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Temporal Trends and Dental Metric Variation in the *Macaca sylvanus* Lineage

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Temporal Trends and Dental Metric Variation
in the *Macaca sylvanus* Lineage

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Anthropology

by

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Abstract

The extensive collection of fossil macaques from Europe, spanning from the Late Miocene to the Late Pleistocene period, is believed to be of the species *Macaca sylvanus*. However, there has been a prolonged discussion regarding the classification of these specimens into a single taxonomic group as the existing dental sample exhibits a large amount of morphological and metric variation. Specifically, researchers have attempted to identify multiple subspecies based on chronological data of the paleontological locality and, secondly, based on dental metric variation. In this study, I assess temporal trends in the fossil record of *Macaca sylvanus* and compare overall variation in the extinct sample to variation in extant species and subspecies of cercopithecids and hominoids.

Results indicate a slight decrease in the mesiodistal length or buccolingual breadth of the upper and lower molars from the Plio-Pleistocene sample compared to the extant sample of *M. sylvanus*, but found mixed results between the Early/Middle Pleistocene samples that do not support a directional temporal trend. Instead, models indicate a spatial trend where buccolingual breadth of the lower third molars decreased from the west to the east of the continent. Moreover, the overall variation in the complete fossil sample is so high that the possibility of multiple subspecies is plausible. However, metric variation in the subsamples is contradictory, showing higher variation in the Late Pliocene-Early Pleistocene sample and lower variation in the Middle-Late Pleistocene sample. Through this study, I highlight how metric data of cercopithecines only help to differentiate individuals widespread geographically, as the North African and European fossils. Temporal variation is considered secondarily. In the case of European fossil macaques, the lack of crania from different time periods and geographic regions will keep the debate about the accuracy of chronological subspecies open.

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Introduction

Plio-Pleistocene macaque samples from Europe are known in the literature to represent the evolutionary stages of one species, *Macaca sylvanus* (the Barbary macaque). This species is represented today by the nominotypical subspecies *Macaca sylvanus sylvanus* in northern Africa and Gibraltar, but it was widespread in the past (Fig. 1). The first evidence of *M. sylvanus* in the circum-Mediterranean area came from the Late Miocene (5.9–5.3 Ma) of Spain and Italy (Köhler et al., 2000; Alba et al., 2014). With respect to the fossil record, three subspecies are recognized as belonging to the *sylvanus* lineage: *Macaca sylvanus prisca* (from the Early-Middle Pliocene), *Macaca sylvanus florentina* (Late Pliocene – Early Pleistocene), and *Macaca sylvanus pliocena* (from the Middle-Late Pleistocene). One additional species, *Macaca majori*, has been described from the island of Sardinia; this species was most likely affected by insular dwarfing (Szalay and Delson, 1979; Delson, 1980; Fooden, 2007).

Most taxonomic interpretations of Plio-Pleistocene European macaques follow Delson (1980). He argues for an anagenetic evolution of the *sylvanus* subspecies without major cladogenesis from the Late Miocene form to modern populations. Previous investigators have briefly noted body size fluctuations in this lineage; for example, *M. s. prisca* is the smaller form, *M. s. florentina* is larger and overlapped with the extant form, and the molars of *M. s. pliocena* are relatively broader when compared with *M. s. sylvanus* (Delson, 1980; Alba et al., 2011). Since the alpha taxonomy of the mentioned subspecies is still discussed, scientists often make assignments of fossil specimens on their temporo-geographical position and/or metric analyses.

Few studies have been conducted on the extinct European macaques and their dental variation. Alba et al. (2011, 2018, 2019) made multiple comparisons between fossil macaques from the Iberian Peninsula and Italy. The metrical data tend to overlap, but overall, differences

could be observed between the averages of the absolute values of the teeth for both mesiodistal length and buccolingual breadth. A recent study by Konidaris et al. (2021) describes the dental morphology and dimensions of a Middle Pleistocene fossil from Greece; they used multivariate analysis (analysis of variance) and biochronology to assign the fossils to subspecies. Therefore, these studies emphasize the necessity of a correlation of geographic and/or temporal differences with a morphologic and metrical variation, as some authors use open nomenclature for taxonomical assignments (Alba et al., 2019; Fidalgo et al., 2023) and others refrain from a subspecific designation (Bona et al., 2016; Konidaris et al., 2021).

As a group, macaques are known for their conservative morphology and intra-specific sexual dimorphism, but geographic patterns of variation still tend to emerge. Molecular analysis of living species shows that macaques are more genetically diverse as an adaptation to different geographical areas (Roos et al., 2019 and references therein). Asahara and Nishioka (2017) analyzed possible geographical variations and patterns of size in populations of *Macaca fuscata* (the Japanese macaque). Their results on the population average of M_1 size indicated differences between the eastern and western populations of Japanese macaques. They also identified correlations between geographic variation and phylogeographic structures of dental traits, as well as between dental traits and climate, showing that M_1 size correlates negatively with temperature and precipitation among populations by sex. The study of Ito et al. (2014) on craniofacial variation in extant macaques revealed modifications in facial form as body size increases with latitude (Bergmann's rule). But the same study argued that the *sylvanus* group may be more influenced by factors such as sex rather than latitude (Ito et al., 2014).

It is also possible that temporal trends are present in the fossil macaques. The results of Anezaki et al. (2006) on morphometry of mandibular cheek teeth in a relatively small population

of *M. fuscata* showed a decrease in size from archaeological macaque specimens to modern individuals. More evidence of temporal trends in body size reduction has come from studies on hominoids. Orangutans have been described as showing a progressive reduction in overall dental size from Pleistocene to modern forms (Cameron, 2001; Harrison et al., 2021). Tshen (2016) argues for a reduction of dental metrics in *Pongo* based on geographical differences and adaptation to the environment. Lockwood et al. (2000) tested the hypothesis of stasis in dental and mandibular dimensions in one fossil species, *Australopithecus afarensis*. Using statistical methods (CV resampling; Fligner-Killeen test), they compared the overall levels of variation of the fossil sample with those of extant hominoid species. The comparative sample included subspecies (geographical populations) of *Pan*, *Gorilla*, and *Pongo*, a much larger sample than those present in macaque studies that mostly used living species as a baseline for possible expectations for fossil variations. Lockwood et al. (2000) demonstrated a temporal trend in their *Australopithecus* sample by acknowledging the importance of particular criteria of the fossil record: stratigraphic and geochronological control, reasonably large samples of identifiable specimens, and analyzing taxonomically informative skeletal elements.

Three extinct European subspecies of *Macaca sylvanus* are recognized as descending from a north African ancestor (de Vries and Beck, 2023; Szalay and Delson, 1979). Even though a large proportion of fossils consist of isolated teeth, jaw, and bone fragments, our knowledge of geographic variation in this *sylvanus* lineage requires more investigation to assess the validity of these proposed subspecies. In this study, I use dental metrics as proxy for body size and propose for investigation two specific research questions:

- 1) Are there temporal trends in dental size in circum-Mediterranean *Macaca* from the Pliocene to the present day? Specifically, I predict that the European *Macaca sylvanus*

lineage experienced a trend toward dental size reduction, corresponding to a reduction in body size.

- 2) What are the levels of variation in the fossil samples compared to modern species? Here I anticipate that the range of dental variation in the European *Macaca sylvanus* lineage is consistent with the range of variation observed in living species that vary geographically.

Materials

Macaca sylvanus extinct sample

Data describing craniofacial variation in European *Macaca sylvanus* ssp. was pulled from the literature; this excluded samples of *Macaca majori* (Plio-Pleistocene of Sardinia; Rook and O'Higgins, 2005). For the present purpose, we consider subspecies temporo-geographical attribution as defined by Delson (1980). The sample (Table 1) includes adults from present-day Spain, France, Italy, Germany, Netherlands, Albania, Greece, Czech Republic, Slovakia, and Israel (Alba et al., 2011; Bona et al., 2016; Konidaris et al., 2021; NYCEP's PRIMate Morphometrics Online (PRIMO) database, <http://primo.nycep.org>). Specimens with unknown locality or temporal range were excluded from this study.

The sample size is different for each class of teeth of macaque specimens from the Plio-Pleistocene of Europe (Table 1). For each specimen, details of the specimen origin were recorded, including information about paleontological locality (country, region, locality, latitudinal and longitudinal coordinates expressed in decimal degrees), geological time (eras/sub-eras, mammalian/isotopic MN/MNQ/MIS zones, absolute ages in millions of years [Ma]), and

information about museum collection. When not known, geographic coordinates were estimated based on the position of the paleontological site on a map (Table 2).

Comparative sample

Variation in the sample of fossil macaques is compared to multiple levels of variation in extant primates (Table 3):

1. Two geographically restricted species: *Macaca sylvanus sylvanus*; *Colobus satanas satanas*.
2. Three species within a single genus: *Cercopithecus cephus cephus*, *Cercopithecus nictitans nictitans*, *Cercopithecus pogonias grayi*.
3. One species with considerable geographic variation: *Macaca fascicularis*.
4. One species with two subspecies: *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*.

One of the goals of using comparative samples is to examine current variation in order to compare it with the fossil record. First, I compared variation in the fossil *M. sylvanus* lineage to living members of that same lineage, *M. sylvanus sylvanus*. Then, fossils were compared to other species that are relatively geographically constrained (*Cercopithecus* sp., *Colobus* sp.), and others (*Macaca fascicularis*, *Pan troglodytes*) that are more variable. For example, *Macaca fascicularis* has a broad distribution along insular and peninsular habitats of Southeast Asia, which made Fooden (2006) recognize as many as ten subspecies of *M. fascicularis*. In contrast, the classification of *P. troglodytes* into three subspecies is strengthened on both geographical origins and modern phylogenetic studies (e.g., Ely et al., 2005). This combination of multiple taxa with

different levels of geographic and taxonomic variation provides a broad background against which to compare levels of fossil variation.

The sample for extant *Macaca sylvanus sylvanus* (Table 3) was drawn from the literature and NYCEP'S PRIMO (Primate Morphometrics Online) database (<http://primo.nycep.org>). Other data were provided by Lucas Delezene (for *C. cephus cephus*, *C. nictitans nictitans*, *C. pogonias grayi*, *Co. satanas satanas*, *M. fascicularis*; Table 3). The sample was extended with dental measurements of casts of *M. fascicularis* ssp. and *Pan troglodytes* ssp. provided by Siobhan Cooke. Casts were originally collected as part of a separate research project; as part of this, museum specimens were molded with President Jet Epoxy and cast using Epotek 301 epoxy resin. Tooth measurements were collected directly on the casts by C.S. using sliding digital calipers. Specimens range from young adults (third molar not fully erupted) to old individuals (wearing into the dentine). Individuals with advanced attrition or dental pathologies were excluded from this study. Samples for all species are evenly divided between males and females, though sexes are not considered in the analyses because fossil specimens were not always able to be attributed to sex.

The *Macaca sylvanus* species is the only species with a range outside of the Asian continent, in northwestern Africa (Fooden, 2007) and with fossil evidence in Africa and Europe from ca. 7-6 million years ago (Ma; Fooden, 2007; Alba et al., 2014). Extant populations inhabit deciduous and coniferous forests in Algeria, Morocco, and Gibraltar (not native), manifesting a large ecological plasticity (Ménard, 2003; Modolo et al., 2005; Fooden, 2007). The individuals in our comparative sample are reported from Algerian and Moroccan populations (Delson in PRIMO database).

Specimens of *Cercopithecus cephus cephus* are collected from different districts of southern Cameroon. This species is distributed in rainforests in western Africa. The sample of *Cercopithecus nictitans nictitans* come from different locations in Southern Cameroon, Gabon, Democratic Republic of Congo (DRC). Generally, this species is spread across a variety of dense forest habitats ranging from western Africa (Guinea) to the DRC in the east. *Cercopithecus pogonias grayi* is endemic to southern Cameroon, parts of southern Nigeria, and Bioko. They are primarily found in lowland and submontane rainforests. The individuals in this sample are described from different districts in southern Cameroon. Our sample of *Colobus satanas satanas* includes individuals found along the Ongue and N'Yong River, Cameroon. There are two subspecies of *Co. satanas*, *Co. s. satanas* and *Co. s. anthracinus*, distributed in the forests of Gabon, Congo, southwest Cameroon, and Equatorial Guinea.

For the purposes of this study, individuals of *M. fascicularis* are grouped considering their geographic position and distance from the ocean into mainland, continental (on the continental shelf), and oceanic (oceanic islands), while the chimp samples are represented by two subspecies. Due to the lower number of individuals registered on mainland localities (Table 4), only the continental and oceanic categories were considered for statistical analyses. The chimp sample is comprised of individuals identified as coming from two different subspecies separated by Congo and Ubangi River: *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii* (Table 4).

Methods

Measurements and variables

For analyses of the dentition, upper and lower tooth rows from P4 to M3 were analyzed. Dental data consists of maximum mesiodistal crown length (MD, in mm), buccolingual crown breadth (BL, in mm), and their breadth/length index. In the case of molars, buccolingual breadth is taken at the mesial lobe (BLm). Dental measurements of extant specimens of *M. fascicularis* and *P. troglodytes* were collected with a digital caliper (0.1 mm error) by C.S. Mesiodistal measurements were not corrected for interstitial wear, potentially introducing errors. The breadth/length index was calculated as the proportion between BLm and MD ($BLm/MD * 100$). Dental measurements of the fossil samples were collected from the literature as explained above.

Most data fail to assume normality, and the variance is not consistent between tooth variables or tooth classes per species. I used the nonparametric statistic Spearman rank correlation to correlate and compare data. Boxplots and bivariate plots of MD vs. BL were used to visualize the degree of overlap between fossil and comparative samples for each tooth class.

Research question 1. *Temporal trends*

My first research question predicts that I will observe a tendency toward body size reduction (and by proxy, craniodental dimensions) in time, and subspecies variation determined by their wide geographical range. To test this prediction, each tooth category for the fossil sample was analyzed in relationship with the temporal period (era/sub-era, absolute age) and geographical information (longitude, latitude, and country) of the specimen. One-way ANOVAs were used to test for differences in dental metrics between time periods and countries. Pairwise post hoc comparisons were performed using Tukey's Honestly Significant Difference (HSD) test. All one-

way ANOVAs and Tukey's HSD tests were performed in R Studio v. 4.2.2, with a critical alpha of 0.05 and a confidence level of Tukey's HSD of 0.95%. Spearman rank correlations were used to assess the correlation between dental size and longitude, latitude, and absolute age in the fossil record. The fossil individuals are generally distributed between -8.62 decimal degrees (dd) E – 35.57 dd W; 32.68 dd N – 51.93 dd N (Table 2). For sites with multiple individuals, the Spearman rank was calculated with the mean of the dental variable for that site, rather than including all individuals separately.

Research question 2. *Extant sample variation*

The second research question predicts that the range of dental variation in fossil *Macaca* is consistent with living species. To test for variation, three statistical models were created. All following tests were performed in R Studio v. 4.2.2, with a critical alpha of 0.05.

First, I compared my fossil sample to an extant sample of the same species, *Macaca sylvanus*. Because extant samples were small, and data are nonparametric, a Mann-Whitney U test was conducted to assess differences of MD, BL, and BLI means of each tooth in P4-M3 tooth row between the extinct and extant individuals of *M. sylvanus*.

Second, I compared variation in the entire fossil sample separately to *Cercopithecus cephus cephus*, *Cercopithecus nictitans nictitans*, *Cercopithecus pogonias grayi*, *Colobus satanas satanas*, *Macaca fascicularis*, and *Pan troglodytes*. The fossil sample was further compared to the subsamples of *M. fascicularis* (continental and oceanic) and the two subspecies of *Pan*, *P. t. troglodytes* and *P. t. schweinfurthii*. Because sample sizes for these extant taxa were often considerably larger than the fossil sample, I used a bootstrapping methodology with the coefficient of variation (CV) to compare variation in the fossil samples with extant variation. The sample size

was adjusted by calculating the coefficient of variation for small sample size $V = [(1 + \frac{1}{4} * \text{sample_size}) * CV]$ for all sample sizes. Here, I first calculated the CV of the fossil sample and then compared the fossil CV to a bootstrapped distribution (1000 replicates, with replacement) for each of the extant samples matching the fossil sample. This was done separately for the three metrical variables (MD, BL, and BLI) of upper and lower teeth from P4 to M3.

Third, the fossil sample size was split into three subsamples representing the fossil subspecies of *M. sylvanus* as defined by Delson (1980) and Alba et al. (2011; see Introduction). Due to the biases in the fossil record, the sample size of *Macaca sylvanus prisca* is too small to be considered for these purposes (Table 1). Therefore, statistical models only involve subsamples of individuals previously described as *Macaca sylvanus florentina* and *Macaca sylvanus pliocena* (see Table 1 for each tooth category). Once the fossil sample had been split, *M. s. florentina* and *M. s. pliocena* samples were compared with each species and subspecies of extant primates using the CV method as described above.

For all the CVs models, I report one-tailed probability for the highest levels of variation; probability levels were significant when $p < 0.05$. In other words, I test for more variation in the fossil sample compared to the extant sample, and therefore report the right tail probability. When $p < 0.05$, then the variation in the fossil sample exceeds that of the extant sample. R script for the CV analyses was originally created by Dr. Lucas Delezene.

Results

RQ1. Temporal trends

One way ANOVA

Results of the ANOVA comparing geological time periods found significant differences for M^2 BL ($p = 0.007$; $F = 9.308$), M^2 BLI ($p = 0.024$; $F = 6.179$) and for M_1 BLI ($p = 0.024$; $F = 3.589$) (Table 5, Fig. 2). According to the Tukey Post Hoc analyses, M^2 BL ($p = 0.007$) and BLI ($p = 0.024$) values from the Early Pleistocene are significantly larger than those from the Middle Pleistocene (Fig. 2, top). In contrast, M_1 BLI ($p = 0.048$) values increased over time (Fig. 2, bottom). No results were reported for the M^3 sample as it was only registered from a single period of time.

ANOVAs examining geographic differences found significant p-values for M^3 MD ($p = 0.010$; $F = 6.5$) and M_2 BL ($p = 0.030$; $F = 2.485$). The Tukey Post Hoc test showed that the sample from Italy was significantly larger (M^3 MD; $p = 0.008$) than that from Israel (though not Spain or France) (Table 6, Fig. 3, top). For M_2 BL, a boxplot (Fig. 3, bottom) shows that there is substantial variation among countries, though the posthoc test found no significant differences (Table 7). No results are reported for P^4 as individuals are described from the same country.

Spearman rank correlation

The Spearman rank correlation (r_s) reveals that dental variables of extinct *Macaca sylvanus* are influenced differently by longitude, latitude, and geological age (Table 8, Fig. 4). The buccolingual breadth ($r_s = -0.624$; $p = 0.030$) and the buccolingual index ($r_s = -0.818$; $p = 0.002$) of the lower third molar decrease with longitudinal distribution from west to east, with the BLI

showing a high negative correlation (Table 8). Dental metrics were not highly impacted by latitudinal distribution (Table 8). There is a slight increase in the BLI of the M_1 ($r_s = 0.474$; $p = 0.035$) and BL of the M_2 ($r_s = 0.416$; $p = 0.054$) as the specimens are distributed on higher latitudes; however, the results show a low positive correlation of the dental metrics with latitude. Relative to geological age, there is a decrease in the MD and BL of M^2 as time passes (Fig. 4). The factor of time seems to affect both measurements of M^2 , the results expressing a highly positive correlation between dental metrics and geological age (MD: $r_s = 0.744$; $p = 0.021$; BL: $r_s = 0.756$; $p = 0.011$). These results indicate that longitude and latitude have a partial effect on lower molar size, whereas geological age supports the initial hypothesis of size reduction for the upper second molar.

RQ2. Sample variation

Comparisons to extant *Macaca sylvanus*

The result of the Mann-Whitney U tests (Table 9) between the extinct and extant *M. sylvanus* show significant differences for multiple different dental measures for M_1 , M_2 , and M_3 , though significance varies depending on the tooth and measurement. Generally, fossil macaques display absolutely longer molars (M^1 , M^2 , M_1 , M_2 , M_3 ; Fig. 5) and relatively broader molars (M^1 , M^2 , M^3 , M_1 , M_3 ; Fig. 6) as compared to extant individuals

Complete fossil sample compared to extant species

Results of the CV analyses (Tables 10-12) vary by tooth and extant sample used for comparisons. Within the *Cercopithecus* genus (Table 10; Fig. 7), all three species register different

levels of variation depending on the dental variables. Fewer significant ($p < 0.05$) p-values are reported for lower teeth; instead, most significant differences in variation in the fossil sample are for the upper teeth. Patterns are generally similar for all three subspecies of *Cercopithecus* (Fig. 7). In contrast, when the fossil data are compared to the CV distributions for *Colobus*, all but five variables are significant (Table 10).

Comparisons between the entire extinct *Macaca sylvanus* sample and *Macaca fascicularis* are significant for only two variables (Table 11, 12; Fig. 8). However, when the *M. fascicularis* sample is broken into continental and oceanic groups, more variables show elevated variation in the fossil sample compared to the extant taxa. A similar pattern is seen when the fossil sample is compared to *Pan troglodytes*, with the CVs for the fossils only exceeding that for *Pan* in five variables (Table 11, 12; Fig. 8). Comparing the entire fossil sample with subspecies of chimps, there are more significant comparisons of extinct *M. sylvanus* to *P. t. schweinfurthii* (15 of 24 tooth variables) than to *P. t. troglodytes* (4 of 24 tooth variables).

Subsets of the fossil sample compared to extant species

After dividing the extinct sample into subspecies, fewer dental variables express significant results (Tables 13-18).

In *M. sylvanus florentina*, I report no results for P^4 due to the small sample size. When this subspecies is compared to the *Cercopithecus* species, only a handful of variables have fossil CVs that exceed the extant sample. However, the pattern for *Colobus* remains, where most of the fossil variables for *M. s. florentina* have CVs that exceed the extant distribution (14 of 24 tooth variables; Table 13). The buccolingual breadth of P_4 in *M. s. florentina* is statistically more variable for than

all species and subspecies groups to which it was compared (Table 14, 15; Fig. 9), though patterns for other teeth are variable.

Results for *M. sylvanus pliocena* suggest this group is more conservative than *M. s. florentina* (Fig. 10) or the complete fossil sample, having a lower level of general variation among tooth variables (Tables 16-18). In comparison to the *Cercopithecus* species (Table 16), only a handful of comparisons are significant, while the results for *Colobus* continue to show a high number of significant comparisons (12 of 24 tooth variables). There are no significant p-values when *M. s. pliocena* is compared to the entire sample of *M. fascicularis* (Table 17, 18), still a few comparisons of the first and the second molars are significant when the *M. fascicularis* sample is broken down. More comparisons are significant for the *Pan troglodytes* samples (Table 17, 18), though this is primarily for *P. t. schweinfurthii* lower dentition.

Overall, the P₄ BL variable shows a higher degree of variation in the complete fossil sample and also in the *M. s. florentina* subsample, expressing significant results in all CVs. When considering the *M. s. pliocena* subsample, higher variation for this variable is observed in comparisons with *Colobus* and *P. t. schweinfurthii*, two samples with restricted geographical area. The complete fossil sample shows more variation than the broken-down samples. However, *M. s. florentina* displays a larger number of variables indicating increased variation compared to *M. s. pliocena*.

Discussion

Historically, the circum-Mediterranean macaque fossils (Fig. 1) have been attributed to a multitude of distinct species designations (Szalay and Delson, 1979; Delson, 1980). However, the

longevity of *Macaca* starting in the Late Miocene of Europe and throughout the Pliocene and Pleistocene is characterized by a wide geographical distribution and conservative cranial and dental morphology. Modern authorities (Delson, 1980; Alba et al., 2008, 2011, 2019; Marigó et al., 2014; Fidalgo et al., 2023) argue for a distinction between extinct subspecies based primarily on temporal-geographic correlations. However, current knowledge of the European macaque's subspecies anatomy and local geographic conditions are insufficient for a distinguishable taxonomy (e.g., Bona et al., 2016; Reumer et al., 2018). Additionally, as previous studies have shown across multiple primate groups (e.g., Cameron, 2001; Anezaki et al., 2006; Tshen, 2016), associations of dental metric sizes with the environment could potentially reveal different adaptive responses of the species to their habitat if dental size is considered a proxy for body size.

This study focused on two major research questions: (1) potential temporal or geographic trends in the fossil record of European *M. sylvanus* and (2) levels of variation in the fossil sample of *M. sylvanus* compared to extant groups. Unfortunately, the data in this study do not reveal much in the way of geographic or temporal patterns. Yet, consistent with prior research, variation in the sample is high, but how large it is comparatively varies. The analysis of upper and lower postcanine teeth reveals a mix of patterns that help to slightly distinguish temporal subgroups. However, intraspecific comparisons showed dental size does not vary with latitude in the European *M. sylvanus* but could differentiate the European population from the isolated populations from Israel and North Africa.

A similar study that used dental size as proxy for reconstructing body size of fossil *M. sylvanus* was the allometric regression of Delson et al. (2000: Table 15). However, in the mentioned study, only specimens from Valdarno, Italy, were considered in the sample of *M. s. florentina*; *M. s. pliocena* was represented by specimens collected from various sites from Europe,

and the specimens from ‘Ubeidiya, Israel, were recorded as a different population of *M. s. pliocena*. More recently, the same authorities attributed the specimens from ‘Ubeidiya to *M. s. florentina*. For this study, I consider the recent, holistic view of the temporal subspecies of the extant *M. sylvanus*, with all specimens from the Late Miocene-Early Pliocene considered *M. s. prisca*, all specimens from the Late Pliocene-Early Pleistocene considered *M. s. florentina*, and all individuals described from the Middle-Late Pleistocene considered *M. s. pliocena*.

RQ1. Temporal trends

The first goal of this study was to examine temporal and geographic variation of the extinct subspecies of *M. sylvanus*, also considering the change in the environment between different periods of time. Prior investigations of the collection of teeth of macaques available in the literature and databases from the Plio-Pleistocene of Europe suggest a decrease in body size (as reflected by dental size) from the fossil sample to the extant populations (e.g., Delson et al., 2000). The body size of catarrhine primates decreased from the Pleistocene to present day (e.g., Cameron, 2001; Anezaki et al., 2006; Tshen, 2016). However, this trend of dental metrics and body size reduction has only been described for Asian primates and it is therefore not clear if the conditions on the European continent allowed a similar direction for primate evolution.

For *M. sylvanus* subspecies, previous research (e.g., Alba et al., 2011; Konidaris et al., 2021) reports longer and broader upper molars for *M. s. florentina* compared to *M. s. sylvanus*. On the other hand, *M. s. pliocena* is described as having wider molars than other subspecies (Alba et al., 2011, 2019). Although there may be a slight difference in size between the two groups, the measurements of the dental series and the morphology of the crown of the molars do not fully

support differentiation of these subspecies; therefore, some authorities designated their specimens based on (bio)chronology (e.g., Castaños et al., 2011; Konidaris et al., 2021).

Based on the analyses here, most dental variables do not express any type of temporal or geographic patterning. Where there are significant relationships, the patterns conflict. For example, two of the variables exhibit two opposite directions of size modification in the Pleistocene: M^2 BLI decreases from Early to Middle Pleistocene, supporting the initial hypothesis of body size reduction over time, while M_1 BLI increases. Despite the limited sample size for different temporal groups, the size of M_1 increased from the Early to Middle Pleistocene and remained constant between the Middle and Late Pleistocene, as indicated by the buccolingual index.

The Spearman rank correlation on geological age provides additional support for a decrease in M^2 MD and BL but not in the BLI or any significant change in the M^1 BLI. However, between 1.5 and 1 Ma, there is a mix of large and small individuals, outliers in the presented correlation model. This period is interesting as it represents the second part of the Early Pleistocene subdivision and, in accordance with prior work on subspecies designation, a moment of overlap between *M. s. florentina* and *M. s. pliocena* (Zapfe, 2001; Alba et al., 2011; PRIMO data base). The sample from the Late Pliocene to Early Pleistocene is typically linked to *M. s. florentina*, while *M. s. pliocena* is described from the Middle to the Late Pleistocene. Thus, it is observable that a smaller version of *M. s. florentina* was present in the Early Pleistocene of Israel (~1.5-1.2 Ma; Rink et al., 2007; Martínez-Navarro et al., 2009) than the specimens from Europe. During the same time period, the mean BL of *M. s. florentina* from Italy was significantly larger from the Israel group of *M. s. florentina* and smaller than *M. s. ssp.* from Spain. Previous investigations (Alba et al., 2011; Konidaris et al., 2021) that included the sample from ‘Ubeidiya argue for a wider M_2 BL

of *M. s. pliocena* (Middle-Late Pleistocene) than in *M. s. florentina* (Late Pliocene – Early Pleistocene).

It is difficult to fully support the theory that size has decreased over time due to mixed signals and varying patterns in different variables. The upper teeth in this sample are smaller than the one of lower teeth across all time groups. To accurately analyze metric variation, it is important to correlate geological time with geographical coordinates. However, this approach results in an even smaller sample size.

This study also analyzed geographic variation in dental size relative to longitudinal and latitudinal coordinates and country. The sample size is smaller than when the specimens are grouped by time period and is slightly unequal with more specimens reported from Western-Central Europe than Eastern Europe or the Levant. Therefore, it is difficult to establish the relationship between neighboring populations and populations that possibly interbreed, which would help us better understand the level of ecological and geographical segregation of Barbary macaques at a given time (e.g., Albrecht and Miller, 1993).

The results here indicate that the dental size of the European macaques does not differ statistically by country. However, results are mixed and indicate that specimens from Europe and the Levant corridor are significantly different, with the specimens from ‘Ubeidiya, Israel, being significantly smaller than the other samples examined. For example, the ANOVA results show a statistically significant difference between the Italy and Israel samples at the level of M^3 MD but not between the Italian sample and the other European samples at any given time.

This study found a longitudinal gradient at the level of M_3 , which shows a slight decrease in the mesiodistal length and the buccal breadth from west to east. On the other hand, during the

Pleistocene, the European macaques have been generally described from interglacial localities (e.g., Delson, 1980). The Spearman rank correlation shows a low relationship between latitude and dental size (M_1 BLI and M_2 BL) expressed via a large degree of overlap between the European subspecies. Latitude contributes to the level of variation in some cases when comparing European and the Israeli fossil samples. Yet, correlations with geological age are only significant for the M^2 (MD and BL) sample, which lacks individuals from ‘Ubeidiya. This tooth shows a change restricted to the European continent; the other variables are probably influenced by the specimens from Israel.

RQ2. Sample variation

For the second part of this study, I examined levels of variation in the extinct and extant dental samples of *M. sylvanus* relative to several extant species and subspecies of catarrhines. The results of this study support previous research indicating that levels of variation in fossil *M. sylvanus* are high and are consistent with the first part of this study related to the relationship between size, spatial distribution, and age.

The pattern seen in the fossil record of *M. sylvanus* is expected for a sample with different geographical and temporal distribution (e.g., Plavcan, 1973; Albrecht et al., 1990). Variation in tooth samples is high when compared to black colobus and the three groups of *Cercopithecus*, relatively high for chimps, and low compared to *M. fascicularis*. Comparative analysis of species of the genus *Cercopithecus* reveals a pattern of more variation in the upper teeth compared to lower teeth, except for P_4 length and breadth. The picture is slightly different for *Co. satanas*, which show a lower level of variation for all the statistical models. This result could be related to sexual dimorphism of the postcanine teeth (Plavcan, 1973), the highly restricted geographical area of the

colobine sample, and also the fossil sample and subsamples being collected from different parts of Eurasia with a large geographic extent.

However, two tooth variables are consistently higher in variation in fossil *M. sylvanus* compared to all extant comparative groups, M^3 MD and P_4 BL. This could be due to both the development and function of these teeth in primates. The Inhibitory Cascade Model (Kavanagh et al., 2007) directly influences the relative size of the mandibular molars, with secondary consequences on upper molar development. The heritability of this trait also varies among primates, with macaques showing greater heritability of MD molar length relative to body size (Hardin, 2020). Furthermore, the M^3 of cercopithecines usually presents an additional distal cuspule, unlike colobines (Delson, 1973: p. 208). The M^3 length variation is predicted by the M^2/M^1 ratio and/or the presence of hypoconulid on M_3 , which has high variability in cercopithecids (Delson, 1973; Boughner et al., 2021).

The breadth of the P_4 expresses a high level of variation in fossil *M. sylvanus* compared to both species and subspecies comparative groups, probably linked to this tooth's role in mastication. Functional inferences of feeding adaptation suggest a link between premolar enlargement and food processing, especially hard food objects (Daegling et al., 2011; Scott et al., 2018). However, morphological features such as the expression of the lingual cusp of the P_4 are highly variable in cercopithecids and can generate higher intraspecific and interspecific variation (Hornbeck and Swindler, 1967; Delson, 1973).

The results for the proposed subspecies of fossil *M. sylvanus* indicate higher variation in the P_4 BL of *M. s. florentina* compared to *M. s. pliocena*. Additionally, the analysis reveals that the MD length of the P_4 is statistically more variable in the complete fossil sample and *M. s. florentina* than in *M. s. pliocena* when compared to all comparative extant groups. Because of

these considerable differences between the two fossil subgroups, it is plausible to argue for more variation in the *M. s. florentina* and the possible existence of multiple different populations within this sample.

The assessment of variation in the fossil sample of *Macaca sylvanus* depends more on the size of the comparative group than on the measurements. The present study does not report any clear patterns of morphological variation, however, previous scholars showed that the molars of the fossil sample tend to be longer and wider than the extant specimens of *M. sylvanus* (Szalay and Delson, 1979; Alba et al., 2008, 2011; Konidaris et al., 2021). The presence of sexual dimorphism cannot be excluded from the analysis of fossil sample variation. However, macaques generally express moderate sexual dimorphism in their postcanine teeth and strong dimorphism in canine length (e.g., Biggerstaff, 1966).

Paleoenvironmental and climatic implications

Across the European continent, different populations of macaques seem to manifest specific adaptations to climate change and habitat quality in relation to temporal periods, rather than individual temporal trends or geographic trends (Ito et al., 2014; Ménard et al., 2014). Temporal and geographical factors seem to influence the distribution of different dental variables. The clinal variation in size seems more common between African cercopithecids (e.g., Cardini et al., 2007; Grunstra et al., 2018). Examining longitudinal distributions of macaques in Europe opens interesting questions about the type of predators these primates may have encountered and their foraging behaviors in different habitat types due to the geographical barriers (Meloro and Clauss, 2012, Meloro and Elton, 2013). However, the lack of climatic data limits the correlation between M_1 and M_2 morphology and spatial distribution. Previous research has shown that populations

express changes in the size and shape of these teeth as adaptation to cold temperatures, creating differences between western and eastern populations of Japanese macaque (Asahara and Nishioka, 2017). However, other investigations by Cardini et al. (2007) and Elton et al. (2010) on intraspecific variation of the skull of vervet monkeys show that morphology and geographic proximity do not correlate, suggesting that other factors beyond the spatial components may account for variation in the fossil sample.

In this study, elevation is relevant in comparing the fossil macaques from higher latitude sites to the north (e.g., the European continent) with lower latitude sites (the Levantine corridor). As previous studies on the African primates have shown, temperature and seasonality do not necessarily demand an adaptation of body size (Dunbar, 1990; Cardini et al., 2007). If latitude is considered to be a proxy for climatic variables on the European continent, no significant changes in dental sizes in relation to latitude would indicate a strong intracontinental variation (Fig., 4). This tends to contradict expectations based on Pleistocene Asian primates (Albrecht and Miller, 1993; Cameron, 2001; Louys et al., 2007; Harrison et al., 2021) and rather underlines the necessity of understanding the change in resource availability and predation pressure that took place during the Early Pleistocene (Elton and O'Regan, 2014).

As the climate changed from the Late Pliocene to the Early Pleistocene and glaciers start taking over the continent, the vegetative cover was reduced (Szabó et al., 2022), which might explain the contradictory results of the temporal analysis with specimens from the European continent. However, fluctuations of the plant species in relation to glacial cyclicality and changes in mammal communities (Markova, 2007; Meloro and Clauss, 2012; Meloro and Elton, 2013; Elton and O'Regan, 2014) might have reduced the variation in the Middle-Late Pleistocene macaques and selected for relatively larger back teeth as shown for extant temperate macaques (more in

Grunstra et al., 2018). This finding supports previous research (Alba et al., 2011), which argued for larger BL width in the *M. s. pliocena* than in *M. s. florentina*, and a relationship between increased seasonality, larger geographic ranges, and relative tooth size.

The response to habitat pressure on the two continents in the present sample is expressed at the level of the mandibular and maxillary M1 and M2. Even though the occlusal morphology is conserved among macaques over time, the size of the molars, a morphological trait with minimal plasticity across mammals (Gingerich, 1974; Gingerich and Schoeninger, 1979; Grunstra et al., 2018), suggests evolutionary changes. As in the studies on Japanese macaque (Anezaki et al., 2006; Asahara and Nishioka, 2017), changes in the size of M₁ are important when arguing for changes in body size and climate change, its morphology being vulnerable to changes in diet and temperature (e.g., Ingicco et al., 2012; Asahara and Nishioka, 2017).

The longevity of *M. sylvanus* during the Pliocene, Pleistocene, and Holocene allowed for processes of microevolution, with populations adapting temporally and geographically. The climatic conditions from the Pleistocene led to changes in the dynamics of ecological communities (Meloro and Elton, 2013; Elton and O'Regan, 2014). This, along with other ecological pressures, caused a high variation in the mesiodistal-buccolingual indices (BLI) of M¹ in *M. s. pliocena* when compared to extant species and subspecies.

The current fossil record provides little information about the early forms of *M. sylvanus* and there are currently not enough specimens to describe the alpha-taxonomy of the named subspecies. Furthermore, because so many teeth included here are isolated and sex is not possible to identify, it is hard to assess the role of sexual dimorphism in this lineage that could explain some of the variation observed here. With the conservative morphology of the genus and the small sample size of *M. s. prisca*, there are not enough evidence to argue for a temporal trend in the

sylvanus lineage. Even though the Pleistocene of Europe is characterized by seasonality, the effect of resource abundance or local adaptation in the fossil record cannot be fully tested. In general, without empirical testing, the changes in body size of this species related to habitat remain theoretical.

Variation in M. sylvanus over time and space

Macaques are distributed across a wide range of climates and habitats but are quite conservative in their dental morphology. Such a decision to designate all macaque individuals from the Late Pliocene-Early Pleistocene to *M. s. florentina* (Szalay and Delson, 1979; Delson, 1980) oversimplifies our understanding of the complexity of speciation. Due to the scarcity of cranial remains in the fossil record, a comprehensive study of selective pressures in this group cannot be completed. In fact, in discussing variation and subspeciation in primates, previous work has shown teeth do not always express a clear evolutionary pattern (Lockwood et al., 2000; Mottura and Gentili, 2006). The CV results suggesting relatively lower variation in the Middle-Late Pleistocene for *M. s. pliocena* and support the hypothesis of one subspecies; however, the CV results for *M. s. florentina* express a mix of variation, with more diverse variables for some of the analyzed teeth, potentially rejecting the one subspecies hypothesis.

The evolutionary pattern seen in *M. sylvanus* lineage contrasts with the linear trend of body size reduction found in different Pleistocene populations of hominids (Cameron, 2001; Tshen, 2016; Harrison et al., 2021) or cercopithecoids (Anezaki et al., 2006; Hlusko et al., 2016). The diversification of *Macaca* is most likely related to variation of climatic niches rather than a temporal evolution (Delson, 1980; Duran and Pie, 2015). Previous research has shown that primate lineages with higher rate shifts may be associated with mountain geographical distributions or

precipitation patterns, especially those from Southeast Asia (Abegg and Thierry, 2002; Gouveia et al., 2014; Ito et al., 2014; Duran and Pie, 2015). To understand the variation in the *sylvanus* lineage, one could hypothesize a gradual replacement of populations and a continuous migration under the glacial fluctuations from the Pleistocene period that does not imply a linear evolution (Fooden, 2007; Elton and O'Regan, 2014).

Further analysis of this fossil lineage should consider skull metrics and correlations between temperature and humidity, as ecogeographic variation and longitudinal speciation appear more common within the European and African primates (Albrecht et al., 1990; Cardini et al., 2007; Ito et al., 2014; Grunstra et al., 2018). Taxonomic identification in fossil macaques could provide insights about the biology of primates.

Conclusion

In this study, dental metrics were used as a proxy for body size to investigate variation in fossil *Macaca sylvanus* and the potential for this variation to be patterned geo-temporally. Analysis of dental metric variation in the fossil *Macaca sylvanus* reveals a nondirectional change that does not help in the characterization of different subspecies on the European continent. However, notable evidence of the metrical changes of the lower molars across the European and African continents allows a distinction between the extinct and the extant populations of *Macaca sylvanus* and between the Early Pleistocene *M. s. florentina* from Europe and Israel as has been previously shown (e.g., Delson et al., 2000). Within the fossil *M. sylvanus*, the buccolingual breadth of the lower molars suggests a longitudinal west-east decrease in body size with fluctuations over time. On the other hand, the buccolingual index of the upper molars shows opposite trends; from the

Early to Middle Pleistocene, the BLI of M^2 decreased, and the BLI of M^1 increased. Although *M. s. prisca* was only tentatively described as being smaller than the earlier fossils (Delson et al., 2000), the dental morphology studied here does not express a clear temporal trend. Signals from dental parameters are mixed and usually express a pattern of nondirectional change. Thus, these data hint at geographic patterning in the dental metrics of fossil *M. sylvanus*, but do not clearly support the chronogeographic subspecies distinctions previously proposed (Szalay and Delson, 1979; Delson, 1980).

In the second part of the study, levels of dental metric variation were analyzed in the complete fossil sample and temporal subgroups considered fossil subspecies. Additionally, the results were compared with different taxonomic groups of extant species and subspecies. When tooth variables are analyzed individually, M^3 MD and P_4 BL show higher statistical variation for both the complete fossil sample and the subgroup from the Late Pliocene-Early Pleistocene, known as *M. s. florentina*. Dental variation between the two temporal subspecies, *M. s. florentina* and *M. s. pliocena* suggest a higher level of variation in the *florentina* sample, which might indicate the existence of multiple subspecies inhabiting the Eurasian continent.

Finally, understanding the role of geographic variation in the fossil record and extant species can enhance our understanding of biology and evolution. Multiple factors could contribute to the overall variation in the fossil and extant species, and fluctuating temperatures and changes in dietary resources could be only one trigger for the changes in fossil populations. Achieving a deeper understanding of the morphological changes in the evolution of *Macaca sylvanus* will depend on further paleontological samples. This will clarify the anatomical characteristics that are currently lacking. Although there is currently enough information to differentiate between the European and African subspecies of *M. sylvanus*, the validity of the European subspecies remains

questionable. The chronological variation that has been analyzed in this study does not resolve the taxonomic issue mentioned earlier, and the debate over the validity of the European fossil subspecies remains open.

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Tables and Figures

Table 1. Sample sizes of each variable (mesiodistal length, buccolingual breadth, and breadth/length index) of individuals of fossil *Macaca sylvanus* and the three described subspecies: *Macaca sylvanus prisca*, *Macaca sylvanus florentina*, and *Macaca sylvanus pliocena*. Individuals from the complete sample size with lower confidence over their geographical distribution have been eliminated from the subspecies groups.

Upper/Lower Dentition	<i>Macaca sylvanus</i> (entire sample)	<i>Macaca sylvanus prisca</i>	<i>Macaca sylvanus florentina</i>	<i>Macaca sylvanus pliocena</i>
P4 MD	8/30	2/0	1/19	3/9
P4 BL	8/30	2/0	1/19	3/9
P4 BLI	8/30	2/0	1/19	3/9
M1 MD	21/37	4/0	8/22	7/16
M1 BL	21/37	4/0	8/22	7/16
M1 BLI	21/37	4/0	8/22	7/16
M2 MD	25/41	1/2	11/21	7/18
M2 BL	26/41	2/2	11/21	7/18
M2 BLI	25/41	1/2	11/21	7/18
M3 MD	26/21	0/0	9/11	8/9
M3 BL	26/21	0/0	9/11	8/9
M3 BLI	26/21	0/0	9/11	8/9

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 2. Temporo-geographic information of fossil specimens included in this study.

Collection	Catalog No.	Taxon	No. specimens	Locality	Country	Long. (DD)	Lat. (DD)	Time period	MN/ MNQ/MIS Zone	Absolute age (Ma)	Source
—	IPMC-11676	<i>M. s. ssp.</i>	1	Casablanca Almenara M	Spain	0.00	40.00	Miocene	MN13	5.9–5.3	Kohler et al., 2000
MNHN-P	UNCAT	<i>M. s. florentina</i>	1	Montpellier (terrestrial)	France	3.88	43.60	Pliocene	MN14	~5	PRIMO
MNHN-P	UNCAT	<i>M. s. prisca</i>	3	Montpellier	France	3.88	43.60	Pliocene	MN14	~5	PRIMO
MNHN-P	AMA 051	<i>M. s. ssp.</i>	3	Montpellier (terrestrial)	France	3.88	43.60	Pliocene	MN14	~5	PRIMO
UM	BAC-029	<i>M. s. prisca</i>	1	Balaruc 2	France	3.67	43.43	Late Pliocene	MN16	3.6–2.8	PRIMO
NMB	V.J. 88	<i>M. s. prisca</i>	2	RDB Quarry Triversa	Italy	8.10	44.90	Late Pliocene	MN16a	~3.2–3.0	PRIMO
—	V.J. 88	<i>M. s. florentina</i>	3	RDB Quarry Triversa	Italy	8.10	44.90	Late Pliocene	MN16a	~3.2–3.0	Rook et al., 2001
IGF	7519v	<i>M. s. florentina</i>	1	Lower Valdarno; Castelfiorentino	Italy	43.69	10.90	Late Pliocene	—	3.6–1.8 Ma	D.M.A
IPS	IPS14955	<i>M. s. florentina</i>	3	Cal Guardiola	Spain	2.02	41.55	Early Pleistocene	—	1.2-0.8	Alba et al., 2008
—	IN-I 1960	<i>M. s. florentina</i>	1	Incarcal	Spain	2.79	42.20	Early Pleistocene	—	1.5-1.4	Alba et al., 2016
DSTUP	unknown	<i>M. s. pliocena</i>	3	Monte Peglia Orvieto	Italy	12.20	42.82	Early Pleistocene	MIS 35/33 (lower); MIS 34/32 (upper)	ca. 1.072	PRIMO
MUPE	GCP-CV 4052	<i>M. s. florentina</i>	20	Quibas	Spain	-1.05	38.20	Early Pleistocene	—	1.3—1.0	Alba et al., 2011
FSL	40136/40190	<i>M. s. prisca</i>	3	Seneze (Domeyrat)	France	3.52	45.25	Early Pleistocene	MN17	2.12-2.19	PRIMO
FSL	40136/40190	<i>M. s. florentina</i>	1	Seneze (Domeyrat)	France	3.52	45.25	Early Pleistocene	MN17	2.12-2.19	PRIMO
RGM-L/ZMA	47424	<i>M. s. florentina</i>	9	Tegelen	Netherlands	6.17	51.35	Early Pleistocene	—	ca. 2	PRIMO

Table 2 (Cont.)

Collection	Catalog No.	Taxon	No. specimens	Locality	Country	Long. (DD)	Lat. (DD)	Time period	MN/ MNQ/MIS Zone	Absolute age (Ma)	Source
HUJ-ESE	UB 314	<i>M. s. florentina</i>	16	'Ubeidiya	Israel	35.57	32.68	Early Pleistocene	MnQ2	1.5–1.2	PRIMO
IQW	1980/1656 6 (Mei. 16087)d	<i>M. s. florentina</i>	2	Untermassfeld	Germany	11.17	51.17	Early Pleistocene	—	1.14	PRIMO
IGF	13084	<i>M. s. florentina</i>	21	Upper Valdarno	Italy	11.48	43.56	Early Pleistocene	—	2.588–0.781	PRIMO
MAP	10	<i>M. s. florentina</i>	4	Upper Valdarno	Italy	11.48	43.56	Early Pleistocene	—	2.588–0.781	PRIMO
NMB	VA 1088	<i>M. s. florentina</i>	16	Upper Valdarno	Italy	11.48	43.56	Early Pleistocene	—	2.588–0.781	PRIMO
IPH	without no	<i>M. s. florentina</i>	2	Vallonnet	France	7.46	43.77	Early Pleistocene	—	1.1-1.2	PRIMO
IPS	EVT2237 2	<i>M. s. florentina</i>	4	Vallparadis	Spain	2.02	41.55	Early Pleistocene	—	ca. 0.98	Alba et al., 2008
LPHP-S	776/G1	<i>M. s. pliocena</i>	8	Gajtan	Albania	19.05	42.07	Middle Pleistocene	—	0.781–0.126	PRIMO
NMP	without no	<i>M. s. pliocena</i>	4	Gombasek	Slovakia	20.47	48.57	Middle Pleistocene	—	0.781–0.126	PRIMO
ARO17-J8-Xa-934	—	<i>M. s. pliocena</i>	4	Gruta da Aroeira	Portugal	-8.61	39.51	Middle Pleistocene	MIS11	436-390 ka	Alba et al., 2019
EPS-MAR-1-926/587-47	—	<i>M. s. pliocena</i>	5	Marathousa 1	Greece	22.09	37.40	Middle Pleistocene	MIS12-11	500-400 Ka	Konidaris et al., 2021
SMNK	SMNK-Pal 6602	<i>M. s. ssp.</i>	1	Mauer	Germany	8.80	49.35	Middle Pleistocene	—	0.781–0.126	Schreiber & Lösscher, 2011
SMNK	SMNK-PAL 6630	<i>M. s. ssp.</i>	1	Mauer	Germany	8.80	49.35	Middle Pleistocene	—	0.781–0.126	Schreiber, 2020
IG-R	without no	<i>M. s. pliocena</i>	3	Monte Sacro	Italy	12.54	41.94	Middle Pleistocene	—	0.781–0.126	PRIMO
Harle	UNCAT	<i>M. s. pliocena</i>	3	Montsaunes	France	0.94	43.11	Middle Pleistocene	—	0.781–0.126	PRIMO

Table 2 (Cont.)

Collection	Catalog No.	Taxon	No. specimens	Locality	Country	Long. (DD)	Lat. (DD)	Time period	MN/ MNQ/MIS Zone	Absolute age (Ma)	Source
NMP	without no	<i>M. s. pliocena</i>	1	Orgnac-3	France	4.42	44.30	Middle Pleistocene	—	0.781–0.126	PRIMO
IIPU	140-144	<i>M. s. pliocena</i>	4	Pofi	Italy	13.42	41.57	Middle Pleistocene	—	0.781–0.126	PRIMO
MCSNBS	PA 11136	<i>M. s. pliocena</i>	3	Quecchia Quarry	Italy	10.31	45.54	Middle Pleistocene	MIS 7a	0.5-0.3	Bona et al., 2016
—	MCSNBS PA11141	<i>M. s. ssp.</i>	4	Quecchia Quarry	Italy	10.31	45.54	Middle Pleistocene	MIS 7a	0.5-0.3	Bona et al., 2016
Bonifay	UNCAT	<i>M. s. pliocena</i>	4	St. Estève Janson	France	5.40	43.69	Middle Pleistocene	—	0.781–0.126	PRIMO
IAPU-P	UNCAT	<i>M. s. pliocena</i>	2	Valdemino (Borgio)	Italy	8.31	44.16	Middle Pleistocene	—	0.781–0.126	PRIMO
NMP	UNCAT	<i>M. s. pliocena</i>	7	Zlaty Kun C718	Czech Republic	14.07	49.92	Middle Pleistocene	—	0.781–0.126	PRIMO
SIP-V	unknown	<i>M. s. pliocena</i>	1	Cova Negra	Spain	-0.47	38.96	Late Pleistocene	—	0.126–0.01	PRIMO
GOV	100	<i>M. s. pliocena</i>	2	Grotta degli Orsi Volanti	Italy	14.17	42.35	Late Pleistocene	—	0.126–0.01	Mazza et al., 2005
BGDG	LzII.M15.-271.300	<i>M. s. pliocena</i>	3	Lezetxiki II	Spain	-2.48	43.05	Late Pleistocene	last phasse of OIS5	0.7–0.86	Castaños et al., 2011
Verhulsdonck	00177 HvH	<i>M. s. ssp.</i>	1	Maasvlakte 2 and Hoek van Holland	Netherlands	3.98	51.93	Late Pleistocene	MIS 5e	0.126–0.01	Reumer et al., 2018
IPH	UNCAT	<i>M. s. pliocena</i>	1	—	—	—	—	—	—	—	PRIMO
SMF	UNCAT	<i>M. s. pliocena</i>	1	—	—	—	—	—	—	—	PRIMO
SMNS	7683A	<i>M. s. pliocena</i>	6	—	—	—	—	—	—	—	PRIMO
ZIN-L	34600+34601	<i>M. s. pliocena</i>	3	—	—	—	—	—	—	—	PRIMO

Table 3. Total size of the comparative sample of extant *Macaca sylvanus sylvanus*, *Cercopithecus cephus cephus*, *Cercopithecus nictitans nictitans*, *Cercopithecus pogonias grayi*, *Colobus satanas satanas*, *Macaca fascicularis*, and *Pan troglodytes* specimens.

Upper/Lower Dentition	<i>Macaca sylvanus sylvanus</i>	<i>Cercopithecus cephus cephus</i>	<i>Cercopithecus nictitans nictitans</i>	<i>Cercopithecus pogonias grayi</i>	<i>Colobus satanas satanas</i>	<i>Macaca fascicularis</i>	<i>Pan troglodytes</i>
P4 MD	22/19	81/81	83/82	68/68	47/46	181/187	79/75
P4 BL	22/19	81/81	83/80	70/68	47/46	183/186	79/75
P4 BLI	22/19	81/81	83/80	68/68	47/46	180/186	79/75
M1 MD	17/19	81/80	89/81	71/67	53/52	314/214	80/72
M1 BL	13/16	80/80	84/78	72/71	53/52	312/209	80/72
M1 BLI	13/16	80/79	84/77	71/67	53/52	312/209	80/72
M2 MD	24/19	81/57	84/84	71/72	52/51	191/193	82/76
M2 BL	22/18	81/57	84/84	71/73	52/51	191/193	82/76
M2 BLI	22/18	81/57	84/82	71/72	52/51	191/191	82/76
M3 MD	25/18	71/73	75/75	63/64	45/44	161/170	76/76
M3 BL	25/18	72/73	75/77	63/65	43/44	156/170	76/76
M3 BLI	25/18	71/73	75/75	63/64	43/44	156/170	76/76

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 4. Total size of the comparative sample of *Macaca fascicularis* separated geographically and *Pan troglodytes* separated by subspecies.

Upper/Lower Dentition	<i>Macaca fascicularis</i> mainland	<i>Macaca fascicularis</i> continental	<i>Macaca fascicularis</i> oceanic	<i>Pan troglodytes</i> <i>troglodytes</i>	<i>Pan troglodytes</i> <i>schweinfurthii</i>
P4 MD	7/7	101/105	73/73	32/26	47/48
P4 BL	7/7	102/104	73/73	32/26	47/48
P4 BLI	7/7	99/102	73/73	32/26	47/48
M1 MD	7/7	133/134	73/73	33/23	47/48
M1 BL	7/7	131/129	73/73	33/23	47/48
M1 BLI	7/7	131/129	73/73	33/23	47/48
M2 MD	7/7	112/113	72/73	33/27	49/49
M2 BL	7/7	112/113	72/73	33/27	49/49
M2 BLI	7/7	112/111	72/73	33/27	49/49
M3 MD	7/7	84/90	70/73	29/26	47/50
M3 BL	7/7	79/90	70/73	29/26	47/50
M3 BLI	7/7	79/90	70/73	29/26	47/50

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 5. Results of the one-way ANOVAs of cheek teeth in fossil *Macaca sylvanus* with time period and country as cofactors. Data reported by upper and lower dentition. Bold values are significant at $p < 0.05$; empty cells are where the sample sizes were too small for analysis.

	Time period				Country			
	Upper dentition		Lower dentition		Upper dentition		Lower dentition	
	F value	p	F value	p	F value	p	F value	p
P4 MD	2.846	0.234	1.223	0.310			2.384	0.068
P4 BL	0.539	0.539	0.415	0.665			1.465	0.238
P4 BLI	0.016	0.911	0.645	0.532			0.404	0.841
M1 MD	1.254	0.287	2.153	0.112	1.175	0.372	1.188	0.341
M1 BL	3.831	0.076	1.889	0.151	1.473	0.286	1.355	0.259
M1 BLI	0.28	0.607	3.589	0.024	0.383	0.768	1.242	0.312
M2 MD	2.309	0.147	0.709	0.553	0.385	0.816	0.895	0.541
M2 BL	9.308	0.007	1.978	0.135	0.887	0.497	2.485	0.030
M2 BLI	6.179	0.024	0.829	0.487	2.719	0.073	0.756	0.656
M3 MD			0.29	0.751	6.5	0.010	0.952	0.502
M3 BL			1.561	0.237	1.908	0.192	2.521	0.071
M3 BLI			0.466	0.635	3.123	0.0748	0.417	0.875

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 6. Differences of mean of variation (Tukey Post Hoc; $p < 0.05$) of M³ mesiodistal length of fossil *Macaca sylvanus* individuals grouped by country.

	Israel	France	Spain
France	0.848		
Spain	0.848	0.601	
Italy	0.008	0.097	0.381

Table 7. Differences of mean of variation (Tukey Post Hoc; $p < 0.05$) of the M₂ buccolingual breadth of fossil *Macaca sylvanus* individuals grouped by country.

	Israel	Greece	Albania	France	Italy	Czech Republic	Germany	Netherlands	Spain
Greece	1.000								
Albania	1.000	1.000							
France	0.996	1.000	1.000						
Italy	0.677	0.942	0.999	0.994					
Czech Republic	0.707	0.899	0.994	0.978	1.000				
Germany	0.775	0.877	0.979	0.962	0.997	1.000			
Netherlands	0.265	0.551	0.857	0.663	0.908	0.999	1.000		
Spain	0.056	0.257	0.584	0.240	0.429	0.972	1.000	1.000	
Slovakia	0.229	0.372	0.614	0.481	0.697	0.926	0.999	0.996	1.000

Table 8. Results of the Spearman rank correlation coefficients of upper and lower teeth of fossil *Macaca sylvanus* in relation to longitude, latitude, and geological age. Bold/shaded values are significant $p < 0.05$.

	Longitude				Latitude				Age			
	Upper dentition		Lower dentition		Upper dentition		Lower dentition		Upper dentition		Lower dentition	
	p	rho	p	rho	p	rho	p	rho	p	rho	p	rho
P4 MD	0.417	0.600	0.925	-0.032	0.417	-0.600	0.259	0.372	0.333	-0.800	0.572	-0.191
P4 BL	0.333	-0.800	0.926	-0.031	0.333	0.800	0.102	0.519	0.750	0.400	0.939	-0.026
P4 BLI	0.333	-0.800	0.818	0.081	0.333	0.800	0.673	-0.145	0.750	0.400	0.514	0.221
M1 MD	0.548	-0.251	0.138	-0.343	0.588	-0.227	0.932	-0.021	0.306	0.415	0.958	-0.012
M1 BL	0.286	-0.431	0.960	-0.012	0.800	-0.107	0.087	0.392	0.876	0.066	0.534	-0.147
M1 BLI	0.462	-0.309	0.390	0.203	0.793	0.119	0.035	0.474	0.822	-0.095	0.396	-0.201
M2 MD	0.613	-0.200	0.592	-0.121	0.744	-0.133	0.352	0.208	0.021	0.744	0.909	0.025
M2 BL	0.206	-0.437	0.496	-0.153	0.283	-0.376	0.054	0.416	0.011	0.756	0.959	0.011
M2 BLI	0.076	-0.633	0.713	-0.083	0.194	-0.483	0.078	0.384	0.057	0.652	0.758	0.069
M3 MD	0.919	-0.085	0.390	-0.273	0.497	0.371	0.416	0.259	0.175	0.657	0.949	-0.021
M3 BL	0.803	-0.142	0.030	-0.624	0.803	0.142	0.077	0.529	0.714	0.200	0.492	-0.221
M3 BLI	0.919	0.085	0.002	-0.818	1.000	-0.028	0.099	0.503	0.419	-0.428	0.477	-0.227

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 9. Results of the Mann–Whitney U test of tooth variables of fossil *Macaca sylvanus* in relation to extant *M. sylvanus*. Bold/shaded values are significant at $p < 0.05$.

	Upper dentition		Lower dentition	
	F	p - value	F	p - value
P4 MD	0.089	0.424	0.841	
P4 BL	0.403	0.181	0.584	0.845
P4 BLI	0.090	0.475	0.550	0.813
M1 MD	0.755	<0.001	0.301	<0.001
M1 BL	0.919	<0.001	0.229	<0.001
M1 BLI	0.625	0.727	0.728	0.954
M2 MD	0.000	0.001	0.020	0.012
M2 BL	0.212	0.002	0.084	0.088
M2 BLI	0.888	0.749	0.253	0.103
M3 MD	0.358	0.181	0.448	<0.001
M3 BL	0.525	0.044	0.043	0.337
M3 BLI	0.978	0.480	0.119	<0.001

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 10. Results of the coefficient of variation (CV) analysis for the complete fossil sample of *Macaca sylvanus* in comparison to *Cercopithecus* (*C. cephus cephus*, *C. nictitans nictitans*, and *C. pogonias grayi*) and *Colobus satanas*. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>C. c. cephus</i> p-value		<i>C. n. nictitans</i> p-value		<i>C. pogonias grayi</i> p-value		<i>Co. satanas</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD	4.5	8.935	0.751	0.004	0.742	0.004	0.694	0.007	0.403	<0.001
P4 BL	7.3	10.345	0.229	0.024	0.114	<0.001	0.153	<0.001	0.002	<0.001
P4 BLI	9.34	8.27	0.040	0.275	0.058	0.115	0.042	0.001	0.004	<0.001
M1 MD	6.921	5.195	0.007	0.459	0.025	0.797	0.012	0.229	<0.001	<0.001
M1 BL	5.921	6.378	0.522	0.162	0.198	0.399	0.260	0.209	<0.001	<0.001
M1 BLI	5.81	5.47	0.001	0.193	0.001	0.766	0.011	0.836	<0.001	0.001
M2 MD	4.37	6.163	0.959	0.085	0.944	0.519	0.716	0.004	0.149	<0.001
M2 BL	7.1	6.868	0.044	0.057	0.001	0.014	0.065	0.032	<0.001	<0.001
M2 BLI	5.1	5.67	0.003	0.143	0.134	0.630	0.777	0.140	<0.001	<0.001
M3 MD	12.11	6.015	0.004	0.783	0.015	0.786	<0.001	0.188	<0.001	0.479
M3 BL	7.783	6.408	0.253	0.614	0.065	0.578	0.027	0.602	<0.001	<0.001
M3 BLI	5.72	6.25	0.753	0.067	0.915	0.423	0.935	0.268	0.058	0.440

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 11. Results of the coefficient of variation (CV) analysis for the complete fossil sample of *Macaca sylvanus* in comparison to *Macaca fascicularis*. Bolded/shaded values are significant at p<0.05.

	Fossil CV		<i>M. fascicularis</i> p-value		<i>M. f. continental</i> p-value		<i>M. f. oceanic</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD	4.5	8.935	0.896	0.196	0.866	0.091	0.795	0.236
P4 BL	7.3	10.345	0.367	<0.001	0.242	0.001	0.467	<0.001
P4 BLI	9.34	8.27	0.168	0.110	0.050	0.084	0.176	0.110
M1 MD	6.921	5.195	0.151	0.766	0.074	0.806	0.082	0.610
M1 BL	5.921	6.378	0.999	0.449	0.513	0.295	0.508	0.268
M1 BLI	5.81	5.47	0.950	0.536	<0.001	0.141	0.002	0.873
M2 MD	4.37	6.163	0.981	0.293	0.990	0.269	0.862	0.145
M2 BL	7.1	6.868	0.219	0.624	0.185	0.498	0.153	0.715
M2 BLI	5.1	5.67	0.492	0.688	0.240	0.193	0.520	0.937
M3 MD	12.11	6.015	<0.001	0.976	<0.001	0.981	<0.001	0.824
M3 BL	7.783	6.408	0.300	0.821	0.459	0.834	0.029	0.743
M3 BLI	5.72	6.25	0.166	0.692	0.237	0.481	0.049	0.581

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 12. Results of the coefficient of variation (CV) analysis for the complete fossil sample of *Macaca sylvanus* in comparison to *Pan troglodytes*. Bolded/shaded values are significant at p<0.05.

	Fossil CV		<i>P. troglodytes</i> p-value		<i>P. t. troglodytes</i> p-value		<i>P. t. schweinfurthii</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD	4.5	8.935	0.925	0.111	0.981	0.177	0.778	0.028
P4 BL	7.3	10.345	0.148	<0.001	0.230	<0.001	0.039	<0.001
P4 BLI	9.34	8.27	0.233	0.728	0.412	0.750	0.043	0.665
M1 MD	6.921	5.195	0.214	0.496	0.276	0.072	<0.001	0.241
M1 BL	5.921	6.378	0.332	0.015	0.626	0.178	0.015	0.002
M1 BLI	5.81	5.47	0.005	0.510	0.019	0.967	<0.001	0.010
M2 MD	4.37	6.163	0.986	0.204	0.996	0.122	0.896	0.010
M2 BL	7.1	6.868	0.071	0.012	0.254	0.306	<0.001	<0.001
M2 BLI	5.1	5.67	0.744	0.344	0.878	0.644	0.530	0.048
M3 MD	12.11	6.015	<0.001	0.929	<0.001	0.894	<0.001	0.844
M3 BL	7.783	6.408	0.112	0.050	0.260	0.030	0.015	0.056
M3 BLI	5.72	6.25	0.872	0.451	0.579	0.162	0.841	0.359

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 13. Results of the coefficient of variation (CV) analysis for the subsample set of fossil *Macaca sylvanus florentina* in comparison to *Cercopithecus* (*C. cephus cephus*, *C. nictitans nictitans*, and *C. pogonias grayi*) and *Colobus satanas*. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>C. c. cephus</i> p-value		<i>C. n. nictitans</i> p-value		<i>C. pogonias grayi</i> p-value		<i>Co. satanas</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD		8.47		0.033		0.045		0.053		<0.001
P4 BL		12.25		0.004		>0.001		>0.001		<0.001
P4 BLI		7.910		0.225		0.296		0.052		<0.001
M1 MD	4.57	4.978	0.600	0.591	0.670	0.800	0.585	0.346	0.037	0.005
M1 BL	4.88	6.77	0.760	0.112	0.610	0.263	0.611	0.126	0.009	<0.001
M1 BLI	8	5.32	0.750	0.306	0.619	0.750	0.864	0.818	0.093	0.011
M2 MD	4.889	4.7	0.734	0.722	0.681	0.901	0.442	0.402	0.086	0.028
M2 BL	6.18	6.57	0.381	0.211	0.175	0.316	0.412	0.183	<0.001	<0.001
M2 BLI	4.370	4.920	0.162	0.423	0.357	0.818	0.837	0.536	0.124	0.008
M3 MD	6.859	6.17	0.804	0.654	0.694	0.648	0.451	0.209	0.001	0.368
M3 BL	3.925	6.18	0.970	0.617	0.949	0.596	0.944	0.626	0.316	<0.001
M3 BLI	5.25	7.95	0.712	0.007	0.188	0.154	0.869	0.025	0.251	0.230

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 14. Results of the coefficient of variation (CV) analysis for the subsample set of fossil *Macaca sylvanus florentina* in comparison to *Macaca fascicularis* groups. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>M. fascicularis</i> p-value		<i>M. f. continental</i> p-value		<i>M. f. oceanic</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD		8.48		0.340		0.229		0.390
P4 BL		12.25		>0.001		>0.001		>0.001
P4 BLI		7.700		0.281		0.236		0.312
M1 MD	4.57	4.978	0.757	0.784	0.718	0.809	0.664	0.690
M1 BL	4.88	6.77	0.982	0.299	0.732	0.189	0.676	0.180
M1 BLI	8	5.32	0.988	0.564	0.719	0.248	0.780	0.848
M2 MD	4.889	4.7	0.794	0.824	0.850	0.865	0.558	0.512
M2 BL	6.18	6.57	0.525	0.657	0.487	0.554	0.512	0.747
M2 BLI	4.370	4.920	0.647	0.854	0.520	0.555	0.687	0.970
M3 MD	6.859	6.17	0.562	0.893	0.516	0.897	0.441	0.680
M3 BL	3.925	6.18	0.977	0.753	0.981	0.774	0.938	0.710
M3 BLI	5.25	7.95	0.360	0.199	0.411	0.095	0.245	0.149

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 15. Results of the coefficient of variation (CV) analysis for the subsample set of fossil *Macaca sylvanus florentina* in comparison to *Pan troglodytes* groups. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>P. troglodytes</i> p-value		<i>P. t. troglodytes</i> p-value		<i>P. t. schweinfurthii</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD		8.47		0.271		0.328		0.145
P4 BL		12.25		>0.001		>0.001		>0.001
P4 BLI		7.91		0.783		0.328		0.685
M1 MD	4.57	4.978	0.698	0.6	0.715	0.229	0.373	0.401
M1 BL	4.88	6.77	0.603	0.012	0.743	0.089	0.307	0.003
M1 BLI	8	5.32	0.679	0.533	0.718	0.93	0.59	0.059
M2 MD	4.889	4.7	0.818	0.836	0.873	0.822	0.611	0.652
M2 BL	6.18	6.57	0.365	0.081	0.577	0.437	0.131	<0.001
M2 BLI	4.37	4.92	0.828	0.648	0.894	0.838	0.746	0.358
M3 MD	6.859	6.17	0.372	0.803	0.153	0.778	0.475	0.707
M3 BL	3.925	6.18	0.964	0.177	0.982	0.146	0.939	0.19
M3 BLI	5.25	7.95	0.803	0.107	0.695	0.017	0.757	0.096

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 16. Results of the coefficient of variation (CV) analysis for the subsample set of fossil *Macaca sylvanus pliocena* in comparison to *Cercopithecus* (*C. cephus cephus*, *C. nictitans nictitans*, and *C. pogonias grayi*) and *Colobus satanas*. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>C. c. cephus</i> p-value		<i>C. n. nictitans</i> p-value		<i>C. pogonias grayi</i> p-value		<i>Co. satanas</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD	6.43	8.47	0.354	0.101	0.361	0.118	0.354	0.122	0.183	0.003
P4 BL	4.48	6.6	0.599	0.504	0.575	0.413	0.585	0.413	0.378	0.074
P4 BLI	9.82	6.750	0.098	0.283	0.083	0.507	0.105	0.335	0.063	0.022
M1 MD	6.14	5	0.205	0.605	0.257	0.776	0.214	0.383	<0.001	0.018
M1 BL	5.25	5.5	0.645	0.568	0.482	0.700	0.501	0.624	0.003	0.001
M1 BLI	9.86	6.1	<0.001	0.966	<0.001	0.444	0.004	0.492	<0.001	0.002
M2 MD	1.56	6.4	0.998	0.116	0.998	0.421	0.995	0.021	0.984	<0.001
M2 BL	4.17	7.58	0.860	0.036	0.770	0.091	0.854	0.020	0.180	<0.001
M2 BLI	4.036	7.180	0.307	0.003	0.400	0.114	0.819	0.007	0.300	<0.001
M3 MD	4.91	6.3	0.952	0.596	0.915	0.594	0.829	0.208	0.215	0.337
M3 BL	4.092	6.51	0.949	0.510	0.916	0.491	0.909	0.508	0.253	<0.001
M3 BLI	3.88	4.062	0.931	0.734	0.960	0.841	0.971	0.872	0.667	0.673

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 17. Results of the coefficient of variation (CV) analysis for the subsample set of fossil *Macaca sylvanus pliocena* in comparison to *Macaca fascicularis* groups. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>M. fascicularis</i> p-value		<i>M. f. continental</i> p-value		<i>M. f. oceanic</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD	6.43	8.47	0.514	0.366	0.485	0.289	0.397	0.391
P4 BL	4.48	6.6	0.617	0.594	0.552	0.568	0.673	0.603
P4 BLI	9.82	6.750	0.185	0.489	0.101	0.422	0.175	0.559
M1 MD	6.14	5	0.404	0.759	0.345	0.783	0.288	0.688
M1 BL	5.25	5.5	0.964	0.732	0.624	0.666	0.575	0.659
M1 BLI	9.86	6.1	0.537	0.265	<0.001	0.082	0.002	0.532
M2 MD	1.56	6.4	0.999	0.249	0.999	0.247	0.999	0.192
M2 BL	4.17	7.58	0.879	0.341	0.852	0.288	0.880	0.347
M2 BLI	4.036	7.180	0.665	0.132	0.573	0.018	0.706	0.303
M3 MD	4.91	6.3	0.871	0.843	0.876	0.860	0.742	0.625
M3 BL	4.092	6.51	0.958	0.662	0.970	0.681	0.904	0.594
M3 BLI	3.88	4.062	0.735	0.947	0.791	0.896	0.591	0.932

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

Table 18. Results of the coefficient of variation (CV) analysis for the subsample set of fossil *Macaca sylvanus pliocena* in comparison to *Pan troglodytes* groups. Bolded/shaded values are significant at $p < 0.05$.

	Fossil CV		<i>P. troglodytes</i> p-value		<i>P. t. troglodytes</i> p-value		<i>P. t. schweinfurthii</i> p-value	
	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition	Upper dentition	Lower dentition
P4 MD	6.43	8.47	0.554	0.308	0.690	0.343	0.392	0.230
P4 BL	4.48	6.6	0.532	0.417	0.608	0.755	0.482	0.156
P4 BLI	9.82	6.750	0.212	0.816	0.313	0.806	0.101	0.799
M1 MD	6.14	5	0.357	0.602	0.412	0.291	0.082	0.443
M1 BL	5.25	5.5	0.512	0.358	0.649	0.649	0.222	0.203
M1 BLI	9.86	6.1	0.007	0.27	0.007	0.728	<0.001	0.007
M2 MD	1.56	6.4	0.999	0.209	0.999	0.148	0.995	0.03
M2 BL	4.17	7.58	0.814	0.013	0.882	0.189	0.727	<0.001
M2 BLI	4.036	7.18	0.813	0.054	0.864	0.093	0.764	0.002
M3 MD	4.91	6.3	0.849	0.748	0.675	0.73	0.902	0.661
M3 BL	4.092	6.51	0.94	0.122	0.963	0.103	0.905	0.135
M3 BLI	3.88	4.062	0.95	0.902	0.94	0.798	0.915	0.875

Abbreviations: MD mesiodistal length; BL buccolingual breadth; BLI breadth/length index.

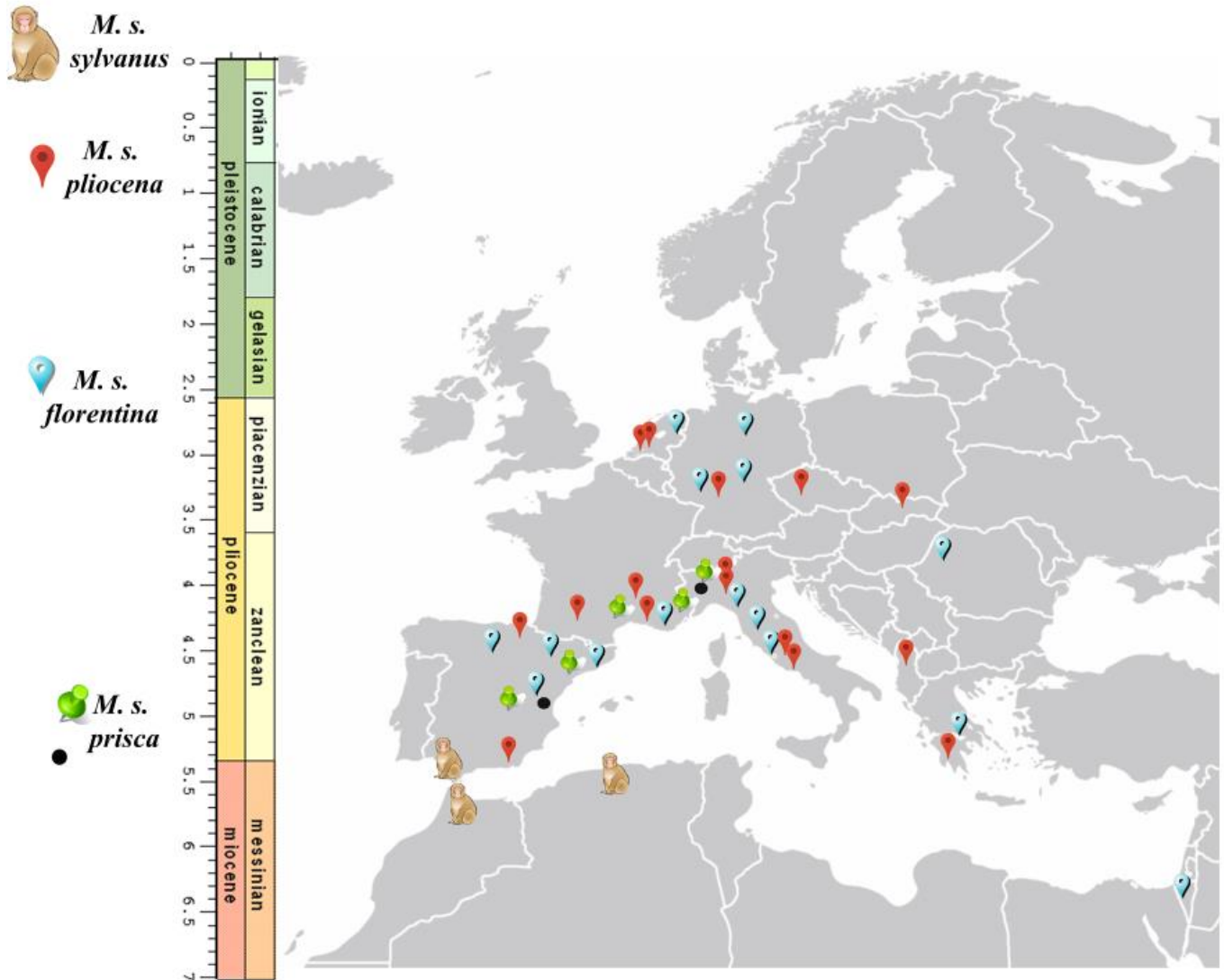


Figure 1. Fossil *Macaca* findspots in Europe and Caucasus from the Late Miocene to the Late Pleistocene and the present African distribution (not all Pliocene-Pleistocene *Macaca* sites in Europe are shown).

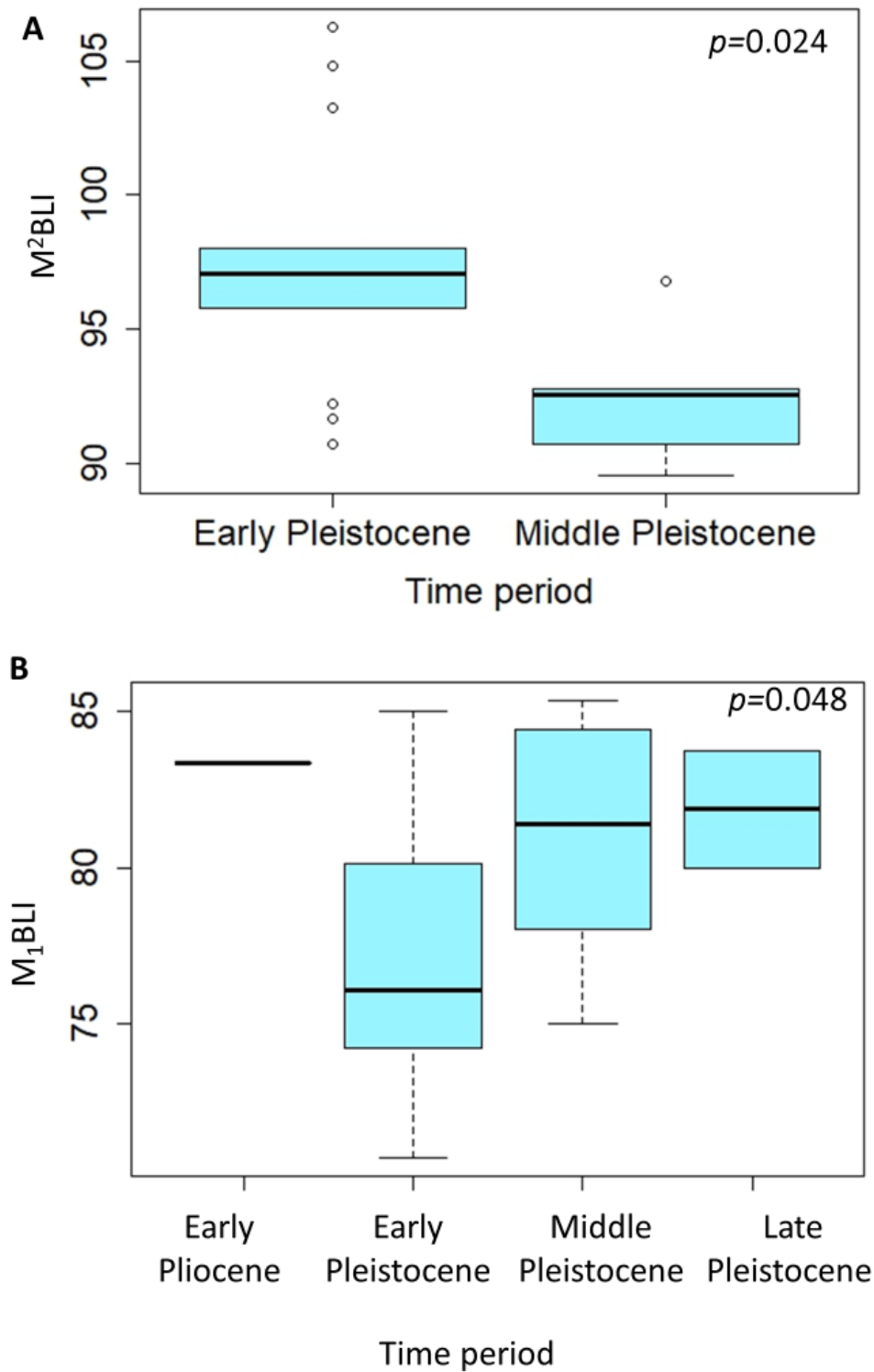


Figure 2. Boxplots showing the differences between extinct *Macaca sylvanus* individuals from different time period in dental metrics of M^2 (top) and M_1 (bottom) breadth/length index (BLI).

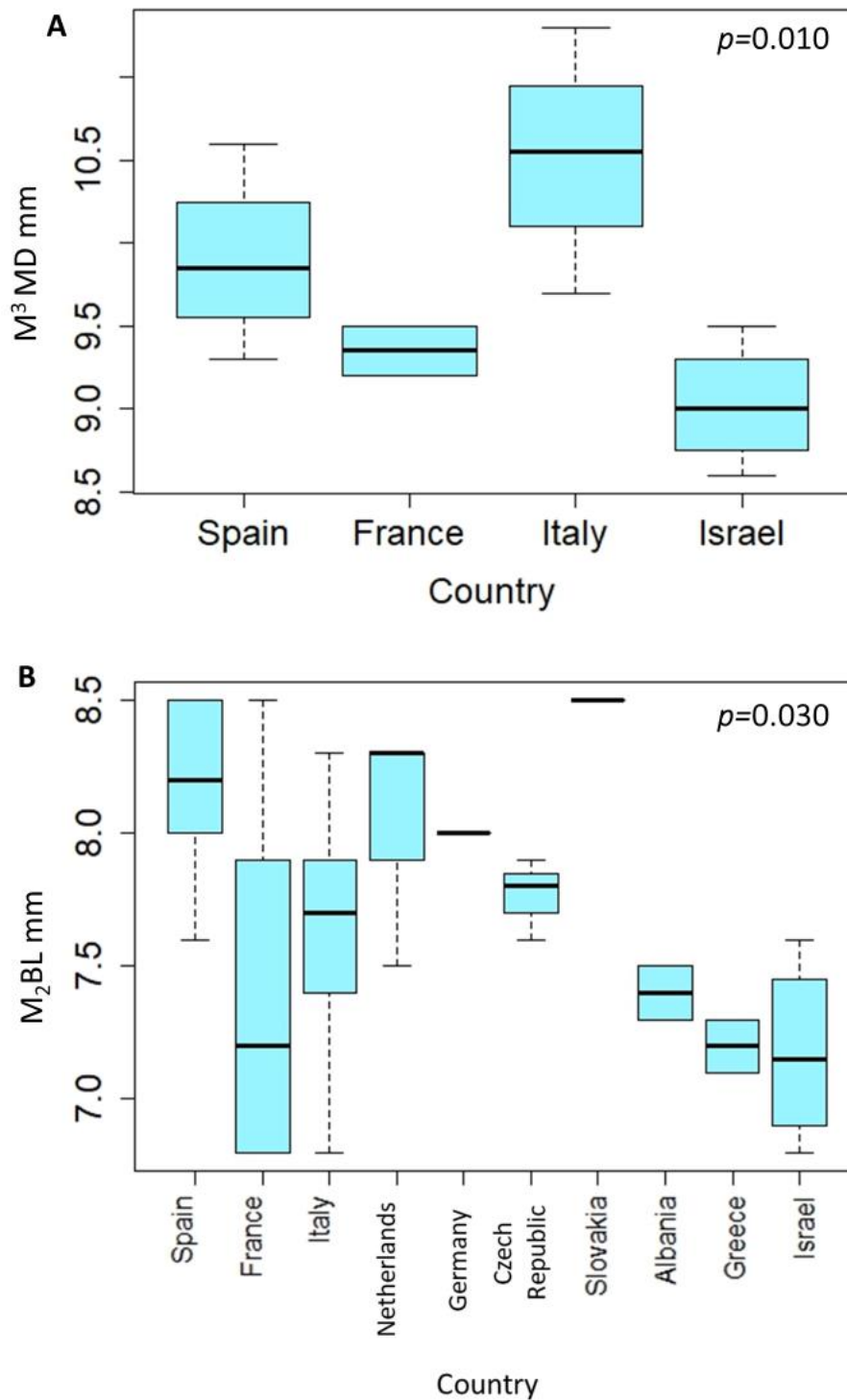


Figure 3. Boxplots showing the differences between extinct *Macaca sylvanus* individuals from different countries in dental metrics (mm) of M^3 (top) mesiodistal length (MD) and M_2 (bottom) buccolingual breadth (BL).

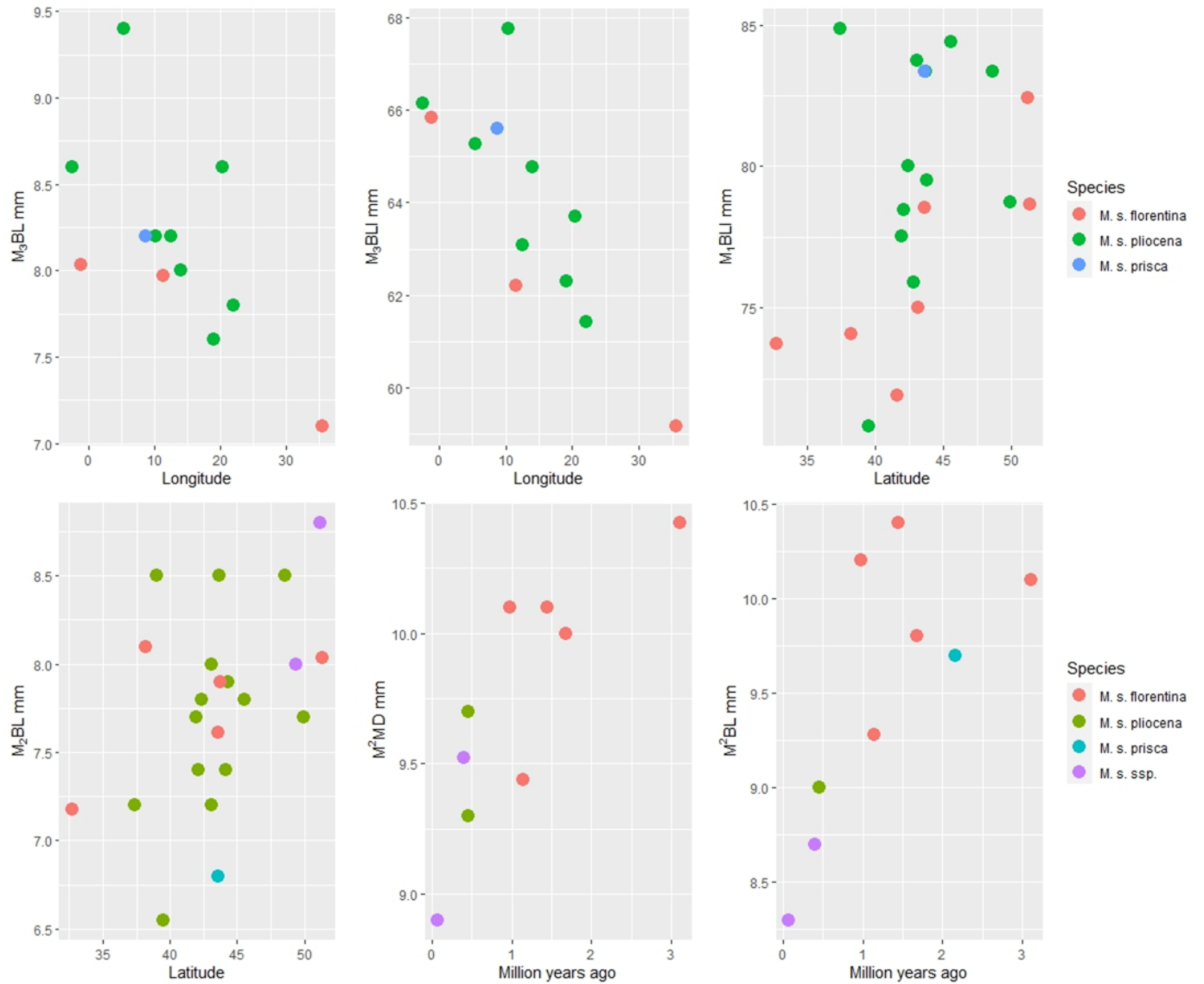


Figure 4. Scatter plots of different tooth variables of *Macaca sylvanus* distributed by longitude, latitude, and geological age (Million years ago). Abbreviations: BL – buccolingual breadth; MD – mesiodistal length.

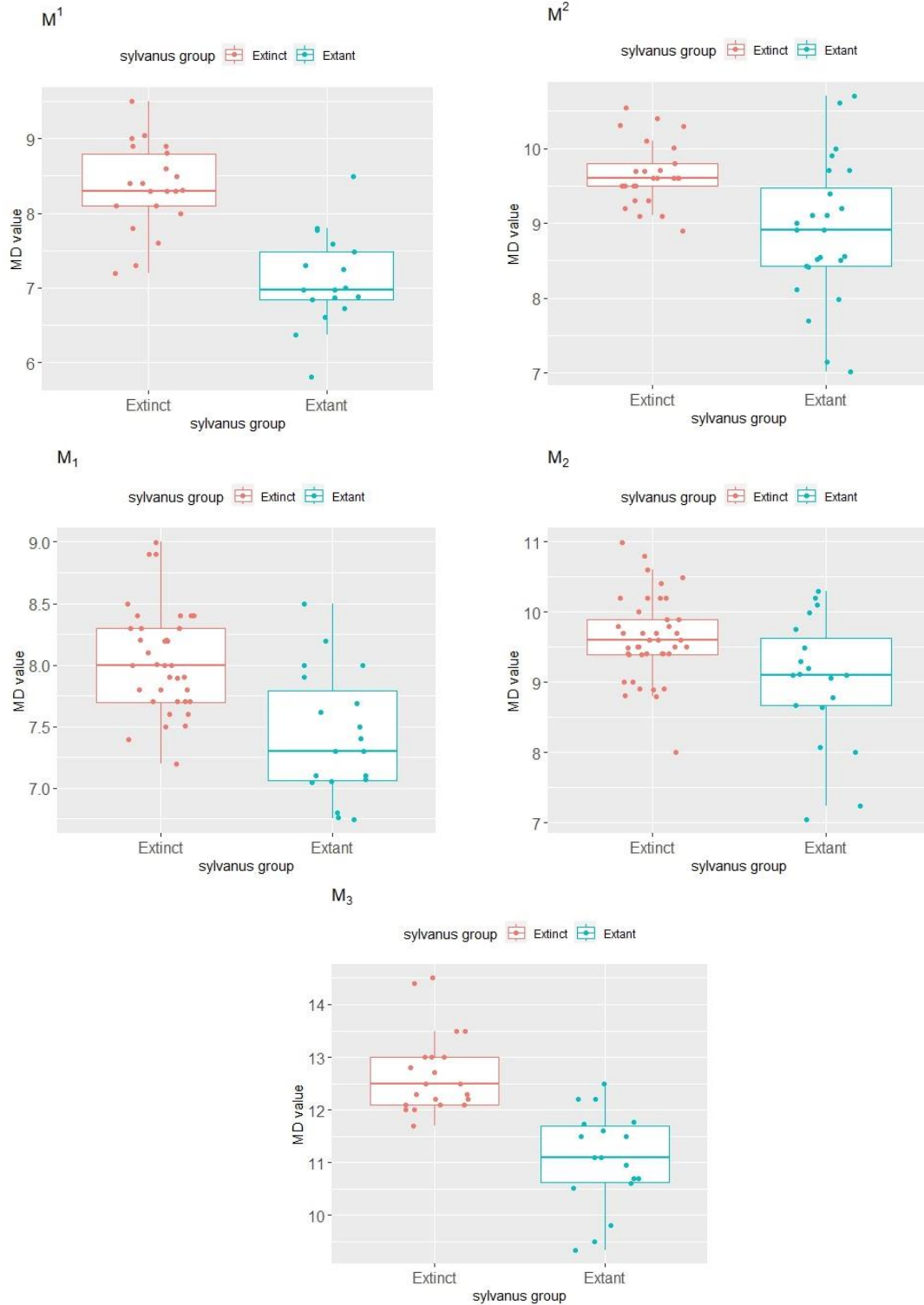


Figure 5. Boxplots of different tooth variables (in mm) showing the difference between extinct and extant *Macaca sylvanus*. Abbreviations: MD – mesiodistal length.

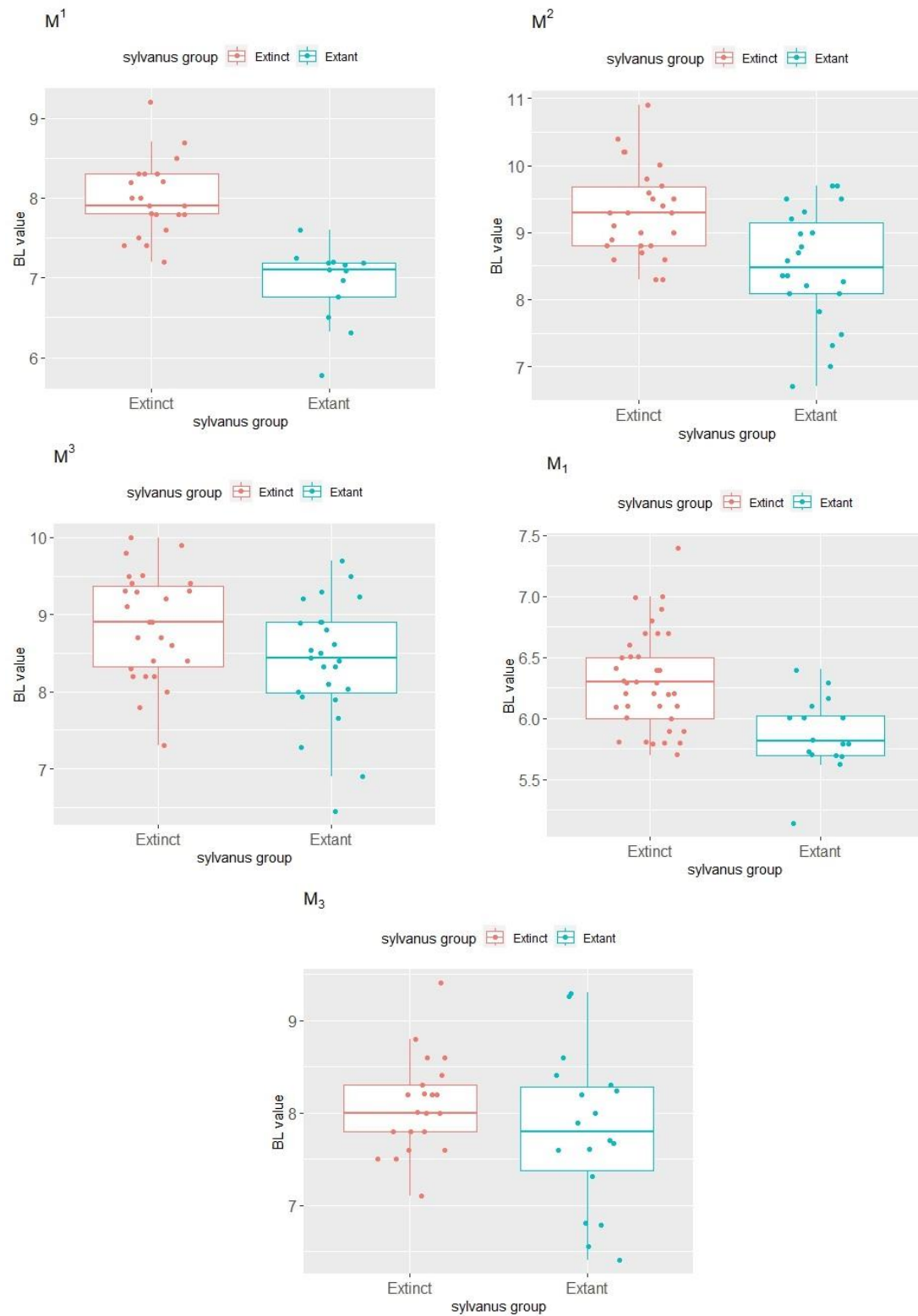


Figure 6. Boxplots of different tooth variables (in mm) showing the difference between extinct and extant *Macaca sylvanus*. Abbreviations: BL – buccolingual breadth.

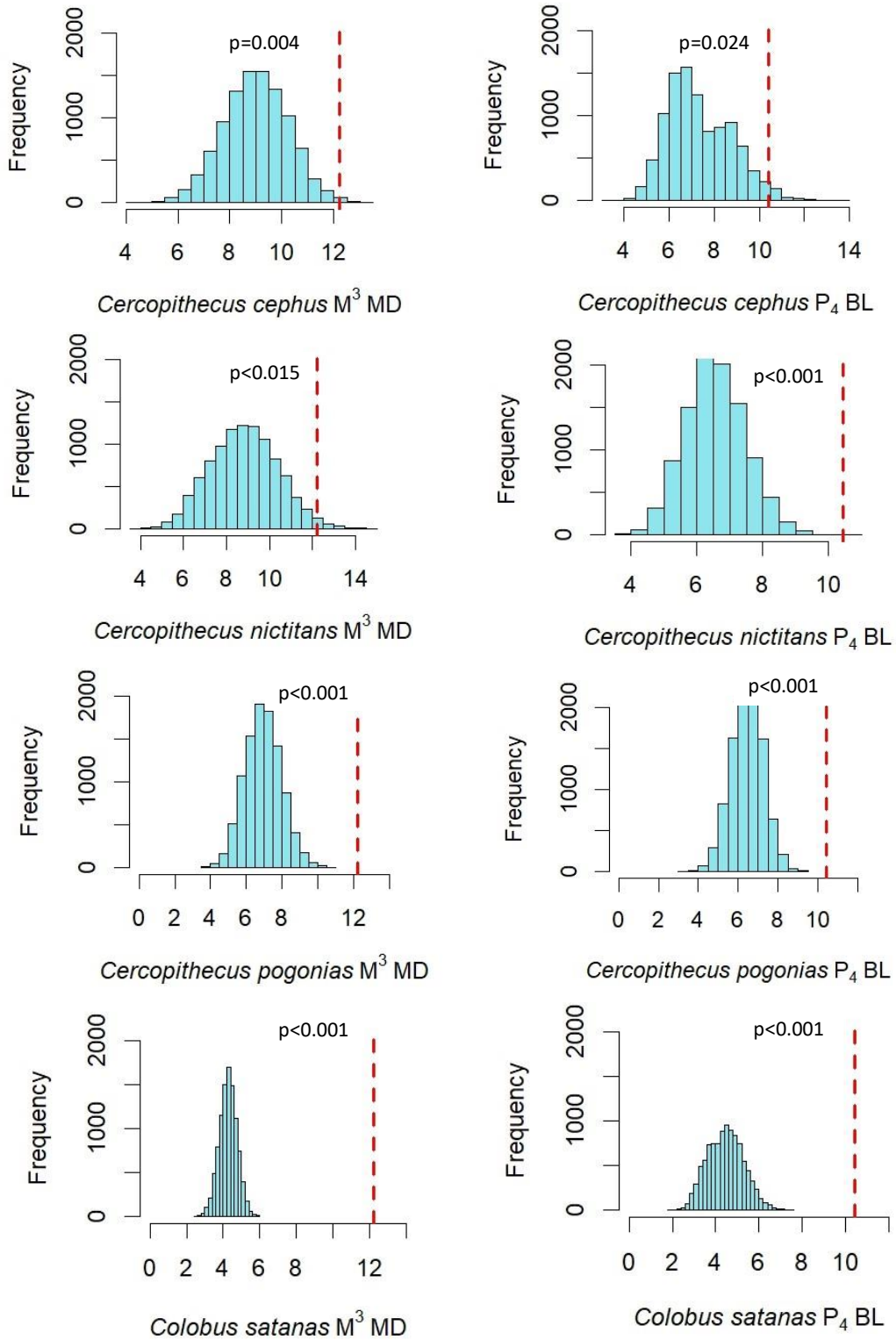
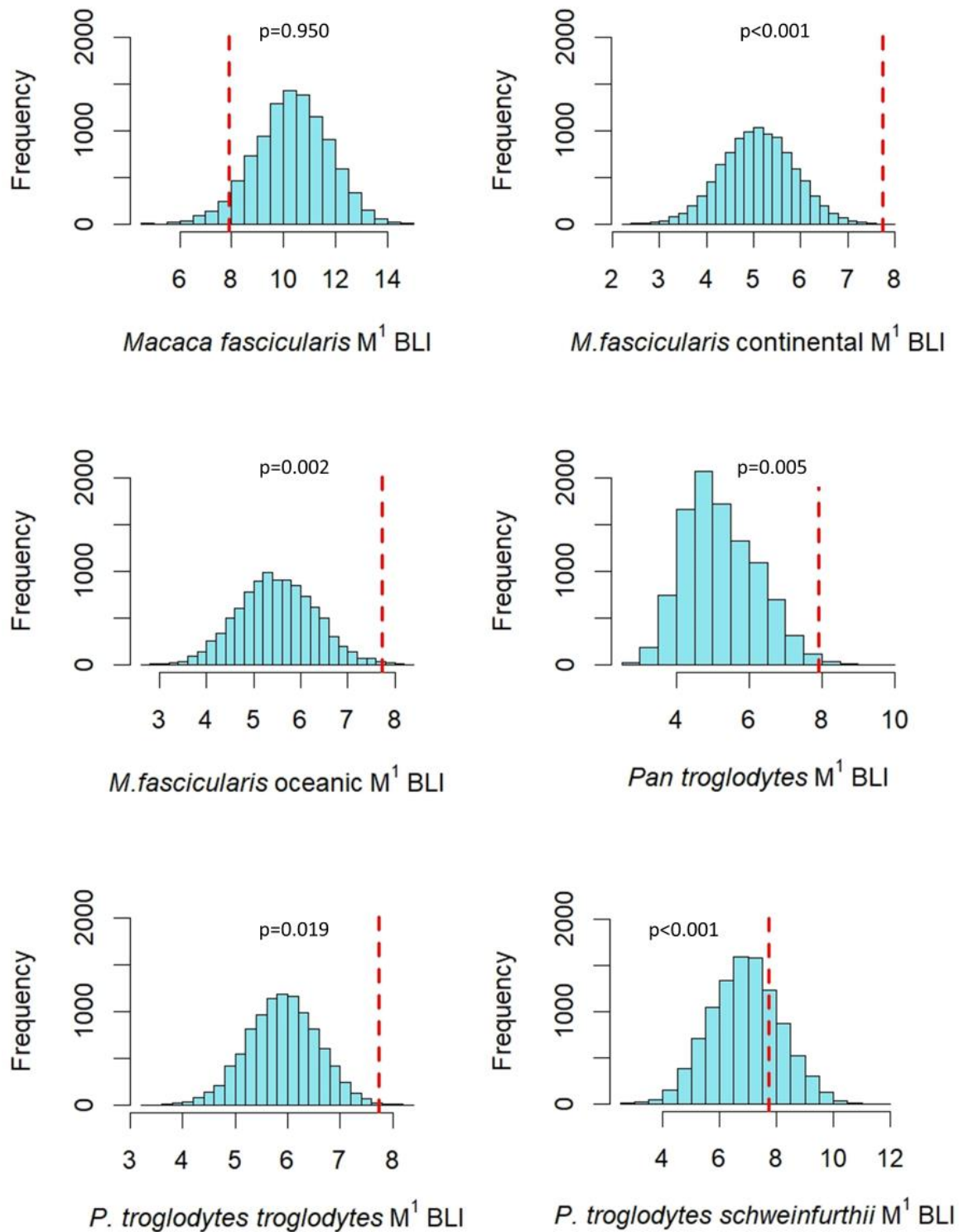


Figure 7. Histograms showing the distributions of resampled coefficient of variations (CV) in M¹ and M³ mesiodistal length (MD) and P₄ buccolingual breadth (BL) for *Cercopithecus* and *Colobus*. The red line represents the measured CV in the fossil sample of *M. sylvanus*.



Figures 8. Histograms showing the distribution of resampled coefficient of variations (CV) in M¹ buccolingual index (BLI) for the groups and subgroups of *Macaca fascicularis* and *Pan troglodytes*. The red line represents the measured CV in the fossil sample of *M. sylvanus*.

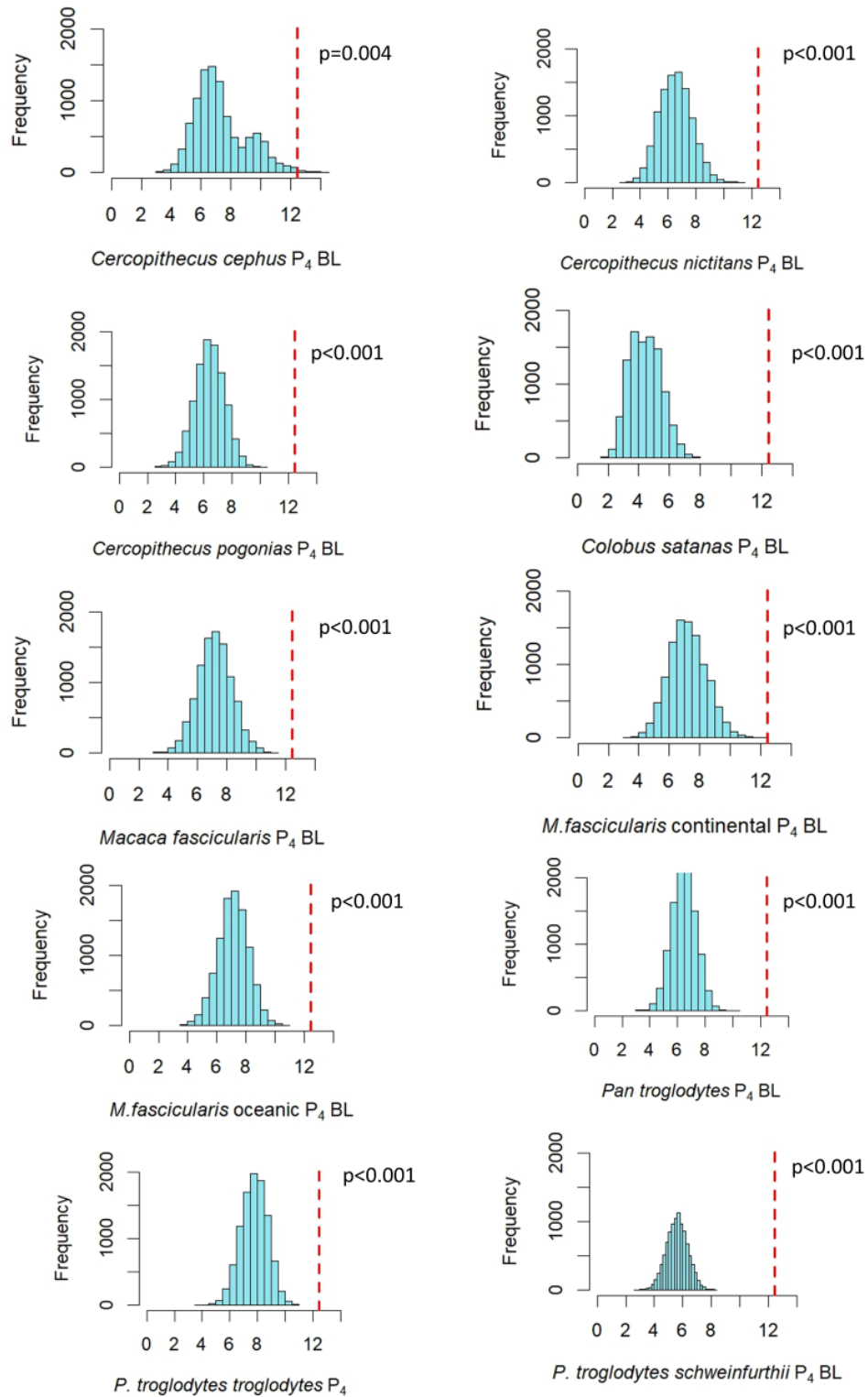


Figure 9. Histograms showing the distribution of resampled coefficient of variations (CV) in P₄ buccolingual breadth (BL) for *Cercopithecus*, *Colobus*, *M. fascicularis*, and *P. troglodytes*. The red line represents the measured CV in the fossil sample of *M. s. florentina*.

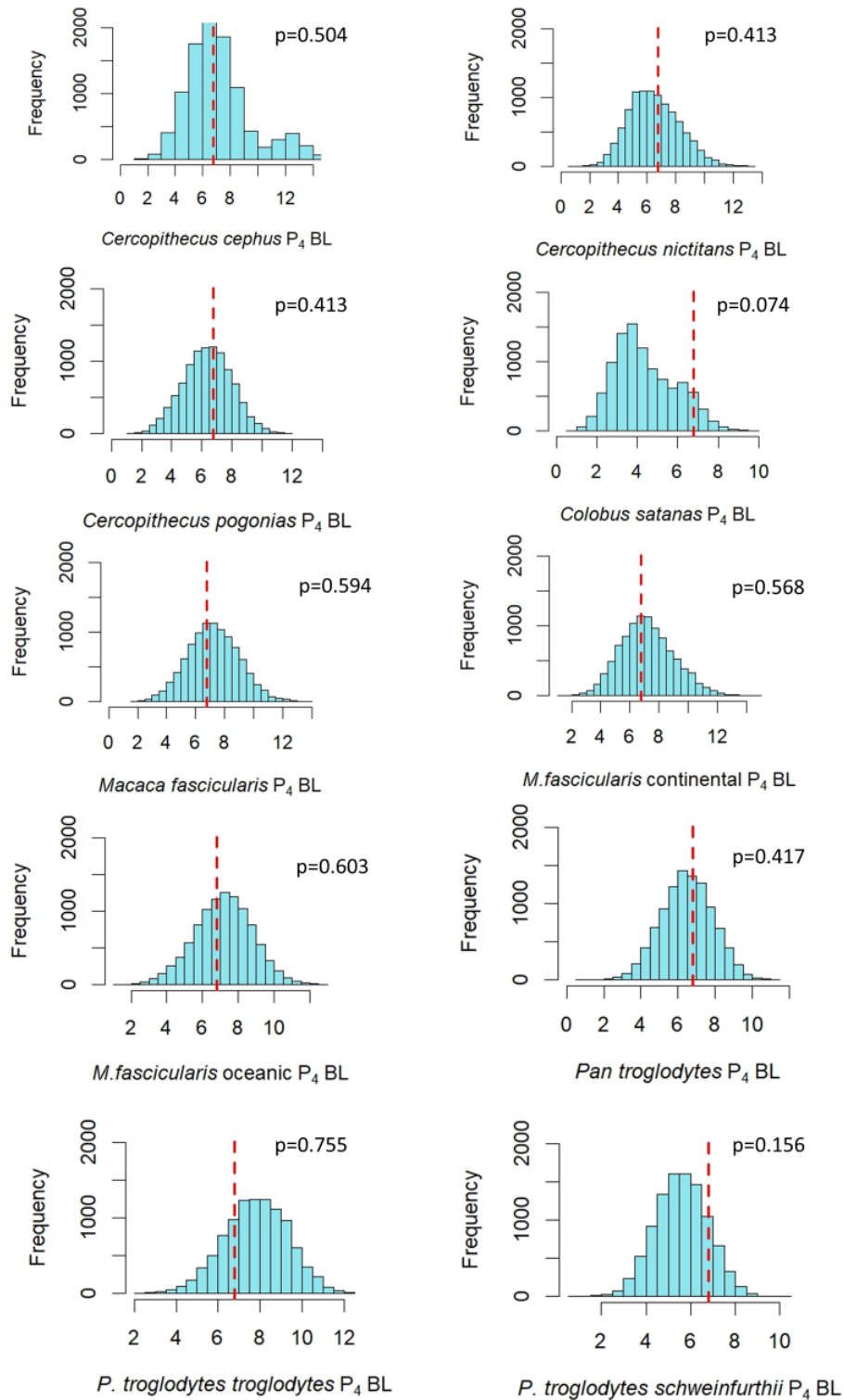


Figure 10. Histograms showing the distribution of resampled coefficient of variations (CV) in P_4 buccolingual breadth (BL) for *Cercopithecus*, *M. fascicularis*, and *P. troglodytes*. The red line represents the measured CV in the fossil sample of *M. s. pliocena*.