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(Article begins on next page)

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

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Abstract

Cercopithecid 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 cercopithecid 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 cercopithecid 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 cercopithecid 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 MioceneePliocene 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 Moncucco 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 Moncucco 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 0e30 cm-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 0.30e0.50 cm 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 remainswere 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 cercopithecid 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 cercopithecids (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 cercopithecid 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 leftM3MGPT-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 profilewith a distinct third lobe, which are characteristic features of M3. The third lobe bears a welldeveloped 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 cuspule-like 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 buccolinguallycompressed 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 thePliocene 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 notwarranted. 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 straighforward. 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. 2l-q and 8a)

Description and comparisons

Talus The right talus MGPT-PU 127000 (Fig. 2leq) 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,n 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 welldeveloped 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 26.0e32.0, N ¼ 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 cercopithecid 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 as a group 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 Mesopithec s specimens. The cluster analysis distinguishes two main groups: hominoids þ atelids versus cercopithecids. 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 Pikermi. 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 buccolinguallycompressed 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 bya 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 cercopithecid 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 cercopithecid 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 cercopithecid 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 displayedby 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. Theradial 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 cercopithecidlike, 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 cheeketooth 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 substantitate 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; moderatelycurved 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 theMoncucco 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 functionallyrelevant 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 ¼ 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 localites 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) fromWadi 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 NWItaly 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-evaporiti cage (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 cercopithecid 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 relativelywarm 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 therarity 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 MoncuccoTorinese 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 (lessarboreal 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, poorlywooded 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 cercopithecid 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 onsistent 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 cercopithecid 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.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at 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

Measurementsa 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. Me. pentelicus pentelicus 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

MGPT-PU 130509 Cercopithecidae indet. Proximal phalanx >17.9 e e (5.3) (3.8) 5.9 4.4

MGPT-PU 130504 Cercopithecidae indet. Intermediate phalanx 16.2 6.3 4.9 4.2 3.1 4.7 3.1

Catalogue No. Taxon Dental measurements MDb BLm BLd 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: BLd, buccolingual crown width (on distal lobe of molars); BLI, breadth/length crown index, computed as (maximum BL/MD)*100; BLm, 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.

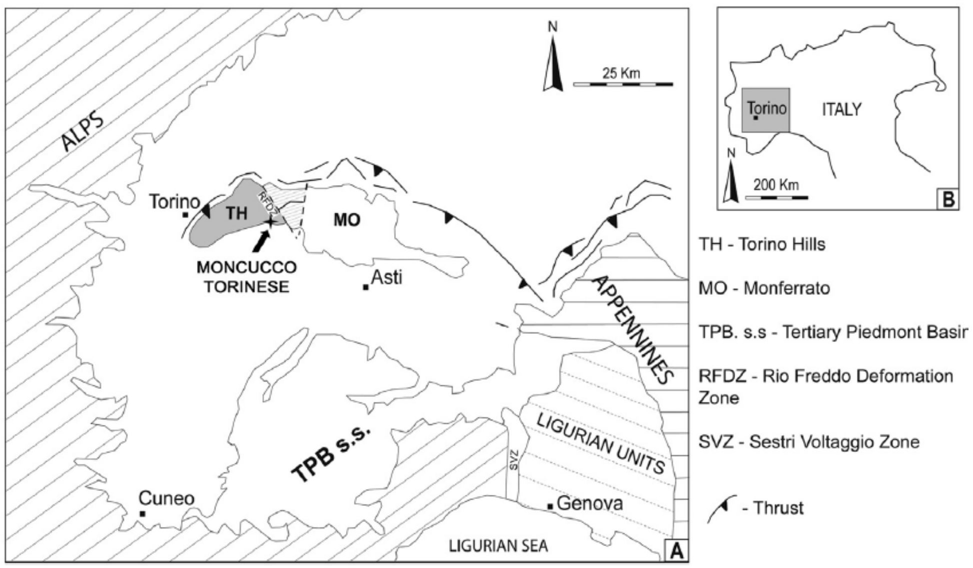

Figure 1. Schematic geological map showing the geographic location and geological setting of Moncucco Torinese. Modified from Zunino and Pavia (2009).

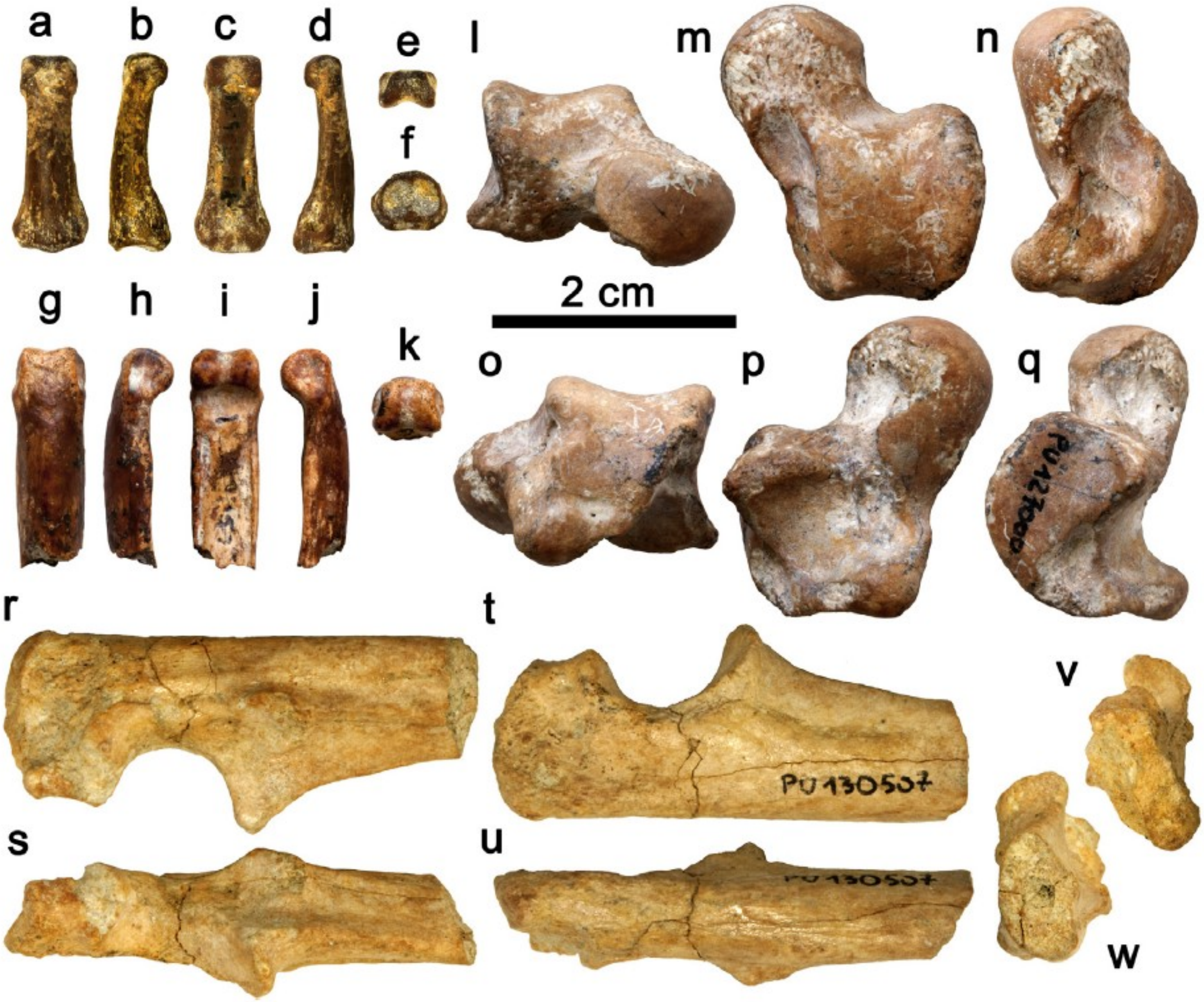

Figure 2. Cercopithecid postcranial remains from Moncucco Torinese (see Table 1 for further details on geological unit provenance). aef, Intermediate phalanx MGPT-PU 130504 of Cercopithecidae indet., in dorsal (a), volar (c), medial/lateral (b, d), distal (e) and proximal (f) views; gek, Distal fragment 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.

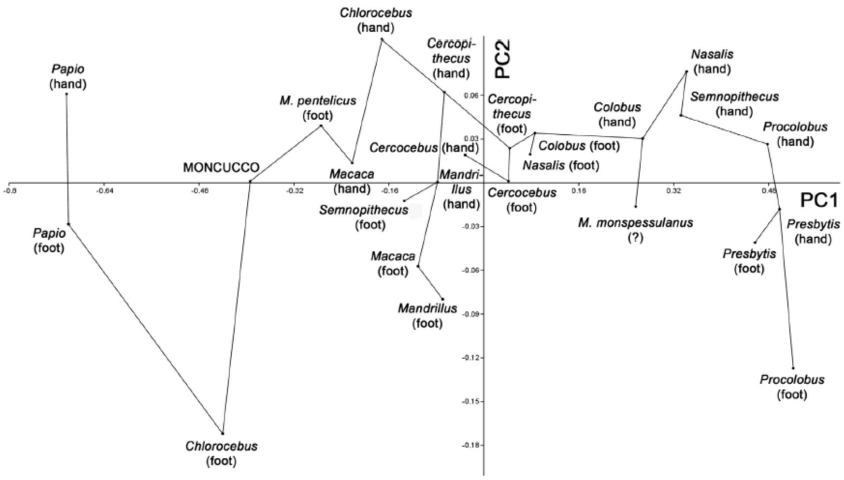

Figure 3. Results of the Principal Components Analysis (PCA) performed with the covariance matrix based on the Mosimann shape variables of intermediate phalanges reported in Table S1 (see also Table S2), depicted as a bivariate plot of PC2 versus PC1 and a minimum spanning tree.

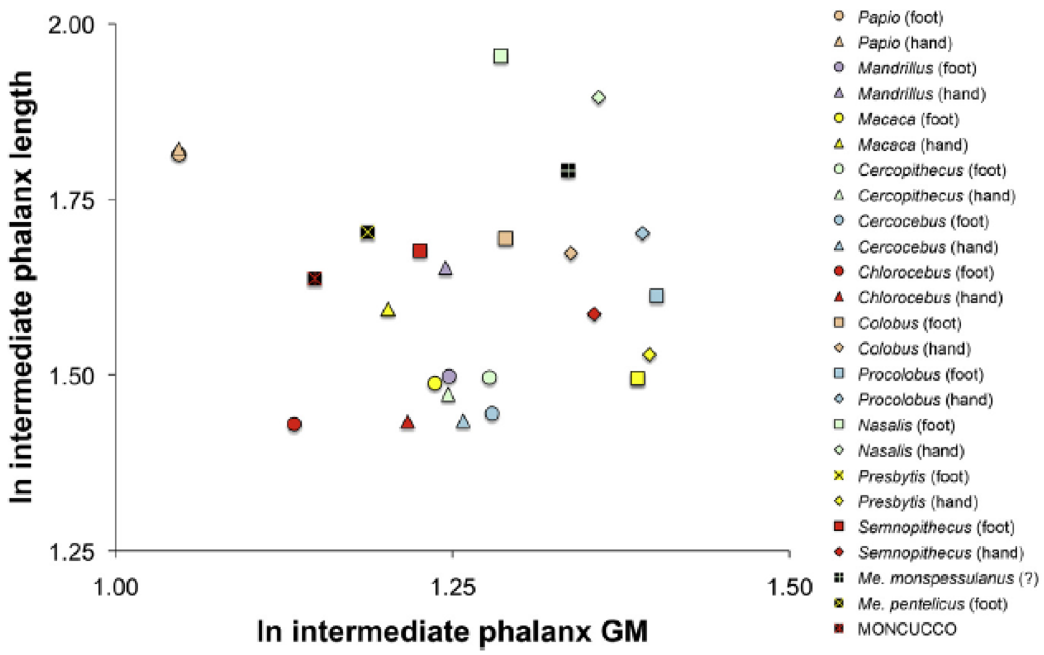

Figure 4. Bivariate plot of log-transformed species mean data for intermediate phalanx length versus the geometric mean of the linear measurements reported in Table S1.

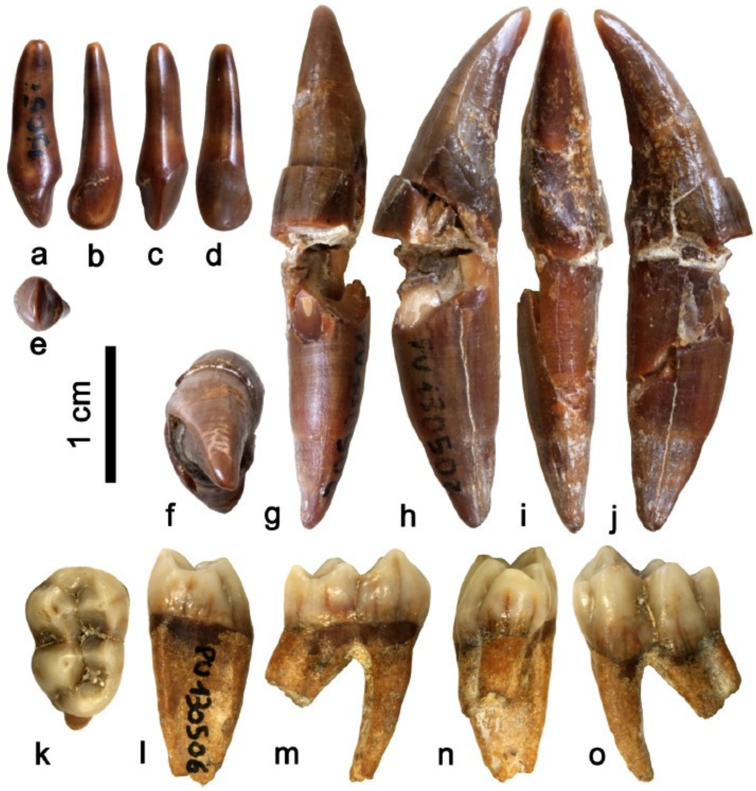

Figure 5. Cercopithecid dental remains from Moncucco Torinese (see Table 1 for further details on geological unit provenance). aee, Right upper lateral incisor MGPT-PU 130501 of cf. Macaca sp., in mesial (a), lingual (b), distal (c), labial (d) and occlusal (e) views; fej, Right male lower canine MGPT-PU 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.

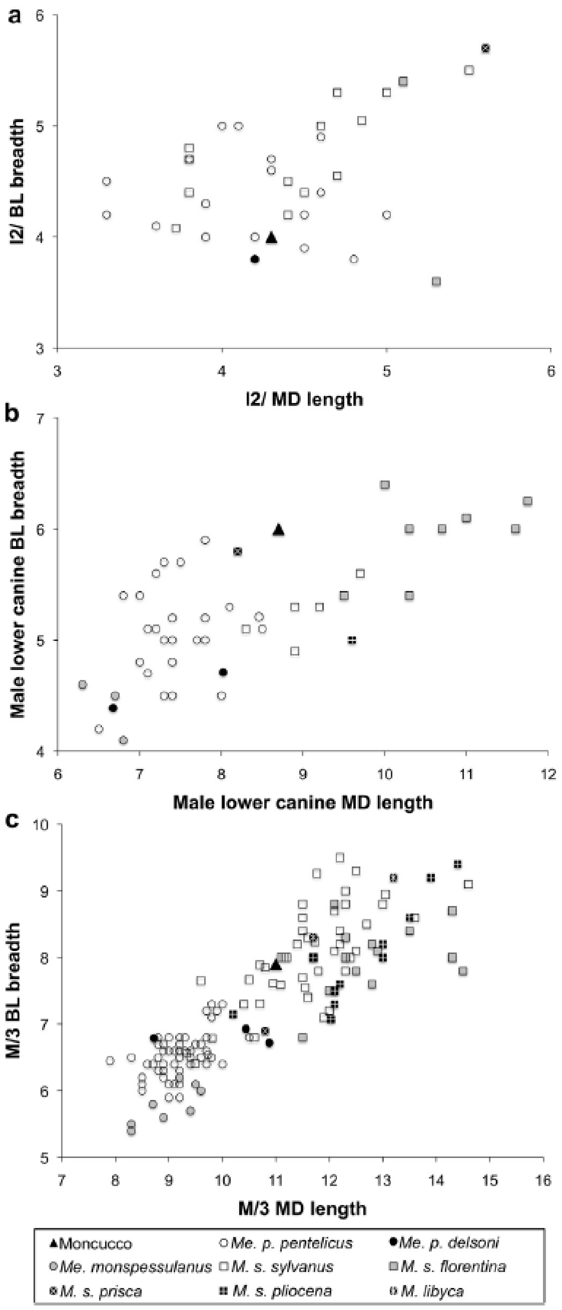

Figure 6. Bivariate plots of breadth (BL) versus length (MD) for the dental remains from Moncucco Torinese, compared with Mesopithecus and Macaca. a, I2; b, lower canine; c, M3. Data for the comparative sample were measured by the authors, taken from NYCEP's PRIMO (PRImate Morphometrics Online) database (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).

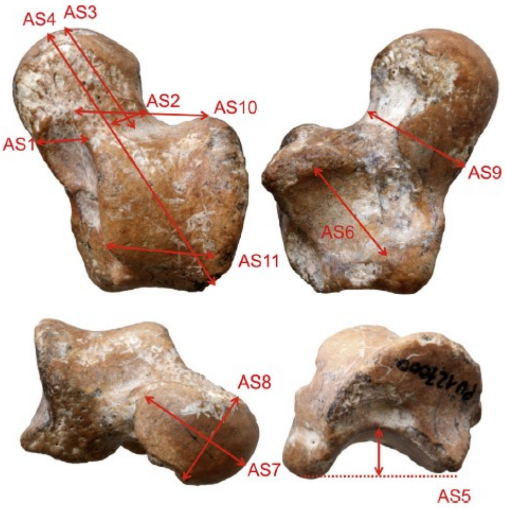

Figure 7. Illustration of the 11 talar measurements employed in this paper (following Youlatos, 1999) on the right talus from Moncucco Torinese MGPT-PU 127000. Abbreviations: AS1, length of talotibial facet on the dorsomedial plane; AS2, length of the neck on the dorsolateral plane; AS3, maximum length 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.

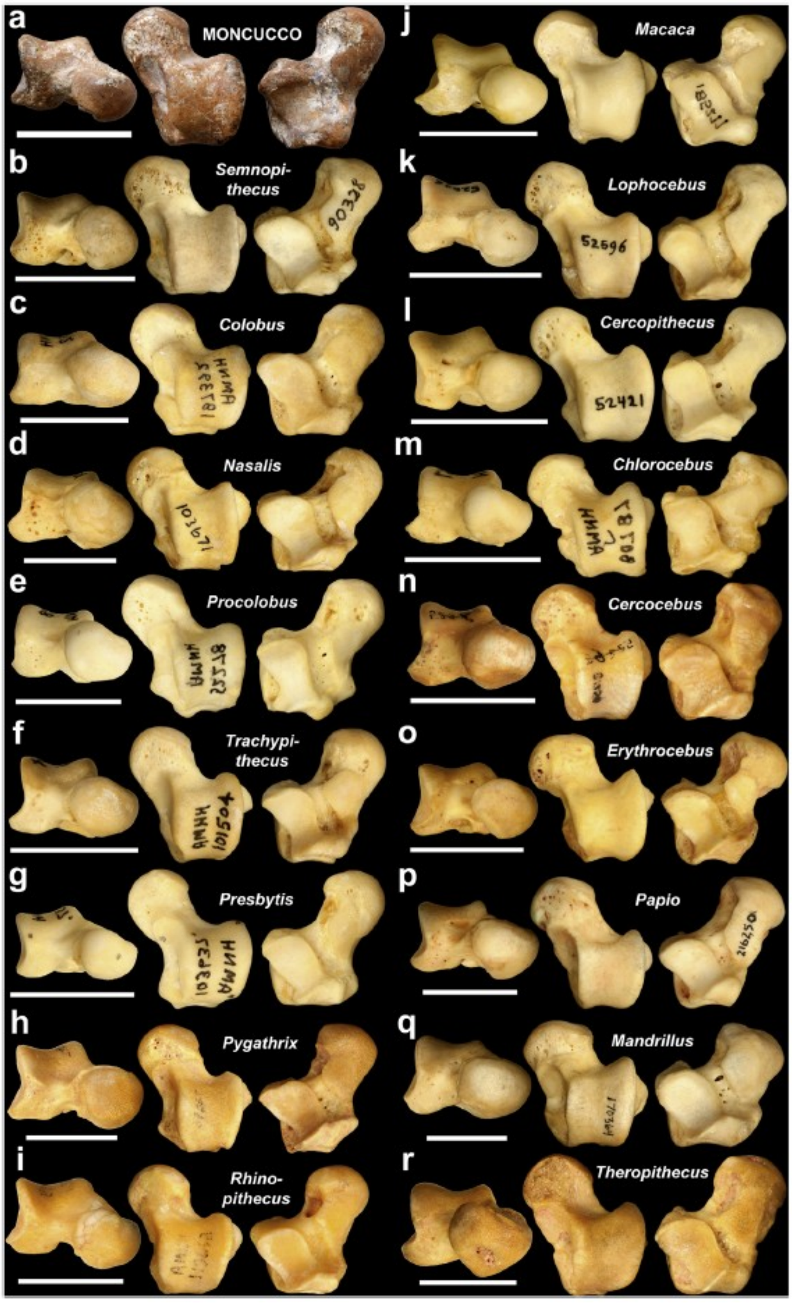

Figure 8. The Moncucco Torinese talus compared with a sample of selected cercopithecid tali, depicted at approximately the same size (scale bars equal 2 cm), in distal, dorsal and plantar views (from left to right); all specimens depicted as right (indicated below when left reversed). a. Mesopithecus 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).

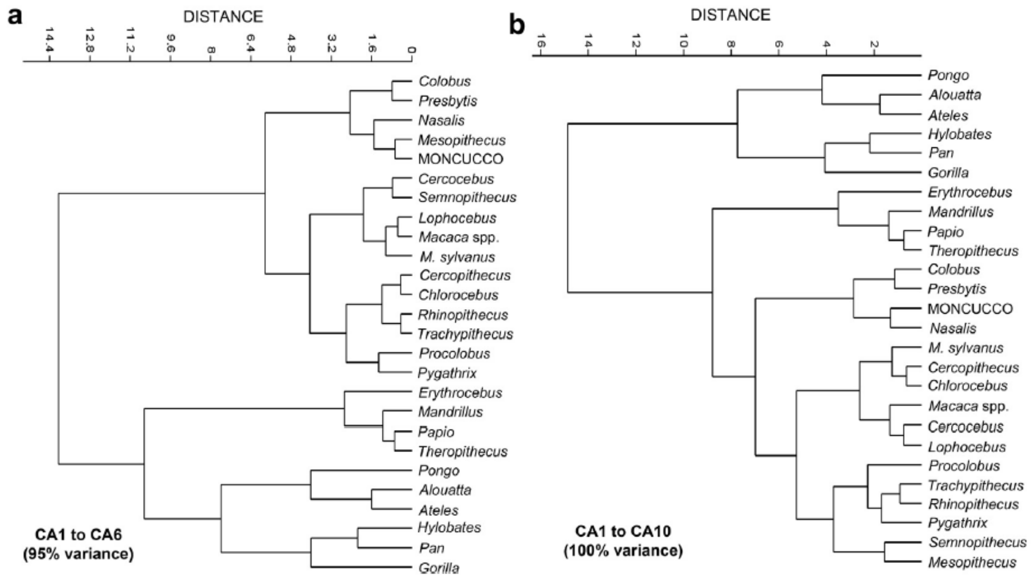

Figure 9. Cluster analysis (Ward's method) based on the results of the CVA performed on the basis of log-transformed Mosimann shape variables of the talus, i.e., on the canonical scores for the Moncucco Torinese talus and the group centroids for extant anthropoids as well as Mesopithecus (Table 5). a. 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.