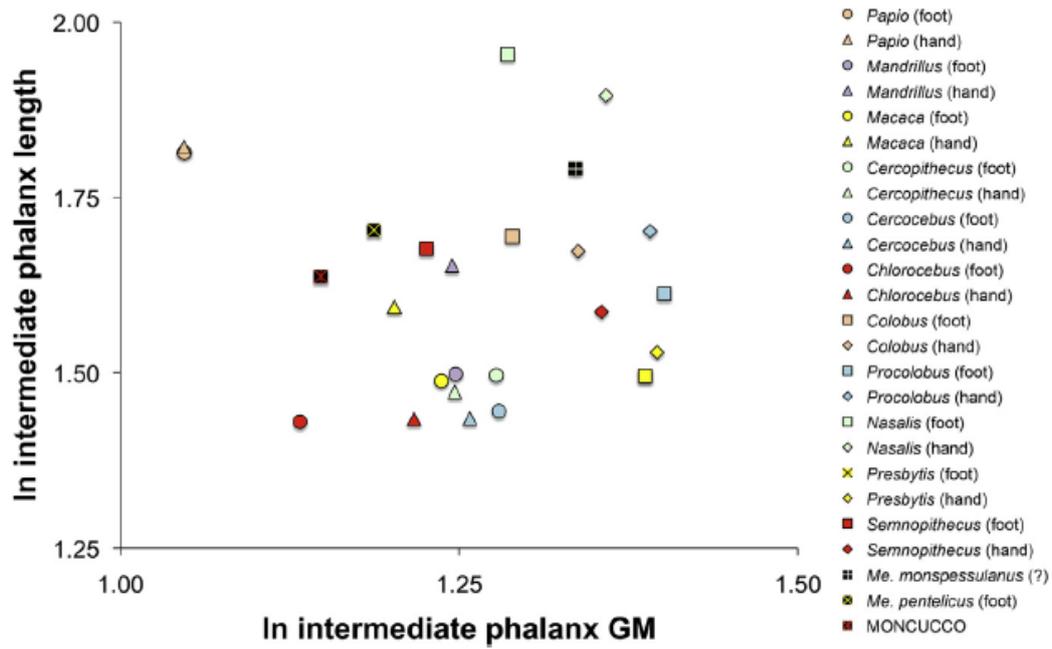


Figure 4. Bivariate plot of log-transformed species mean data for intermediate phalanx length versus the geometric mean of the linear measurements reported in Table S1.

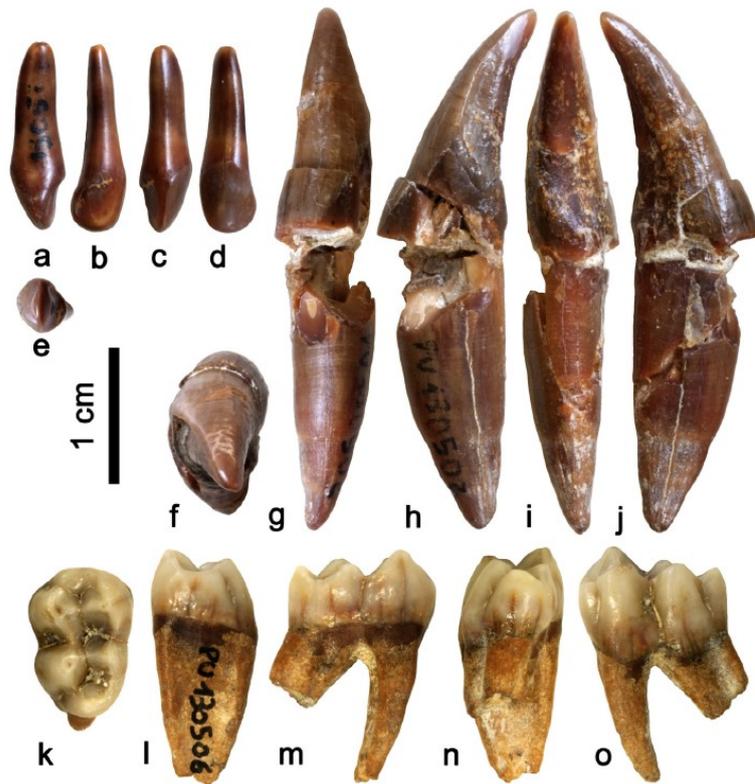


Figure 5. Cercopithecoid dental remains from Moncucco Torinese (see Table 1 for further details on geological unit provenance). aee, Right upper lateral incisor MGPT-PU 130501 of cf. *Macaca* sp., in mesial (a), lingual (b), distal (c), labial (d) and occlusal (e) views; fejj, Right male lower canine MGPT-PU 130502 of cf. *Mesopithecus pentelicus pentelicus*, in occlusal (f), mesial (g), lingual (h), distal (i) and labial (j) views; kem, Left M3 MGPT-PU 130506 of cf. *Macaca* sp., in occlusal (k), mesial (l), lingual (m), distal (n) and buccal (o) views.

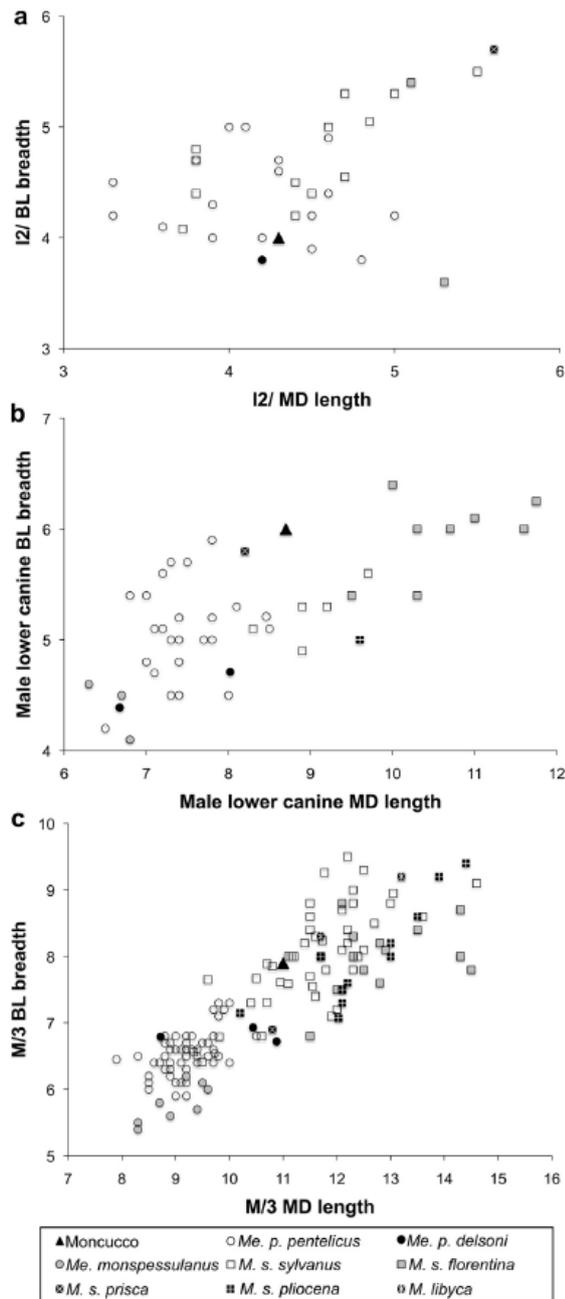


Figure 6. Bivariate plots of breadth (BL) versus length (MD) for the dental remains from Moncucco Torinese, compared with Mesopithecus and Macaca. a, I2; b, lower canine; c, M3. Data for the comparative sample were measured by the authors, taken from NYCEP's PRIMO (PRimate Morphometrics Online) database (<http://primo.nycep.org>), or taken from the literature (Zapfe, 1991, 2001; Mottura and Ardito, 1992; Zanaga, 1998; Koufos et al., 2004; Koufos, 2006; Alba et al., 2008, 2011).

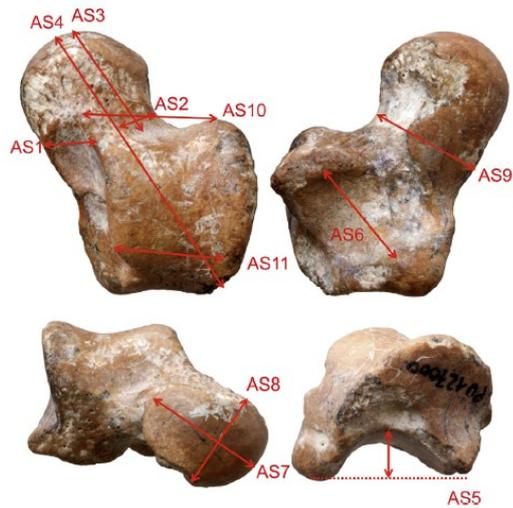


Figure 7. Illustration of the 11 talar measurements employed in this paper (following Youlatos, 1999) on the right talus from Moncucco Torinese MGPT-PU 127000. Abbreviations: AS1, length of talotibial facet on the dorsomedial plane; AS2, length of the neck on the dorsolateral plane; AS3, maximum length of the neck and head; AS4, maximum length of the talus; AS5, height of the posterior talocalcaneal facet; AS6, length of the posterior talocalcaneal facet; AS7, length of the head; AS8, height of the head, perpendicular to the former measurement; AS9, maximum length of the neck on the dorsal plane; AS10, distal length of the trochlea; and AS11, proximal length of the trochlea.

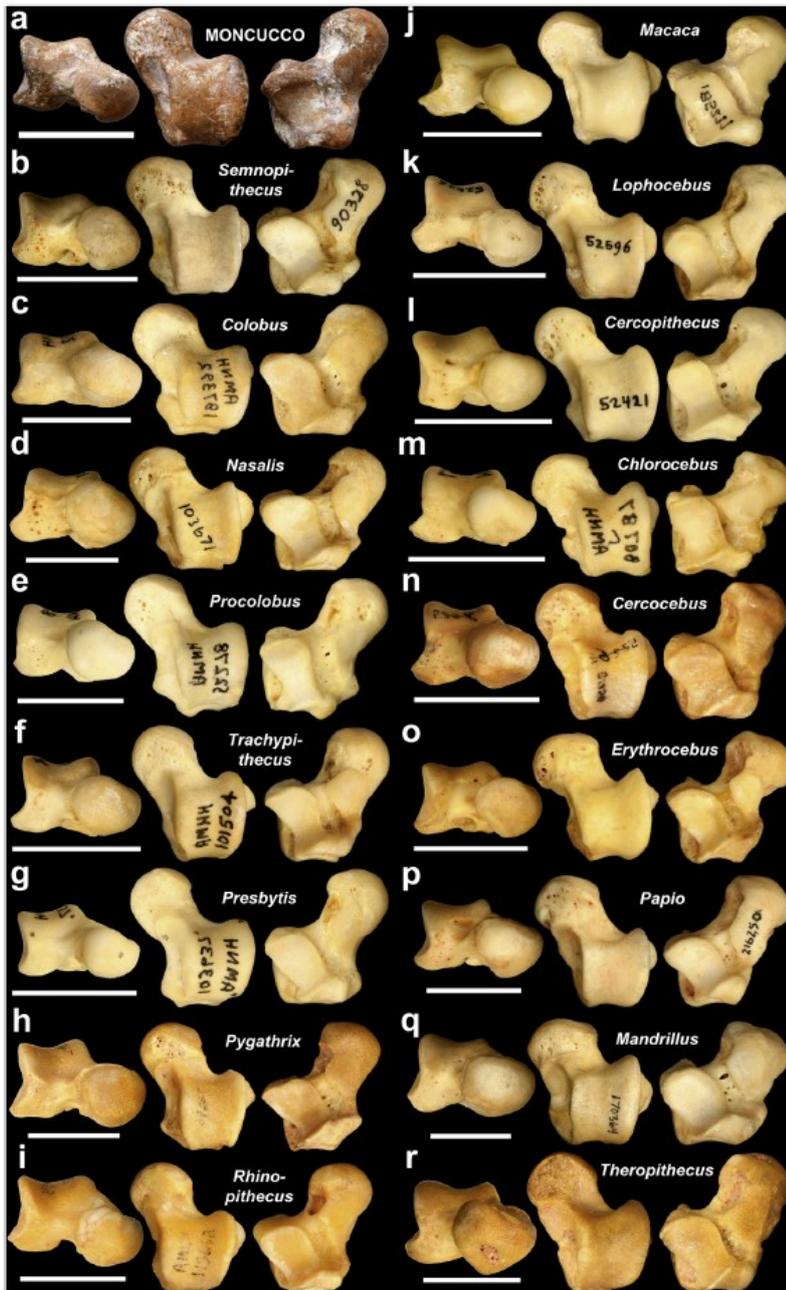


Figure 8. The Moncucco Torinese talus compared with a sample of selected cercopithecoid tali, depicted at approximately the same size (scale bars equal 2 cm), in distal, dorsal and plantar views (from left to right); all specimens depicted as right (indicated below when left reversed). a. *Mesopithecus pentelicus pentelicus* MGPT-PU 127000; b. *Colobus guereza* AMNH 187392 (reversed); c. *Semnopithecus entellus* AMNH90328; d. *Nasalis larvatus* AMNH 103671; e. *Procolobus badius* AMNH 52278 (reversed); f. *Trachypithecus cristatus*

AMNH101504; g. *Presbytis rubicunda* AMNH 103637 (reversed); h. *Pygathrix nemaeus* AMNH 87255; i. *Rhinopithecus roxellana* AMNH 119648; j. *Macaca sylvanus* AMNH 185277 (reversed); k. *Lophocebus albigena* AMNH52596; l. *Cercopithecus neglectus* AMNH52421; m. *Chlorocebus cynosurus* AMNH80787 (reversed); n. *Cercocebus agilis* AMNH 81250 (reversed); o. *Erythrocebus patas* AMNH34713; p. *Papio ursinus* AMNH 216250; q. *Mandrillus sphinx* AMNH170364; r. *Theropithecus gelada* AMNH60568 (reversed).

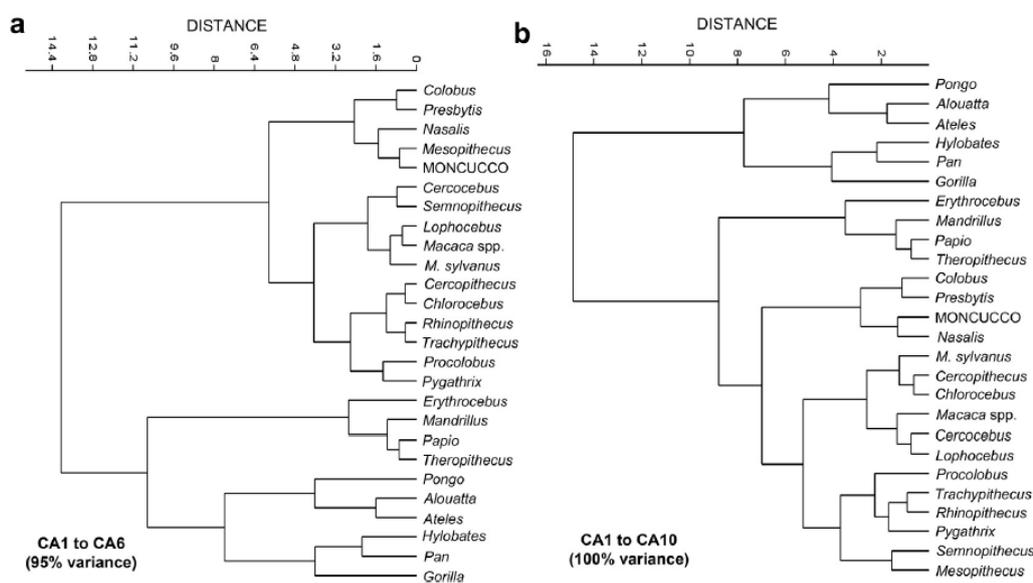


Figure 9. Cluster analysis (Ward's method) based on the results of the CVA performed on the basis of log-transformed Mosimann shape variables of the talus, i.e., on the canonical scores for the Moncucco Torinese talus and the group centroids for extant anthropoids as well as *Mesopithecus* (Table 5). a. Cluster based on canonical axes CA1eCA6 (95% variance); b. Cluster based on CA1eCA10 (100% variance). Note the slightly different results for *Mesopithecus* from Pikermi but not from Moncucco Torinese.