New macaque fossil remains from Morocco

David M. Alba [a,*], Antonio Rodríguez-Hidalgo [b,c,d], Hassan Aouraghe [e], Jan van der Made [f], Aïcha Oujaa [g], Hamid Haddoumi [e], Palmira Saladié [c,h,i], Al Mahdi Aissa [e], Juan Marín [c], Mourad Farkouch [c,e], Carlos Lorenzo [h,c], Said Bengamra [e], Eric Delson [j,k,l,m,a], M. Gema Chacón [c,h,n], Robert Sala-Ramos [c,h]

[a] *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193, Cerdanyola del Vallès, Barcelona, Spain*

[b] *Departamento de Prehistoria, Historia Antigua y Arqueología, Universidad Complutense de Madrid, Facultad de Geografía e Historia, C/ Prof. Aranguren s/n, 28040, Madrid, Spain*

[c] *Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), Tarragona, 43007, Spain*

[d] *Instituto de Evolución en África (IDEA, Madrid), C/ Covarrubias 36, 28010, Madrid, Spain*

[e] *Faculté des Sciences, Département de Géologie, Université Mohamed Premier, BV Mohammed VI, Quartier Al Qods, 60000, Oujda, Morocco*

[f] *Consejo Superior de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, Departamento de Paleobiología, C/ José Gutiérrez Abascal, 2, 28006, Madrid, Spain*

[g] *Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Av. Allal El-Fassi, Hay Riad, 6828, Rabat, Morocco*

[h] *Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain*

[i] *Unidad Asociada al CSIC, Departamento de Paleobiologia, Museo Nacional de Ciencias Naturales, C/ José Gutiérrez Abascal, 2, 28006, Madrid, Spain*

[j] *Department of Anthropology, Lehman College of the City University of New York, 250 Bedford Park Boulevard West, Bronx, NY, 10468, USA*

[k] *Department of Vertebrate Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY, 10024, USA*

[l] *PhD Programs in Anthropology and Earth & Environmental Sciences, The Graduate Center of the City University of New York, 365 Fifth Avenue, New York, NY, 10016, USA*

[m] *New York Consortium in Evolutionary Primatology, New York, NY, USA*

[n] *UMR7194 Histoire naturelle de l'Homme préhistorique (HNHP), Museum National d'Histoire Naturelle (MNHN), CNRS, Université Perpignan Via Domitia, Alliance Sorbonne Université – Musée de l'Homme, Place du Trocadéro 17, 75016 Paris, France*

Corresponding author.

Email: david.alba@icp.cat (D.M. Alba)

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Short Communications

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1. Introduction

1.1. Cercopithecoids from Late Miocene and Plio-Pleistocene North Africa

The Late Miocene and Plio-Pleistocene record of cercopithecoids from North Africa is quite meager as compared with that from tropical and southern Africa (Delson, 1973, 1974, 1975, 1980; Szalay and Delson, 1979; Geraads, 1987; Benefit et al., 2008; Jablonski, 2002; Jablonski and Frost, 2010; Roos et al., 2019; these references are relevant to all occurrences in this paragraph and the next and will not be repeated). During the Late Miocene, cf. *Macaca* sp. and '*Colobus*' *flandrini* are recorded from Menacer (=Marceau; ~7.0–5.8 Ma), Algeria (Arambourg, 1959). Slightly thereafter, *Macaca libyca* and the colobine *Libypithecus markgrafi* co-occur at Wadi Natrun (~6.2–5.0 Ma), Egypt (Stromer, 1913, 1920), and possibly also at As Sahabi (~6.3–5.3 Ma), Libya (Meikle, 1987; Jablonski, 2002; but see Benefit et al., 2008 regarding uncertainty in such attributions).

Macaca sp. is also recorded, together with *Theropithecus* '*atlanticus*'[1], in the earliest Pleistocene of Ahl al Oughlam (~2.5 Ma), Morocco (Raynal et al., 1990; Geraads et al., 1998; Alemseged and Geraads, 1998; Delson et al., 2000), and is probably present as well in the Pliocene site of Garaet Ichkeul (~3 Ma), Tunisia (e.g., Szalay and Delson, 1979; Delson, 1993; Fooden, 2007; but see Geraads, 1987; Alemseged and Geraads, 1998), while *Macaca* aff.

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[1] Although *T. atlanticus* was recognized as a distinct species by Alemseged and Geraads (1998), we do not recognize it here pending nomenclatural action in process by E.D. and D.M.A. and colleagues relating to its priority vis-à-vis subspecies of *T. oswaldi*.

sylvanus has been identified from the Pliocene of Aïn Brimba (~3 Ma), Tunisia (Arambourg and Coque, 1959; Arambourg, 1979; Szalay and Delson, 1979; van den Brink, 1981; Fooden, 2007). Subsequently, *Macaca sylvanus* is recorded from various Middle and Late Pleistocene sites in Algeria (Pomel, 1892, 1896; Fooden, 2007). In turn, *T.* '*atlanticus*' has also been documented from Aïn Jourdel in Algeria (~2.5 Ma; Thomas, 1884; Delson, 1993), while *Theropithecus oswaldi* has been recovered from Tighennif (=Ternifine; ~1.0 Ma; Sahnouni and van der Made, 2009) in Algeria (Jolly, 1972; Delson and Hoffstetter, 1993) and from Thomas Quarries I and III (=Oulad Hamida 1 Quarry; ~700–500 ka; Raynal et al., 2010; Rhodes et al., 2006; Daujeard et al., 2020) in Morocco (Geraads, 1980, 1987; Delson, 1993).

1.2. The site of Guefaït

An ongoing interdisciplinary Spanish-Moroccan project focused on the Aïn Béni-Mathar/Guefaït region, in the northern part of the High Plateaus (Jerada Province, Eastern Morocco), started in 2006 with the aim of mapping the archeological sites and establishing their geochronological and paleontological context (Aouraghe et al., 2016; Chacón et al., 2016). Systematic surveys led to the discovery of Pleistocene archeological sites (Sala et al., 2016) and some paleontological localities ranging in age from the Late Miocene (Blain et al., 2013) to the Plio-Pleistocene (Piñero et al., 2019). The excavation in 2017–2019 of a 28 m^2 surface trench in the locality of Guefaït-4.2 (Supplementary Online Material [SOM] Fig. S1) has yielded 3269 macrovertebrate remains (Sala et al., 2017; Aouraghe et al., 2019a, 2019b; Piñero et al., 2019; authors' unpublished data), including a few cercopithecid teeth. Here we describe these dental remains to provide a taxonomic assignment and discuss their paleoenvironmental, paleobiogeographic, and biochronological implications.

The fossil site of Guefaït-4 (Aïn Béni Mathar-Guefaït Basin) is located at the base of Unit 2 of the Dhar Iroumyane (=Dhar Irroumine) stratigraphic section (Aouraghe et al., 2019a). The fossiliferous layer of Guefaït-4, which consists of clays and marls with nodular calcretes, has delivered a diverse faunal assemblage of vertebrates at the 4.2 locality trench (reptiles, amphibians, and both small and large mammals; Hajji, 2010; Agustí et al., 2017; Aouraghe et al., 2019a, 2019b; Piñero et al., 2020). Paleomagnetic analysis of the series containing Guefaït-4.2 is currently underway. Although some preliminary results have been presented (Alvarez Posada et al., 2015), an interpolated age for Guefaït-4.2 is not available yet. The site was initially correlated broadly to the earliest Pleistocene (Agustí et al., 2016). The absence of *Equus* (despite the abundance of hipparionin equid remains; Aouraghe et al., 2019a, 2019b) indicates an age older than ~2.4 Ma (Sahnouni et al., 2018), while the murid assemblage further supports an age close to the 2.58 Ma Pliocene/Pleistocene boundary (Agustí et al., 2017; Piñero et al., 2020).

2. Materials and methods

The described material includes 6 teeth and tooth fragments collected in 2018–2019 from Guefaït-4.2 (Table 1). The specimens are currently on loan to the Institut Català de Paleoecologia Humana i Evolució Social in Tarragona, Spain but will be permanenty housed in the Faculty of Science, Mohammed I University in Oujda, Morocco. 3D virtual models are available from MorphoSource.org (SOM Files S1–S6; see methods in SOM S1).

Standard dental measurements of mesiodistal crown length (MD), buccolingual crown breadth (BL), and labial crown height (H; only for the incisor) were taken to the nearest 0.1 mm by D.M.A. For the molars, BL was taken both at the mesial (BLm) and distal (BLd) lophids. A breadth/length index (BLI, in %) was also computed (using BLm for the molars). Body mass (BM) was estimated following Delson et al. (2000)—see SOM S2 for details.

Extant and fossil macaques as well as *Parapapio* (cf.) *ado* (this concept includes both *P. ado* and *P*. cf. *ado*), '*Parapapio*' *lothagamensis*, and *Pliopapio alemui* were included in the comparative sample[2]. Measurements were taken from the PRIMO (PRImate Morphometrics Online) database (http://primo.nycep.org) or the literature (references in SOM Table S1), or taken by D.M.A. Bivariate plots of BL vs. MD and box-and-whisker plots were used to visually compare dental size and proportions. Differences among some taxa from the comparative sample were tested using analysis of variance (ANOVA) and Tukey's pairwise post hoc tests, while the studied specimens were compared to these taxa using z-scores (z = [measurement – mean] / SD). Statistical computations and plots were performed with PAST v. 4.02 for Mac (Hammer et al., 2001; https://www.nhm.uio.no/english/research/infrastructure/past/).

3. Results

3.1. Description

Upper central incisor The left I^1 (Fig. 1a; see Table 1 for measurements) preserves the crown and a small portion of the root. The incisal edge is sharp and only slightly worn, and although some enamel chips are missing from the distal and mesial aspects, MD can be estimated and lingual morphology adequately ascertained. The crown is only slightly longer mesiodistally than buccolingually broad, and much taller than mesiodistally long. In labial/lingual views it displays a subrectangular contour (with subparallel mesial and distal

[2] Other species of *Parapapio*, such as *Parapapio jonesi* and *Parapapio broomi*, were not included because the described molars are clearly smaller and do not overlap the range of variation of these species.

edges that converge toward the base), which is slightly asymmetrical (somewhat tilted mesially). The incisal edge is horizontal except on the distal-most portion. The crown progressively becomes labiolingually wider rootward. The root displays a subtriangular cross section close to the cervix. The latter is V-shaped mesially and distally, and lingually it extends somewhat further rootward than labially. The labial crown aspect is smooth and uniformly convex, whereas the lingual side is slightly excavated and displays a distinct median sulcus (flanked by two subparallel grooves) that separates the steep mesiolingual crown portion from the more bulging distolingual one. The damaged distal ridge and the apparently thicker mesial ridge converge basally into a narrow lingual cingulum located above a protruding basal bulge.

Lower molars The lower molars are represented by several molar crown and germ fragments plus two almost complete lower molars (see measurements in Table 1). The right M_1 fragment (Fig. 1b), which preserves 7.4 mm of the buccal wall, is smaller than, but shows a similar morphology to, the complete M_2 (Fig. 1e; see below), except for displaying a tiny cuspulid-like enamel thickening in the median buccal cleft. The right mesial germ fragment (Fig. 1c) preserves most of the metalophid (up to the metaconid) and, based on size, probably belongs to an M_2 or M_3. The right distal germ fragment (Fig. 1d) preserves the whole hypolophid and, given its size and the lack of a hypoconulid, must belong to an M_2. Both germ fragments might belong to the same tooth (although this cannot be confirmed based on spatial association; Table 1), but must belong to a different individual than the complete M_2 and M_3.

The right M_2 (Fig. 1e) preserves the whole crown (which is moderately worn, with dentine exposure at the protoconid apex) and the obliquely oriented distal root. The occlusal contour is subrectangular (longer than wide, and slightly wider across the metalophid). It displays a bilophodont occlusal pattern with a moderately deep median lingual notch (down to slightly below crown midheight, far from the cervix) and some buccal flare. The four main cuspids are quite bulbous, and the lingual ones are slightly more mesial than the corresponding buccal cuspids. The mesial fovea is restricted, with a short preprotocristid, a slightly protruding mesial marginal ridge, and a faint mesial buccal cleft. The distal fovea is shorter than the trigonid basin but more spacious than the mesial fovea and distally enclosed by a thicker and more protruding semicircular marginal ridge. The median buccal cleft is not very wide and lacks secondary cuspulids.

The left M_3 (Fig. 1f) preserves most of the crown (except for the missing protoconid apex), which is broken at the cervix level and presents only slight wear. This molar displays the same occlusal pattern as the M_2, with the following differences: (1) the lingual cuspids are somewhat more buccolingually compressed; (2) the median lingual notch is shallower (ending above crown midheight); (3) the median buccal cleft is more restricted (narrower and shallower); (4) the crown is relatively narrower, and although crown breadth at the hypolophid is minimally narrower than at the metalophid, it displays a distally tapering oval contour with a well-developed third lobe; and (5) the distal lobe bears a buccally-located large hypoconulid (subequal in size to the remaining main cuspids and aligned with the remaining buccal cuspids), as well as a smaller tuberculum sextum between the entoconid and the hypoconulid (more centrally located than the two lingual cuspids). The hypoconulid lobe is smaller than is usual in macaques and other papionins, although this shape is not unique; the four main cuspids seem ‘normal’, with the distal portion of the tooth compressed mesiodistally.

3.2. Morphological comparisons

Upper central incisor Cercopithecoid upper incisors are not particularly diagnostic. Nonetheless, the I^1 from Guefaït-4.2 differs from that of colobines by being taller than long and by displaying a distinct median sulcus on the lingual side, which is characteristic of papionins (Delson, 1973; Swindler, 2002). The continuous lingual cingulum, lacking a rootward oriented excavated pit (as is typical of *Papio*; Delson, 1973), further agrees well with the macaque I^1 morphology (SOM Fig. S2), while the rootward extension of the labial cervix appears less marked than in *Lophocebus* sp. from Koobi Fora, Kenya (1.87–1.56 Ma; Jablonski et al., 2008: Figs. IV.18 and IV.20).

Lower molars Although the faint mesial buccal cleft (so that the mesial ridge does not constitute a distinct ledge-like protrusion) is somewhat reminiscent of colobines, other features of the Guefaït-4.2 specimens (moderately deep median lingual notches, moderate buccal flare of the crown, and distal marginal ridge uninterrupted by the distal buccal cleft) denote cercopithecine affinities (Delson, 1973). The presence of a hypoconulid on the M_3 rules out an assignment to cercopithecins (Delson, 1973, 1975), while the presence of a tuberculum sextum further supports a papionin assignment, since this feature is rare in colobines (Delson, 1973). Indeed, the two lower molars display a generalized papionin occlusal morphology that is compatible with both *Macaca* (e.g., *M. sylvanus* [SOM Fig. S3B–F], known from this region) and dentally conservative papioninans (e.g., *Parapapio*, *Pliopapio* and *Papio*). This morphology differs from the more derived pattern of *Theropithecus*, which is characterized by greater occlusal relief (with deeper foveae and notches), obliquely oriented lophids and trigonid, large distal accessory cuspulid on M_2, and less buccal flare (Delson, 1973, 1975; Szalay and Delson, 1979). In molar proportions and buccal flare, the Guefaït molars do not differ much from *Lophocebus* sp. from Koobi Fora (Frost, 2001; Jablonski et al., 2008). However, they can be distinguished from the latter by the smaller dimensions, and the more buccally located hypoconulid and better developed tuberculum sextum on the M_3 (albeit variable within papionin taxa, the tuberculum sextum is only incipiently developed in some Koobi Fora specimens and more consistent with an attribution to *Macaca*).

3.3. Metrical comparisons

Estimated BM for the Guefaït-4.2 M_2 is around 11–12.5 kg (SOM S2), more similar to female (10.1 kg) than male (14.5 kg) average BM for extant *M. sylvanus* (Delson et al., 2000). Dental measurements for the Guefaït-4.2 specimens are visually compared with those of macaques and similarly-sized extinct papionins of *Parapapio* and *Pliopapio* by means of bivariate plots (Fig. 2) and boxplots (Fig. 3). Statistical comparisons are provided in SOM Tables S2–S4 and discussed in SOM S3.

Although metrical comparisons for the Guefaït-4.2 I^1 are limited by the small fossil samples, it comfortably fits within the variation of extant *M. sylvanus*, not only in length and width, but also in crown height (Figs. 2A, B and 3A–C; SOM Table S2). In turn, the Guefaït-4.2 molars (Figs. 2C, D and 3D–I; SOM Table S2) fit well in size with *M. s. sylvanus*, *M. majori*, '*P.*' *lothagamensis*, and *Pl. alemui*, but appear too short for *P.* (cf.) *ado*, *M. s.* (cf.) *pliocena*, *M. s. florentina*, and *M. libyca*; the Guefaït-4.2 M_3 is further relatively too broad as compared with these fossil macaques and *Pl. alemui*. It is noteworthy that the Guefaït-4.2 M_3, like those of extant *M. sylvanus*, not only lacks the elongation of fossil European *M. sylvanus* but displays a particularly broad (or short) crown in relative terms (albeit within the variation of extant *M. sylvanus*). While the I^1 from Guefaït-4.2. falls toward the upper size range of *M. sylvanus*, the lower molars display the opposite pattern, suggesting that the former derives from a different (larger) individual.

4. Discussion and conclusions

The occlusal morphology of the Guefaït-4.2 upper incisor and lower molars appears compatible with *Macaca* and other fossil papionins. However, in size and proportion the Guefaït-4.2 sample only fits well with *M. s. sylvanus*, as well as '*P.*' *lothagamensis*, which despite a markedly tapering distal contour similarly displays a buccally located hypoconulid and frequently a tuberculum sextum (Leakey et al., 2003). The Guefaït-4.2 lower molars are somewhat unusual due to the slightly projecting mesial fovea and the unusually 'shortened' appearance of the M_3. However, the latter is not caused by a poorly developed hypoconulid per se, but due to the shortness of the hypoconulid lobe as a whole. This is probably the most variable dental complex among cercopithecoids (Delson, 1973). The hypoconulid has been lost in cercopithecins and is reduced in smaller Asian colobines (Swindler, 1983, 2002; Szalay and Delson, 1979) but is almost invariably present in papionins, where it shows some degree of intraspecific variation (Swindler, 1983). It is only rarely missing in some *Papio*, *Cercocebus* and *Macaca* individuals (Delson, 1973, 1975; Szalay and Delson, 1979; Phillips-Conroy, 1982), resulting in the reduction of the hypoconulid lobe (Phillips-Conroy, 1982). However, the development of the hypoconulid in the Guefaït-4.2 M_3 is comparable to that of *M. sylvanus* (SOM Fig. S3). Furthermore, its overall proportions fit well within the variation of extant *M. sylvanus* from northern Africa, while it can be metrically distinguished from those of European Plio-Pleistocene *M. sylvanus* (which generally display better developed hypoconulid lobes).

'*Parapapio*' *lothagamensis* is a stem papionin (Gilbert, 2013) from the Late Miocene and earliest Pliocene of eastern Africa (Leakey et al., 2003). Therefore, an assignment to *Macaca* is favored on biogeographical and chronological grounds. Given that *M. sylvanus* is the only macaque species previously recognized in the African Plio-Pleistocene (see Introduction), an assignment to this species seems warranted—although, given the small available sample, we prefer to use open nomenclature to keep our assignment tentative (i.e., *M.* cf. *sylvanus*). Other authors might prefer an assignment to cf. *Macaca* or even Papionini indet. (Benefit et al., 2008). However, an attribution to *M.* cf. *sylvanus* is in agreement with standard taxonomic practice for European Plio-Pleistocene macaques, which following Szalay and Delson (1979) are regularly allocated to *M. sylvanus* despite the lack of more diagnostic cranial material (e.g., Alba et al., 2011, 2014, 2018).

The roughly coeval Moroccan site of Ahl al Oughlam (~2.5 Ma; Geraads, 2006, 2010) also records the presence of *Theropithecus* (Alemseged and Geraads, 1998; Geraads et al., 1998; Geraads, 2006), which raises the question as to why this genus is not recorded at Guefaït. The fauna from Ahl al Oughlam displays close affinities with both eastern and southern Africa (Geraads, 2006), indicating that—even if the Sahara belt acted as a biogeographic barrier that promoted the divergence between Macacina and Papionina in the Late Miocene (Delson, 1973; Roos et al., 2019)—it did not completely prevent the dispersal of *Theropithecus* and other mammals from lower latitudes into northern Africa sometime during the Late Pliocene (Geraads, 2006). During the Late Pliocene, eastern Africa experienced a progressive aridification trend punctuated by more humid episodes, including a brief humidity peak at 2.7–2.5 Ma (Trauth et al., 2007), which might have facilitated the northward dispersal of *Theropithecus*, as it roughly coincides with the appearance in eastern Africa of *T. oswaldi oswaldi* (Jablonski and Frost, 2010). Hypothetically, Guefaït-4.2 might predate the dispersal of *Theropithecus* into northern Africa only if it is somewhat older than Ahl al Oughlam—as tentatively suggested by the presence of some Late Pliocene murids that are absent from the latter site (Agustí et al., 2017; Piñero et al., 2019).

Alternatively, the absence of *Theropithecus* from Guefaït-4.2 might reflect paleoenvironmental differences relative to Ahl al Oughlam. Preliminary accounts of the Guefaït 4.2 paleoenvironment based on the micromammal and paleoherpetological assemblage suggest an open woodland habitat characterized by dry conditions within a rocky landscape and with a permanent (lacustrine or riverine) water body nearby (Agustí et al., 2017; Sala-Ramos et al., 2017). Such a paleoenvironmental reconstruction seems highly suitable for macaques, based on the preferences of extant *M. sylvanus*, which is dependent on water availability but occupies a wide variety of seasonal habitats—from forests to grasslands and rocky escarpments—as long as there are trees nearby (Deag, 1974; Camperio Ciani et al., 2001; Ménard, 2002; Fooden, 2007). However, this is unlikely to rule out the presence of *Theropithecus*—particularly *T. o. oswaldi*, which was better adapted to open habitats than its predecessor *T. oswaldi darti* (Leakey, 1993; Teaford, 1993; Jablonski et al., 2002; Folinsbee, 2008). Furthermore, based on the accompanying fauna, Ahl al Oughlam has similarly been reconstructed as recording an open (and probably seasonal) environment (Geraads et al., 1998; Geraads, 2006).

Given the rarity of primate finds and the restricted sample currently available for some large mammals (such as suids and giraffids) from Guefaït-4.2, the absence of *Theropithecus* might simply be a sampling artifact. In any case, it is noteworthy that the macaques from Ahl al Oughlam and Guefaït-4.2 represent the last known record of *Macaca* in Africa until its reappearance in the late Middle Pleistocene of Aïn Mefta (~200 ka; Pomel, 1892, 1896; Geraads, 1987). This gap of more than 2 Myr contrasts with the more continuous record of macaques in Europe throughout the Pleistocene and their subsequent greater abundance in the Late Pleistocene of North Africa (e.g., Fooden, 2007, and references therein). It is uncertain whether this pattern is also attributable to the biases of the record or whether it might represent a local extinction followed by a subsequent redispersal of macaques from elsewhere into northern Africa toward the end of the Middle Pleistocene. Additional fieldwork would be required to clarify further papionin evolution and paleobiogeography during the Pleistocene of northern Africa.

References

Agustí, J., Blain, H.-A., Piñero, P., Hajji, N.-e., Aouraghe, H., Haddoumi, H., El Hammouti, K., El Harradji, A., 2016. Les petits vertébrés des sites de Guéfait : Biostratigraphie et paléoenvironment. In: 10 Ans de Recherches & de Coopérations Scientifiques Maroco-Espagnole dans la Province de Jerada (Maroc Oriental). Séminaire International sur le Patrimoine Archéologique de la Province de Jerada. Recueil du Séminaire, Jerada, 2016, pp. 12–13.

Agustí, J., Piñero, P., Blain, H.-A., Aouraghe, H., Haddoumi, H., El Hammouti, K., Chacón, G., Sala, R., 2017. The Early Pleistocene small vertebrates from Guefeit 4 (Jerada, Morocco). In: La 9ème Rencontre des Quaternaristes Marocains (RQM9). Recueil des Résumés. “Programme et Guide de l’Excursion”. Cadi Ayyad University, , Faculté Polydisciplinaire, Safi, p. 54.

Alba, D. M., Carlos Calero, J.A., Mancheño, M.Á., Montoya, P., Morales, J., Rook, L., 2011. Fossil remains of *Macaca sylvanus florentina* (Cocchi, 1872) (Primates, Cercopithecidae) from the Early Pleistocene of Quibas (Murcia, Spain). J. Hum. Evol. 61, 703–718.

Alba, D.M., Delson, E., Carnevale, G., Colombero, S., Delfino, M., Giuntelli, P., Pavia, M., Pavia, G., 2014. First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. J. Hum. Evol. 67, 1–18.

Alba, D.M., Delson, E., Morales, J., Montoya, P., Romero, G., 2018. Macaque remains from the early Pliocene of the Iberian Peninsula. J. Hum. Evol. 123, 141–147.

Alemseged, Z., Geraads, D., 1998. *Theropithecus atlanticus* (Thomas, 1884) (Primates: Cercopithecidae) from the late Pliocene of Ahl al Oughlam, Casablanca, Morocco. J. Hum. Evol. 34, 609–621.

Alvarez Posada, C., Parés, J.M., Carrancho Alonso, A., Villalain, J.J., Aouraghe, H., Haddoumi, H., El Mammouti, K., El Harradji, A., Sala, R., Chacón, M.G., 2015. Paleomagnetic studies in the northwestern margin of the Aïn Beni Mathar–Guefait Basin (High Plateaus, Morocco). In: II Meeting of African Prehistory. CENIEH, Burgos, p. 17.

Aouraghe, H., Sala, R., Chacón, M.G., 2016. Bilan de dix ans de recherches archéologiques dans la région de Jerada (Maroc Oriental). In: 10 Ans de Recherches & de Coopérations Scientifiques Maroco-Espagnole dans la Province de Jerada (Maroc Oriental). Séminaire International sur le Patrimoine Archéologique de la Province de Jerada. Recueil du Séminaire, Jerada, 2016, pp. 8–9.

Aouraghe, H., Haddoumi, H., Rodríguez-Hidalgo, A., Van der Made, J., Piñero, P., Agustí, J., Álvarez, C., Benito-Calvo, A., Blain, H.-A., Duval, M., El Hammouti, K., Expósito, I., Marín, J., Mejías, D., Oujaa, A., Parés, J.M., Pla, S., Ramírez-Pedraza, I., Rivals, F., Saladié, P., Tornero, C., Chacón, M.G., Sala-Ramos, R., 2019a. Nouvelles données sur le site du Pliocène Final/Pléistocène Inférieur de Guefaït 4: Mission 2019. In: 10ème Rencontre des Quaternaristes Marocains, Kénitra. Recueil des Résumés, pp. 47–48.

Aouraghe, H., Haddoumi, H., Hajji, N.-E., Sala, R., Rodríguez-Hidalgo, A., Van der Made, J, Saladié, P., Chacón, M. G., El Hammouti, K., 2019b. Découverte d'un nouveau site paléontologique plio-quatenaire dans le Maroc oriental (Guefaït 4, province de Jerada).

In: Recueil des Résumés, 23ème Colloque des Bassins Sédimentaires. Fès, 21 – 23 novembre 2019, pp. 34–35.

Arambourg, C., 1959. Vertébrés continentaux du Miocène Supérieur de l'Afrique du Nord. Publ. Serv. Carte Géol. Algérie Paléontol. 4, 5–159.

Arambourg, C., 1979. Vertébrés villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). Édition de la Fondation Singer-Polignac, Paris.

Arambourg, C., Coque, R. 1959. Le gisement villafranchien de l'Aïn Brimba (Sud-Tunisien) et sa faune. Bull. Soc. Géol. Fr. 8, 607–614.

Benefit, B.R., McCrossin, M., Boaz, N.T., Pavlakis, P., 2008. New fossil cercopithecoids from the Late Miocene of As Sahabi, Libya. Garyounis Sci. Bull. Special Issue No. 5, 265–282.

Blain, H.-A., Agustí, J., López-García, J.M., Haddoumi, H., Aouraghe, H., El Hammouti, K., Pérez-González, A., Chacón, M.G., Sala, R., 2013. Amphibians and squamate reptiles from the late Miocene (Vallesian) of eastern Morocco (Guefaït-1, Jerada Province). J. Vert. Paleontol. 33, 804–816.

Camperio Ciani, A., Martinoli, L., Capiluppi, C., Arahou, M., Mouna, M., 2001. Effects of water availability and habitat quality on bark-stripping behavior in Barbary macaques. Cons. Biol. 15, 259–265.

Chacón, M.G., Aouraghe, H., Agustí, J., Àlvarez, C., Arnold, L., Benito-Calvo, A., lain, H.-A., Carrancho, A., de Lombera, A., Duval, M., El Hammouti, K., El Harragji, A., Haddoumi, H., Menéndez, L., Parés, J.M., Piñero, P., Tarriño, A., Villalaín, J.J., Sala, R., 2016. Ten years of archaeological research in the Aïn Béni-Mathar/Guefaït region (Eastern Morocco): Results and perspectives. In: 58th Annual Meeting in Budapest. March 29th – April 2nd 2016. Hugo Obermaier-Gesellschaft für Erforschung des Eiszeitalers und der Steinzeit e.V., Erlangen, pp. 21–22.

Daujeard, C., Falguères, C., Shao, Q., Geraads, D., Hublin, J.-J., Lefèvre, D., El Graoui, M., Rué, M., Gallotti, R., Delvigne, V., Queffelec, A., Ben Arous, E., Tombret, O., Mohib, A., Raynal, J.-P., 2000. Earliest African evidence of carcass processing and consumption in cave at 700 ka, Casablanca, Morocco. Sci. Rep. 10, 4761.

Delson, E., 1973. Fossil colobine monkeys of the Circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia). Ph.D. Dissertation, Columbia University.

Delson, E., 1974. Preliminary review of cercopithecid distribution in the Circum Mediterranean region. Mém. Bur. Rech. Géol. Min. Fr. 78, 131–135.

Delson, E., 1975. Evolutionary history of the Cercopithecidae. Contrib. Primatol. 5, 167–217.

Delson, E., 1993. *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In: Jablonski, N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 157–189.

Delson, E., Hoffstetter, R., 1993. *Theropithecus* from Ternifine, Algeria. In: Jablonski, N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 191–208.

Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J., Jablonski, N.G., Dechow, P.C., 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. Anthropol. Papers Am. Mus. Nat. Hist. 83, 1–159.

Folinsbee, K.A., 2008. Evolutionary history and biogeography of papionin monkeys. Ph.D. Dissertation, University of Toronto.

Fooden, J., 2007. Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). Fieldiana Zool. 113, 1–60.

Frost, S.R., 2001. Fossil Cercopithecidae of the Afar depression, Ethiopia: Species systematics and comparison to the Turkana Basin. Ph.D. Dissertation, The City University of New York.

Geraads, D., 1980. La faune des sites à «*Homo erectus*» des carrières Thomas (Casablanca, Maroc). Quatemaria 22, 65–94.

Geraads, D., 1987. Dating the Northern African cercopithecid fossil record. Hum. Evol. 2, 19–27.

Geraads, D., 2006. The late Pliocene locality of Ahl al Oughlam, Morocco: vertebrate fauna and interpretation. Trans. R. Soc. S. Afr. 61, 97–102.

Geraads, D., 2010. Biochronologie mammalienne du Quaternaire du Maroc atlantique, dans son cadre régional. L'Anthropologie 114, 324–340.

Geraads, D., Amani, F., Raynal, J.-P., Sbihi-Alaoui, F.-Z., 1998. La faune de Mammifères du Pliocène terminal d'Ahl al Oughlam, Casablanca, Maroc. C. R. Acad. Sci. Paris 326, 671–676.

Gilbert, C.C., 2013. Cladistic analysis of extant and fossil African papionins using craniodental data. J. Hum. Evol. 64, 399–433.

Hajji, N.E., 2010. Le Mio-Pliocène de la région de Guéfait (Maroc oriental) : stratigraphie et sédimentologie de la coupe de Dhar Irroumine. Master’s Thesis, Université Mohamed 1er.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 4.

Jablonski, N.G., 2002. Fossil Old World monkeys: the late Neogene radiation. In: Hartwig, W.C. (Ed.), The Primate Fossil Record. Cambridge University Press, Cambridge, pp. 255–299.

Jablonski, N., Frost, S., 2010. Cercopithecoidea. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 393–428.

Jablonski, N.G., Leakey, M.G., Kiarie, C., Antón, M., 2002. A new skeleton of *Theropithecus brumpti* (Primates: Cercopithecidae) from Lomekwi, West Turkana, Kenya. J. Hum. Evol. 43, 887–923.

Jolly, C.J., 1972. The classification and natural history of *Theropithecus (Simopithecus)* (Andrews, 1916), baboons of the African Plio-Pleistocene. Bull. Brit. Mus. Nat. Hist. Geol. 22, 1–123.

Kato, A., Tang, N., Borries, C., Papakyrikos, A.M., Hinde, K., Miller, E., Kunimatsu, Y., Hirasaki, E., Shimizu, D., Smith, T.M., 2014. Intra- and interspecific variation in macaque molar enamel thickness. Am. J. Phys. Anthropol. 155, 447–459.

Kopp, G.H., Roos, C., Butynski, T.M., Wildman, D.E., Alagaili, A.N., Groeneveld, L.F., Zinner, D., 2014. Out of Africa, but how and when? The case of hamadryas baboons (*Papio hamadryas*). J. Hum. Evol. 76, 154–164.

Leakey, M.G., 1993. Evolution of *Theropithecus* in the Turkana Basin. In: Jablonski, N.G (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 85–123.

Leakey, M.G., Teaford, M.F., Ward, C.V., 2003. Cercopithecidae from Lothagam. In Leakey, M.G., Harris, J.M. (Eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 201–248.

Meikle, W.E., 1987. Fossil Cercopithecidae from the Sahabi Formation. In: Boaz, N.T., El-Arnauti, A., Gaziry, A.W., de Heinzelin, J., Boaz, D.D. (Eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York, pp. 119–127.

Ménard, N., 2002. Ecological plasticity of Barbary macaques (*Macaca sylvanus*). Evol. Anthropol. 11(S1), 95–100.

Phillips-Conroy, J.E., 1982. Symmetrical reduction of M3 and hypoconulid loss in *M. mulatta*. Am. J. Phys. Anthropol. 58, 27–35.

Piñero, P., Agustí, J., Haddoumi, H., El Hammouti, K., Chacón, M.G., Sala-Ramos, R., 2019. *Golunda aouraghei*, sp. nov., the last representative of the genus *Golunda* in Africa. J. Vert. Paleontol. 39, e1742726.

Pomel, A., 1892. Sur un macaque fossile des phosphorites quaternaires de l'Algérie, *Macacus trarensis*. C. R. Séanc. Acad. Sci. 115, 157–160.

Pomel, A., 1896. Singe et homme. Publ. Serv. Carte Géol. Algérie Paléontol. 11, 1–32.

Raynal, J.-P., Texier, J.-P., Geraads, D., Sbihi-Alaoui, F.-Z., 1990. Un nouveau gisement paléontologique plio-pléistocène en Afrique du Nord : Ahl Al Oughlam (ancienne carrière Deprez) à Casablanca (Maroc). C. R. Acad. Sci. Paris. 310, 315–320.

Raynal, J.-P., Sbihi-Alaoui, F.-Z., Mohib, A., El Graoui, M., Lefèvre, D., Texier, J.-P., Geraads, D., Hublin, J.-J., Smith, T., Tafforeau, P., Zouak, M., Grün, R., Rhodes, E. J., Eggins, S., Daujeard, C., Fernandes, P., Gallotti, R., Hossini, S., & Queffelec, A., 2010. Hominid Cave at Thomas Quarry I (Casablanca, Morocco): Recent findings and their context. Quat. Int. 223–224, 369–382.

Rhodes, E.J., Singarayer, J.S., Raynal, J.-P., Westaway, K.E., Sbihi-Alaoui, F.Z., 2006. New age estimates for the Palaeolithic assemblages and Pleistocene succession of Casablanca, Morocco. Quat. Sci. Rev. 25, 2569–2585.

Roberts, P., Delson, E., Miracle, P., Ditchfield, P., Roberts, R.G., Jacobs, Z., Blinkhorn, J., Ciochon, R.L., Fleagle, J.G., Frost, S.R., Gilbert, C.C., Gunnell, G. F., Harrison, T., Korisettar, R., Petraglia, M.D., 2014. Continuity of mammalian fauna over the last 200,000 y in the Indian subcontinent. Proc. Nat. Acad. Sci. USA 111, 5848–5853.

Roos, C., Kothe, M., Alba, D.M., Delson, E., Zinner, D., 2019. The radiation of macaques out of Africa: Evidence from mitogenome divergence times and the fossil record. J. Hum. Evol. 133, 114–132.

Sahnouni, M., van der Made, J., 2009. The Oldowan in North Africa within a biochronological framework. In: Schick, K.D., Toth, N. (Eds.), The Cutting Edge: New Approaches to the Archaeology of Human Origins. Stone Age Institute Press, Bloomington, pp. 179–210.

Sahnouni, M., Parés, J.M., Duval, M., Cáceres, I., Harichane, Z., van der Made, J., Pérez-González, A., Abdessadok, S., Kandi, N., Derradji, A., Medig, M., Boulaghraif, K., Semaw, S., 2018. 1.9-million- and 2.4-million-year-old artifacts and stone tool–cutmarked bones from Ain Boucherit, Algeria. Science 362, 1297–1301.

Sala, R., Chacón, M.G., De Lombera, A., Menéndez, L., Tarriño, A., 2016. L'industrie lithique des regions d'Aïn Béni Mathar et Guéfait. In: 10 Ans de Recherches & de Coopérations Scientifiques Maroco-Espagnole dans la Province de Jerada (Maroc Oriental). Séminaire International sur le Patrimoine Archéologique de la Province de Jerada. Recueil du Séminaire, Jerada, 2016, pp. 10–11.

Sala-Ramos, R., Aouraghe, H., Chacón, M.G., Agustí, J., Alvarez, C., Aranold, L., Bengarmra, S., Benito-Calvo, A., Blain, H.A., Burjachs, F., Canals, A., Carrancho, Á., De Lombera-Hermida, A., Duval, M., El Atmani, A., El Harradji, A., El Hammouti, K., Expósito, I., Haddoumi, H., Lorenzo, C., Van der Made, J., Menéndez, L., Mhamdi, H., Moreno, E., Parés, J.M., Oujaa, A., Piñero, P., Rivals, F., Rodríguez-Hidalgo, A., Souhir, M., Soto, M., Tarriño, A., Villalaín, J.J., Viñas, R., 2017. Guéfait 4: Un nouveau site paléontologique dans un environnement humide et ouvert au Maroc Oriental. In: La 9ème Rencontre des

Quaternaristes Marocains (RQM9). Recueil des Résumés. “Programme et Guide de l’Excursion”. Cadi Ayyad University, Safi, p. 48.

Stromer, E. 1913. Mitteilungen über die Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). Z. Deutsch. Geol. Ges. 65, 350–372.

Stromer, E., 1920. Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). 5. Nachtrag zu 1. Affen. Sitz. Math.-Phys. Kl. Bay. Akad. Wiss. München 1920, 345–370.

Swindler, D.R., 1983. Variation and homology of the primate hypoconulid. Folia Primatol. 41, 112–123.

Swindler, D.R., 2002. Primate Dentition. An Introduction to the Teeth of Non-Human Primates. Cambridge University Press, Cambridge.

Szalay, F., Delson, E., 1979. Evolutionary History of the Primates. Academic Press, New York.

Teaford, M., 1993. Dental microwear and diet in extant and extinct *Theropithecus*: preliminary analyses. In: Jablonski, N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 331–349.

Thomas, P., 1884. Recherches stratigraphiques et paléontologiques sur quelques formations d’eau douce de l’Algérie. Mém. Soc. Géol. Fr. 3(2), 1–53.

Trauth, M.H., Maslin, M.A., Deino, A.L., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. J. Hum. Evol. 53, 475–486.

van den Brink, S., 1981. A propos du *Cercopithecidae (Mammalia,* primate*)* villafranchien de l'Aïn Brimba, Tunisie. Géobios 14, 421–425.

Figure captions

Figure 1. Teeth of *Macaca* cf. *sylvanus* from Guefaït-4.2 (views from left to right for each specimen): a) GFT4.2'18-1-Q14-70, left I^1 crown in occlusal, occusal, lingual, mesial, labial, and distal views; b) GFT4.2'18-1-Q14-13, right M_1 lingual crown fragment in occlusal, buccal, and lingual (cross-sectional) views; c) GFT4.2'18-1-P13-191, right M_2 or M_3 mesial germ fragment in oblique occlusal and mesial views; d) GFT4.2'19-1-R15-45, right M_2 distal germ fragment in occlusal and distal views; e) GFT4.2'19-1-S15-65, right M_2 crown with distal root in occusal, lingual, mesial, buccal, and distal views; f) GFT4.2'19-1-R13-63, left M_3 crown in occusal, lingual, mesial, buccal, and distal views. 3D virtual models are available from MorphoSource (see SOM Files S1–S6).

Figure 2. Bivariate plots of dental proportions in *Macaca* cf. *sylvanus* from Guefaït-4.2 (star) compared with extant Barbary macaques (*Macaca sylvanus sylvanus*), fossil macaques from the Plio-Pleistocene of Europe (*Macaca sylvanus* subspp. and *Macaca majori*), fossil *Macaca libyca* and *Macaca* aff. *sylvanus* from Aïn Brimba, and selected stem papioninans from eastern Africa (*Parapapio* [cf.] *ado*, '*Parapapio*' *lothagamensis*, and *Pliopapio alemui*): A) I^1 MD vs. H; B) I^1 BL vs. MD; C) M_2 MD vs. BL; D) M_3 MD vs. BL. The variation of extant *M. s. sylvanus* is denoted by the light gray convex hull, while that of extinct *M. sylvanus* subspp. from Europe is denoted by a semitransparent red convex hull. Data sources are reported in SOM Table S1. Abbreviations: H = maximum recorded labial height (mm); BL = buccolingual breadth (BLm, mesial lophid for the molars; mm); MD = mesiodistal length (mm).

Figure 3. Box-and-whisker plots of MD (A, D, G), BL (B, E, H), and BLI (C, F, I) in extant macaques and some fossil papionins compared with *Macaca* cf. *sylvanus* from Guefaït: a–c)

I^1; d–f) M_2; g–i) M_3. Vertical lines denote the median; boxes denote the 25 and 75 percentiles (Q1 and Q3), i.e., the interquartile range (IQR); whiskers denote the maximum-minimum values. Data sources are reported in SOM Table S1. Abbreviations: BL = buccolingual breadth (mm; BLm, mesial lophid for the molars); BLI = breath/length index (%); MD = mesiodistal length (mm).

Table 1

Provenance information and measurements of the *Macaca* cf. *sylvanus* teeth from Guefaït 4.2.

Catalog No.[a]	Tooth	Level	Square	Collection date	x	y	z	MD	H	BL/BLm	BLd	BLI
GFT4.2’18-1-P13-191	R $M_{2/3}$ mesial germ fragment	1	P13	May 5, 2018	—	—	101	—	—	>7.0	—	—
GFT4.2’18-1-Q14-70	L I^1 crown	1	Q14	May 10, 2018	—	—	104	(6.8)[b]	10.0	6.2	—	91.2
GFT4.2’18-1-Q14-13	R M_1 lingual crown fragment	1	Q14	May 10, 2018	—	—	89	—	—	—	—	—
GFT4.2’19-1-R15-45	R M_2 distal germ fragment	1	R15	April 25, 2019	18	22	105	—	—	—	>7.1	—
GFT4.2’19-1-S15-65	R M_2 crown with distal root	1	S15	April 27, 2019	17	69	106	8.6	—	7.1	6.8	82.6
GFT4.2’19-1-R13-63	L M_3 crown	1	R13	April 19, 2019	43	88	88	10.0	—	7.6	7.5	76.0

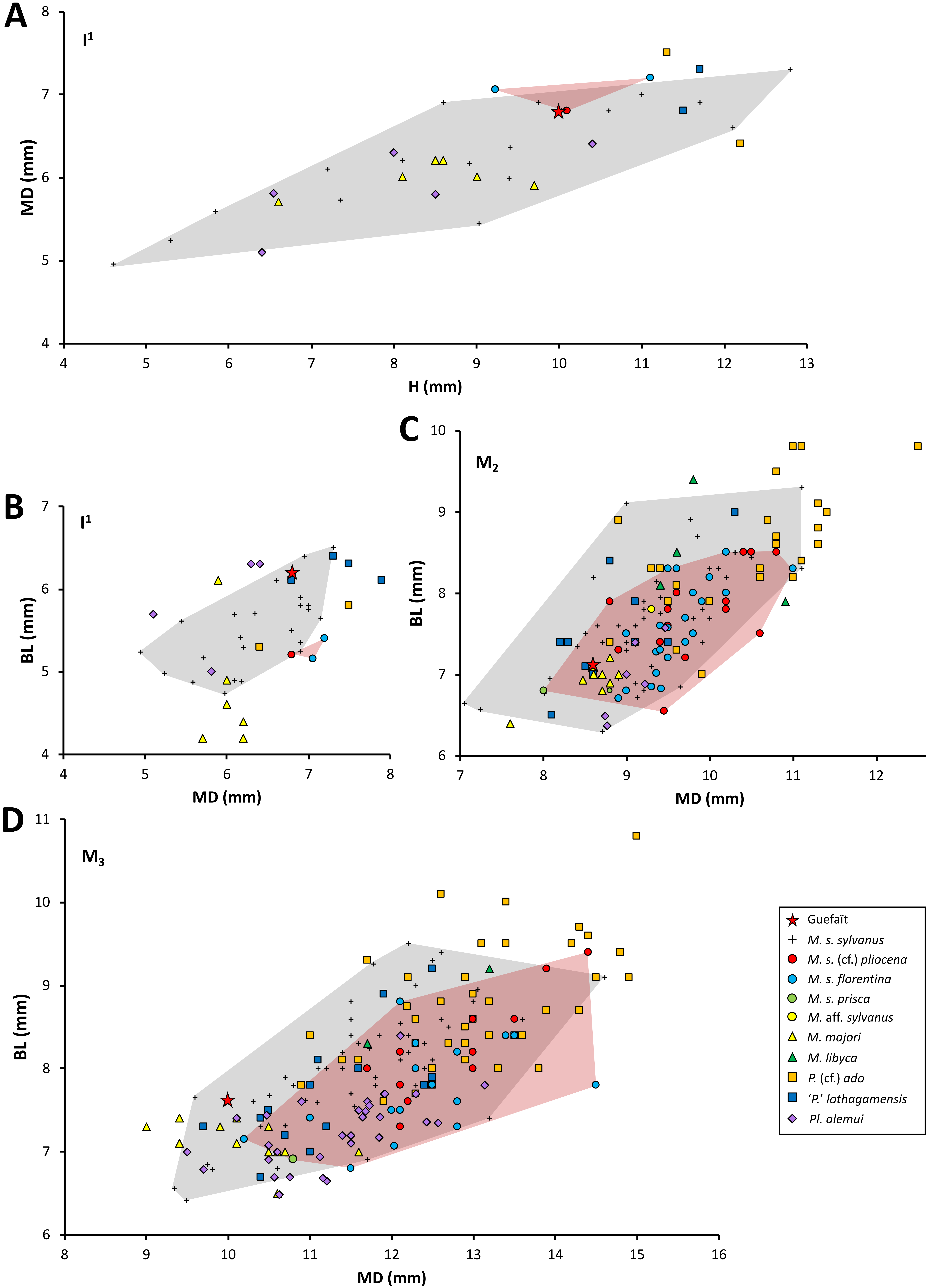
Abbreviations: BL = maximum buccolingual (or labiolingual) crown breadth (mm); BLI = breadth/length index (%), computed as BL / MD × 100 (based on BLm for the molars); BLm = buccolingual crown breadth (mm) at the mesial lophid (only for molars); BLd = buccolingual crown breadth (mm) at the distal lophid (only for molars); H = buccal crown height (mm; only for the incisor); L = left; MD = mesiodistal crown length (mm); R = right.

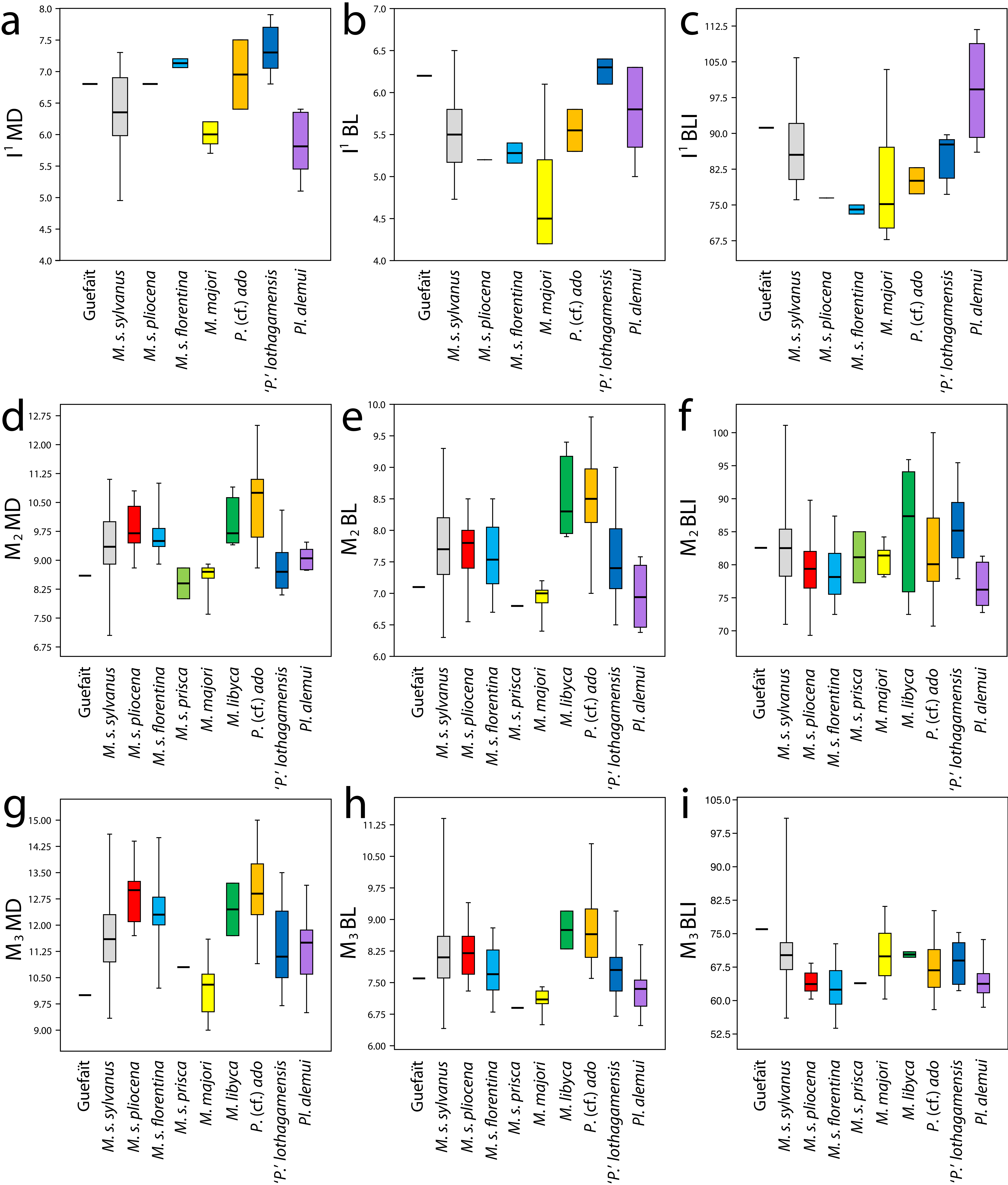
[a] Each specimen is denoted by its accession No., including site acronym (GFT) and locality number (4.2.), followed by year of collection (e.g., ’19 = 2019) and, separated by hyphens, the stratigraphic level, square within the excavation grid (uppercase letter followed by number), and

field No. in the catalog of this locality for each given year. The x, y and z columns indicate the spatial position of the specimen in the locality grid.

[b] Actual measurement is 6.5 mm, but given damage on the mesiolabial side it is estimated that measurement should be increased by ca. 5%.


a
1 cm
b
c
d
e
f


A
I1
MD (mm)
H (mm)
B
I1
BL (mm)
MD (mm)
C
M2
BL (mm)
MD (mm)
D
M3
BL (mm)
MD (mm)
Guefaït
M. s. sylvanus
M. s. (cf.) pliocena
M. s. florentina
M. s. prisca
M. aff. sylvanus
M. majori
M. libyca
P. (cf.) ado
'P.' lothagamensis
Pl. alemui


a
b
c
d
e
f
g
h
i
I1 MD
I1 BL
I1 BLI
M2 MD
M2 BL
M2 BLI
M3 MD
M3 BL
M3 BLI
Guefaït
M. s. sylvanus
M. s. pliocena
M. s. florentina
M. s. prisca
M. majori
M. libyca
P. (cf.) ado
'P.' lothagamensis
Pl. alemui

Supplementary Online Material (SOM):

New macaque fossil remains from Morocco

David M. Alba [a,*], Antonio Rodríguez-Hidalgo [b,c,d], Hassan Aouraghe [e], Jan van der Made [f], Aïcha Oujaa [g], Hamid Haddoumi [e], Palmira Saladié [c,h,i], Al Mahdi Aissa [e], Juan Marín [c], Mourad Farkouch [c,e], Carlos Lorenzo [h,c], Said Bengamra [e], Eric Delson [j,k,l,m,a], M. Gema Chacón [c,h,n], Robert Sala-Ramos [c,h]

[a] *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193, Cerdanyola del Vallès, Barcelona, Spain*

[b] *Departamento de Prehistoria, Historia Antigua y Arqueología, Universidad Complutense de Madrid, Facultad de Geografía e Historia, C/ Prof. Aranguren s/n, 28040, Madrid, Spain*

[c] *Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), Tarragona, 43007, Spain*

[d] *Instituto de Evolución en África (IDEA, Madrid), C/ Covarrubias 36, 28010, Madrid, Spain*

[e] *Faculté des Sciences, Département de Géologie, Université Mohamed Premier, BV Mohammed VI, Quartier Al Qods, 60000, Oujda, Morocco*

[f] *Consejo Superior de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, Departamento de Paleobiología, C/ José Gutiérrez Abascal, 2, 28006, Madrid, Spain*

[g] *Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Av. Allal El-Fassi, Hay Riad, 6828, Rabat, Morocco*

[h] *Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain*

[i] *Unidad Asociada al CSIC, Departamento de Paleobiologia, Museo Nacional de Ciencias Naturales, C/ José Gutiérrez Abascal, 2, 28006, Madrid, Spain*

[j] *Department of Anthropology, Lehman College of the City University of New York, 250 Bedford Park Boulevard West, Bronx, NY, 10468, USA*

[k] *Department of Vertebrate Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY, 10024, USA*

[l] *PhD Programs in Anthropology and Earth & Environmental Sciences, The Graduate Center of the City University of New York, 365 Fifth Avenue, New York, NY, 10016, USA*

[m] *New York Consortium in Evolutionary Primatology, New York, NY, USA*

[n] *UMR7194 Histoire naturelle de l'Homme préhistorique (HNHP), Museum National d'Histoire Naturelle (MNHN), CNRS, Université Perpignan Via Domitia, Alliance Sorbonne Université – Musée de l'Homme, Place du Trocadéro 17, 75016 Paris, France*

Corresponding author.

Email: david.alba@icp.cat (D.M. Alba)

SOM S1

Scanning methods

To derive 3D virtual models of the studied teeth from Guefaït-4.2, the teeth were scanned at the Laboratory of Microscopy of the Centro Nacional de Investigación sobre la Evolución Humana–Unique Scientific & Technical Infrastuctures (Burgos, Spain) with a high-resolution X-ray µCT scanner phoenix v|tome|x s 240 (GE Sensing & Inspections Technologies) with the following parameters: voltage = 120 kV, current = 130 µA, filter = 0.2 mm Cu, resulting in an isometric voxel size of 16.30027 µm. Segmentation was performed with Avizo 7.0 (Visualization Sciences Group, Mérignac) using a combination of automatic and manual segmentation by a technican at the Institut Català de Paleontologia Miquel Crusafont.

SOM S2

Body mass estimation

Body mass (BM, in g) was estimated using Delson et al.'s (2000: Table 7) allometric regression for M_2 mesial buccolingual width (BLm, in mm) for all cercopithecids:

$$\ln BM = 1.839 \ln (M_2\ BLm) + 5.694,\ n = 68,\ SEE = 0.383,\ QMLE = 1.076$$

where SEE is the standard error of estimate and QMLE is the quasi-maximum likelihood estimator to correct for logarithmic transformation bias. Following Ruff (2003), 50% and 95% confidence intervals (CI) were computed as $\pm SEE \times t_{(100\text{-}CI)(2),df} \times QMLE$, where df = n - 2. For df = 66, t = 0.68 for 50% CI and 2.00 for 95% CI, resulting in CIs being calculated as ±0.280 and ±0.824 for 50% and 95% confidence levels, respectively.

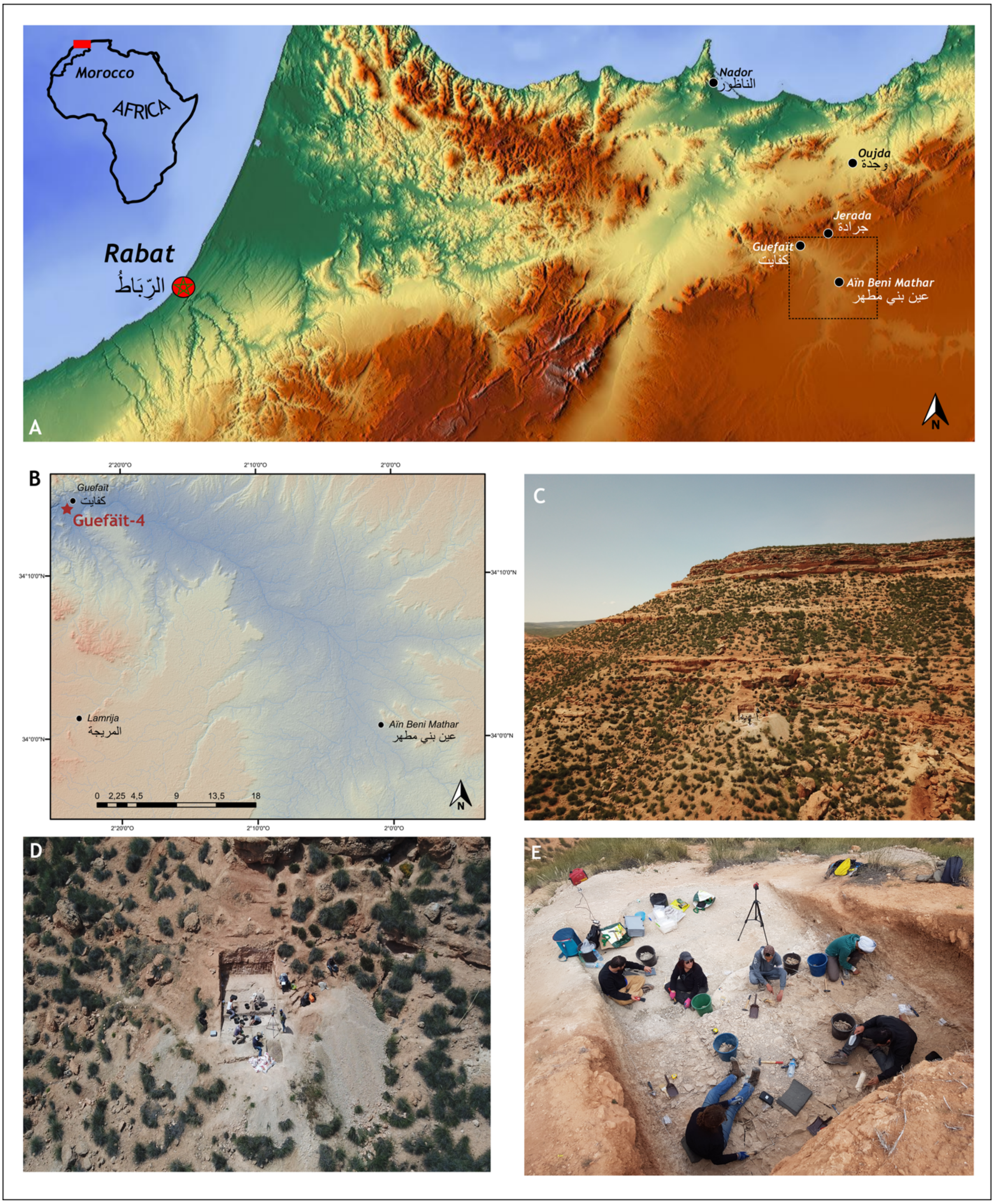
The resulting estimate is 11,753 g, with 50% CI = (11,473, 12,033) and 95% CI = (10,929, 12.577).

SOM S3

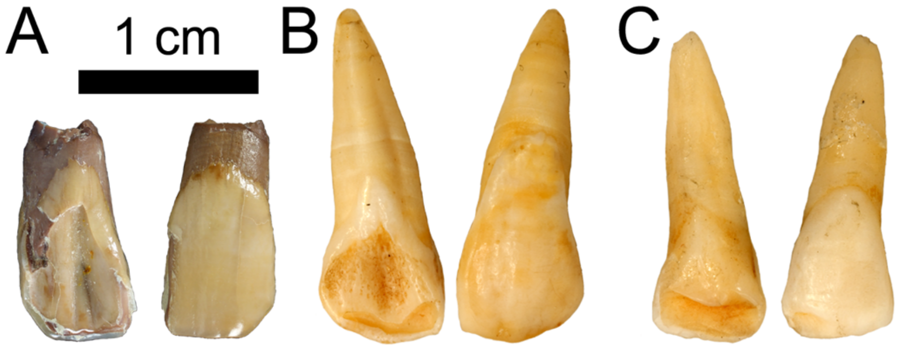
Statistical comparisons

ANOVA results indicate significant differences among the comparative sample for all variables except I^1 H (SOM Table S3), but Tukey's post hoc tests (SOM Table S4) indicate few significant pairwise differences for incisor dimensions (probably due to low statistical power associated with the small fossil samples). Therefore, below we focus on the greater number of significant differences for the lower molars (see SOM Table S4), despite considerable overlap.

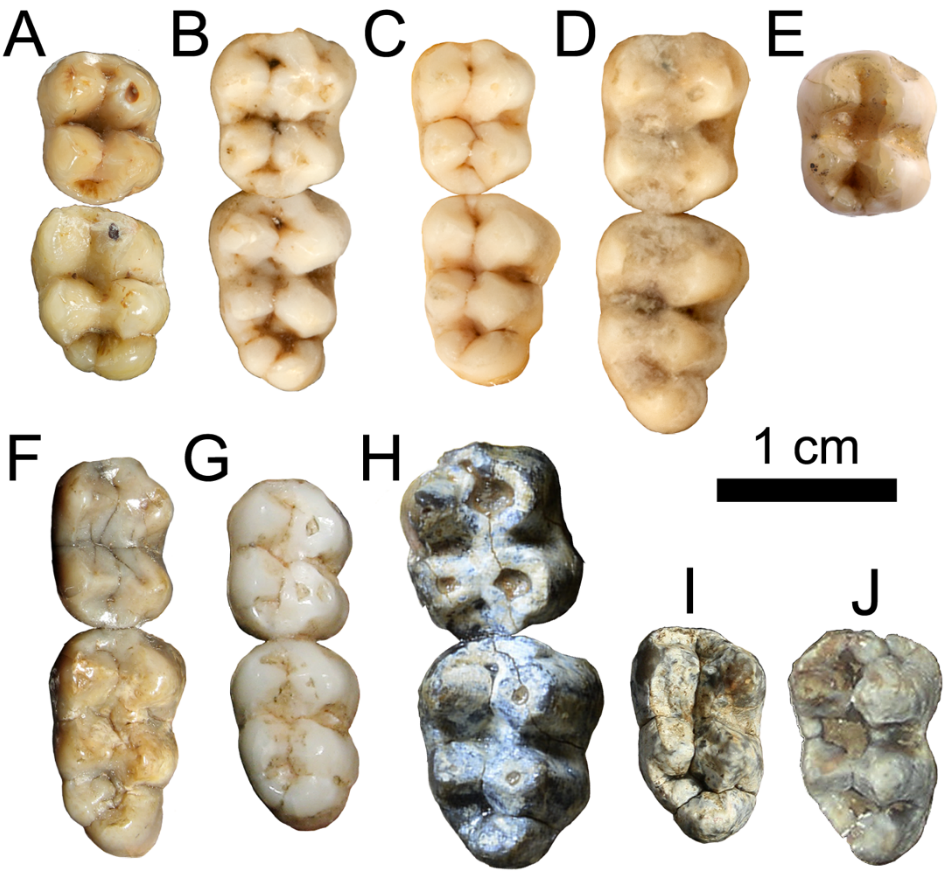
Parapapio (cf.) *ado* displays on average significantly larger molars than '*Parapapio*' *lothagamensis*, *Pliopapio alemui*, and macaques—except for *Macaca libyca* in most instances and also sometimes *Macaca sylvanus pliocena* and *M. sylvanus florentina*. '*Parapapio*' *lothagamensis* and *Pl. alemui* are more similar to macaques in molar dimensions. However, the molars of '*P.*' *lothagamensis* are significantly shorter than in *M. s.* (cf.) *pliocena*. In turn, *Pl. alemui* displays a narrower M_2 than *Macaca libyca*, as well as an M_3 intermediate in length between *Macaca majori* and fossil *M. sylvanus* from Europe; the M_3 of *Pl. alemui* is also narrower than in extant *M. sylvanus* and *M. majori*. Among macaques, *M. libyca* does not display significant differences in molar dimensions compared to *M. sylvanus* sspp., but shows larger M_2 and broader M_3 than *M. majori*. The latter further differs in some molar dimensions from extant and fossil *M. sylvanus*. *Macaca s.*(cf.) *pliocena* and *M. s. florentina* do not significantly differ from one another in molar size or proportions, but they both differ from extant *M. s. sylvanus* by displaying on average a relatively narrower M_3, which is also significantly longer in *M. s.* (cf.) *pliocena*.



SOM Figure S1. Location maps and pictures showing Guefaït-4 site and Guefaït-4.2 locality. A) Partial map of the Kingdom of Morocco (corresponding to the red rectangle overlapping the inset with the African continent); the area of interest (dotted box) is enlarged in panel B; data extracted from Map Tile 7_61/62/63-50 & 7_61/62/63-510 (CC BY-SA). OpenStreetMap© licensed under ODdL 1.0 (https://www.openstreetmap.org/copyright) by the OpenStreetMap Foundation (OSMF). ©OpenStreetMap contributors (https://www.openstreetmap.org/). B) Location map of the Guefaït-4 site (base map taken from ASTER GDEM v. 3, https://ssl.jspacesystems.or.jp/ersdac/GDEM/E/). C–E) Different views of the Guefaït-4 site and Guefaït-4.2 locality (pictures by Alfonso Benito-Calvo and A.R.H).



SOM Figure S2. Left I[1] crown (GFT4.2'18-1-Q14-70) of *Macaca* cf. *sylvanus* from Guefaït-4.2 (A) compared with two I[1] of extant *M. sylvanus* (right specimens, mirrored for comparison): AMNH-M 70269 (B) and AMNH-M 185277 (C). All specimens are shown in lingual (left) and labial (right) views.



SOM Figure S3. Right M_2 (GFT4.2'19-1-S15-65) and left M_3 (GFT4.2'19-1-R13-63, mirrored for comparison) of *Macaca* cf. *sylvanus* from Guefaït-4.2 (A) compared with the M_2–M_3 of three extant *M. s. sylvanus* individuals (B–D), fossil *M.* aff. *sylvanus* from Aïn Brimba (E, only M_2), *M. s. florentina* (F) and *Macaca majori* (G) from Italy, *Parapapio* cf. *ado* from Kanapoi (H), and *Pliopapio alemui* (only M_3) from Gona (I) and Aramis (J): B) AMNH-M 19014 (M_3 mirrored); C) AMNH-M 185277; D) AMNH-M 2060/5484; E) MNHN-F 1958-14-237; F) IGF 13084 (mirrored); G) IGF 2035 (mirrored); H) KNM-KP 286 (reproduced from Frost et al., 2020a: Fig. 1); I) GWM-9m/P256 (mirrored; reproduced from Frost et al., 2020b: Fig. 4); J) ARA-VP-1/2553 (mirrored; reproduced from Frost et al., 2020b: Fig. 4). All specimens are shown in occlusal view.

SOM Table S1

Dental measurements of *Macaca* cf. *sylvanus* from Guefaït-4.2 and the comparative sample, including: maximum recorded crown height (H, in mm; only for incisors), mesiodistal length (MD, in mm), buccolingual (or labiolingual) breadth (BL, in mm; both at the mesial [BLm] and distal [BLd] lophids for the molars), and breadth/length index (BLI, in %; computed based on BLm for molars). Values within parentheses are estimates.

Catalog No.	Species	Site	Tooth	Sex	MD	BL or BLm	BLd or H	BLI	Source
GFT4.2'18-1-Q14-70	*Macaca* cf. *sylvanus*	Guefaït-4.2	I^1	?	(6.8)	6.2	10.0	91.2	This study
AMNH-M 202286	*Macaca sylvanus*	extant	I^1	M	7.3	6.5	12.8	89.0	PRIMO
AMNH-M 185277	*Macaca sylvanus*	extant	I^1	F	5.72	5.17	7.35	90.4	PRIMO
AMNH-M 19014	*Macaca sylvanus*	extant	I^1	F	5.98	4.73	9.39	79.1	PRIMO
AMNH-M 2060/5484	*Macaca sylvanus*	extant	I^1	F	6.95	6.4	—	92.1	D.M.A.
AMNH-M 19178	*Macaca sylvanus*	extant	I^1	F	6.1	5.7	—	93.4	D.M.A.
AMNH-M 70269	*Macaca sylvanus*	extant	I^1	?	6.9	5.25	—	76.1	D.M.A.
MNHN-ZM-AC 1910.166	*Macaca sylvanus*	extant	I^1	M	6.9	5.9	11.7	85.5	PRIMO
MNHN-ZM-AC 1874.343	*Macaca sylvanus*	extant	I^1	M	6.6	6.1	12.1	92.4	PRIMO
NHMUK-Z ZD.1843.5.27.1	*Macaca sylvanus*	extant	I^1	M	6.9	5.8	8.6	84.1	PRIMO
NHMUK-Z ZD.1858.4.5.1	*Macaca sylvanus*	extant	I^1	M	7.0	5.8	11.0	82.9	PRIMO
NHMUK-Z ZD.1911.11.4.1	*Macaca sylvanus*	extant	I^1	F	6.2	5.3	8.1	85.5	PRIMO
NHMUK-Z ZD.1919.8.19.1	*Macaca sylvanus*	extant	I^1	M	6.1	4.9	7.2	80.3	PRIMO
NHMUK-Z ZD.1939.1048	*Macaca sylvanus*	extant	I^1	M	6.8	5.5	10.6	80.9	PRIMO
NMNH 196984	*Macaca sylvanus*	extant	I^1	F	6.35	5.71	9.4	89.9	PRIMO
NMNH 476782	*Macaca sylvanus*	extant	I^1	F	6.18	4.89	8.5	79.1	PRIMO
NMNH 476786	*Macaca sylvanus*	extant	I^1	F	5.24	4.98	5.3	95.0	PRIMO
NMNH 476787	*Macaca sylvanus*	extant	I^1	F	4.95	5.24	4.6	105.9	PRIMO
NMNH 341870	*Macaca sylvanus*	extant	I^1	F	5.44	5.61	9.03	103.1	PRIMO
NMNH 476783	*Macaca sylvanus*	extant	I^1	F	5.59	4.88	5.84	87.3	PRIMO

NMNH 476784	*Macaca sylvanus*	extant	I^1	M	6.17	5.42	8.91	87.8	PRIMO
NMNH 255979	*Macaca sylvanus*	extant	I^1	M	6.9	5.36	9.74	77.7	PRIMO
MCZ 5964	*Macaca sylvanus*	extant	I^1	F	7.15	5.65	—	79.0	D.M.A.
MCZ 5084	*Macaca sylvanus*	extant	I^1	F	7.0	5.75	—	82.1	D.M.A.
IPH UNCAT	*Macaca sylvanus pliocena*	Vallonnet	I^1	?	6.8	5.2	10.1	76.5	PRIMO
HUJ-ESE UB 323	*Macaca sylvanus florentina*	'Ubeidiya	I^1	?	7.06	5.16	9.23	73.1	PRIMO
MHNL 164295	*Macaca sylvanus florentina*	Saint-Vallier	I^1	?	7.2	5.4	11.1	75.0	PRIMO
NMB TY 5203	*Macaca majori*	Capo Figari	I^1	F	6.0	4.6	9.0	76.7	PRIMO
NMB TY 5273	*Macaca majori*	Capo Figari	I^1	?	5.9	6.1	9.7	103.4	PRIMO
NMB TY 5274	*Macaca majori*	Capo Figari	I^1	?	6.2	4.4	8.5	71.0	PRIMO
NMB TY 5275	*Macaca majori*	Capo Figari	I^1	?	6.0	4.9	8.1	81.7	PRIMO
NMB TY 5279	*Macaca majori*	Capo Figari	I^1	?	5.7	4.2	6.6	73.7	PRIMO
NMB TY 5316	*Macaca majori*	Capo Figari	I^1	?	6.2	4.2	8.6	67.7	PRIMO
NMT LAET 77-4595	*Parapapio ado*	Laetoli	I^1	F	6.4	5.3	12.2	82.8	PRIMO
KNM-KP 30149	*Parapapio* cf. *ado*	Kanapoi	I^1	?	7.5	5.8	11.3	77.3	Frost et al. (2020)
KNM-LT 23163	*Parapapio lothagamensis*	Lothagam	I^1	?	7.5	6.3	—	84.0	Leakey et al. (2003)
KNM-LT 24096	*Parapapio lothagamensis*	Lothagam	I^1	?	7.9	6.1	—	77.2	Leakey et al. (2003)
KNM-LT 24100	*Parapapio lothagamensis*	Lothagam	I^1	?	7.3	6.4	—	87.7	Leakey et al. (2003)
KNM-LT 26406	*Parapapio lothagamensis*	Lothagam	I^1	?	6.8	6.1	11.5	89.7	Leakey et al. (2003)
KNM-LT 28792	*Parapapio lothagamensis*	Lothagam	I^1	F	7.3	6.4	11.7	87.7	Leakey et al. (2003)
NME GWM-3/P26	*Pliopapio alemui*	Gona	I^1	?	6.4	6.3	10.4	98.4	Frost et al. (2020b)
NME GWM-9m/P264	*Pliopapio alemui*	Gona	I^1	?	5.8	—	8.5	—	Frost et al. (2020b)
NME GWM-9s/P414	*Pliopapio alemui*	Gona	I^1	?	5.1	5.7	6.4	111.8	Frost et al. (2020b)
NME GWM-44/P1	*Pliopapio alemui*	Gona	I^1	?	—	5.8	9.3	—	Frost et al. (2020b)
NME GWM-67/P55	*Pliopapio alemui*	Gona	I^1	?	6.3	6.3	8.0	100.0	Frost et al. (2020b)
NME ARA-VP 1/816	*Pliopapio alemui*	Aramis	I^1	F	5.81	5	6.54	86.1	PRIMO
GFT4.2’19-1-S15-65	*Macaca* cf. *sylvanus*	Guefaït-4.2	M_2	?	8.6	7.1	6.8	82.6	This study
MNHN-F 1958-14-237	*Macaca* aff. *sylvanus*	Aïn Brimba	M_2	?	9.3	7.8	7.0	83.9	PRIMO

AMNH-M 202286	*Macaca sylvanus sylvanus*	extant	M_2	M	9.1	7.6	7.5	83.5	PRIMO
MNHN-ZM-AC 1910.166	*Macaca sylvanus sylvanus*	extant	M_2	M	10.1	8.3	7.3	82.2	PRIMO
MNHN-ZM-AC 1900.244	*Macaca sylvanus sylvanus*	extant	M_2	F	10.2	8.0	6.8	78.4	PRIMO
MNHN-ZM-AC 1874.343	*Macaca sylvanus sylvanus*	extant	M_2	M	9.5	7.9	6.6	83.2	PRIMO
MNHN-ZM-AC A-1376	*Macaca sylvanus sylvanus*	extant	M_2	F	9.1	6.9	6.1	75.8	PRIMO
NHMUK-Z ZD.1843.5.27.1	*Macaca sylvanus sylvanus*	extant	M_2	M	9.3	7.1	6.1	76.3	PRIMO
NHMUK-Z ZD.1911.11.4.1	*Macaca sylvanus sylvanus*	extant	M_2	F	10.0	8.3	6.7	83.0	PRIMO
NHMUK-Z ZD.1919.8.19.1	*Macaca sylvanus sylvanus*	extant	M_2	M	9.2	6.8	6.2	73.9	PRIMO
NHMUK-Z ZD.1939.1048	*Macaca sylvanus sylvanus*	extant	M_2	M	10.3	8.5	7.5	82.5	PRIMO
AMNH-M 185277	*Macaca sylvanus sylvanus*	extant	M_2	F	8.65	7.6	6.27	87.9	PRIMO
AMNH-M 19014	*Macaca sylvanus sylvanus*	extant	M_2	F	8.08	6.96	6.33	86.1	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_2	?	8.8	8.4	7.3	95.5	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_2	M	9.0	7.4	6.7	82.2	PRIMO
NMNH 196984	*Macaca sylvanus sylvanus*	extant	M_2	F	8.79	6.88	6.16	78.3	PRIMO
NMNH 476782	*Macaca sylvanus sylvanus*	extant	M_2	F	8.68	6.98	6.62	80.4	PRIMO
NMNH 341870	*Macaca sylvanus sylvanus*	extant	M_2	F	7.24	6.57	6.2	90.7	PRIMO
NMNH 341872	*Macaca sylvanus sylvanus*	extant	M_2	F	7.05	6.65	6.3	94.3	PRIMO
NMNH 476783	*Macaca sylvanus sylvanus*	extant	M_2	F	8.01	6.77	6.47	84.5	PRIMO
NMNH 476784	*Macaca sylvanus sylvanus*	extant	M_2	M	9.12	6.72	6.45	73.7	PRIMO
NMNH 255979	*Macaca sylvanus sylvanus*	extant	M_2	M	9.76	8.91	8.1	91.3	PRIMO
AMNH-M 2060/5484	*Macaca sylvanus sylvanus*	extant	M_2	F	10.2	8.2	7.4	80.4	D.M.A.
AMNH-M 19178	*Macaca sylvanus sylvanus*	extant	M_2	F	11.1	8.3	7.3	74.8	D.M.A.
AMNH-M 70269	*Macaca sylvanus sylvanus*	extant	M_2	?	9.65	6.85	6.15	71.0	D.M.A.
MCZ 5964	*Macaca sylvanus sylvanus*	extant	M_2	F	10.0	8.3	6.6	83.0	D.M.A.
MCZ 7098	*Macaca sylvanus sylvanus*	extant	M_2	M	8.6	(8.2)	(7.3)	(95.3)	D.M.A.
MCZ 5084	*Macaca sylvanus sylvanus*	extant	M_2	F	9.4	7.75	6.8	82.4	D.M.A.
MNHN-ZM-MO 1939.1118	*Macaca sylvanus sylvanus*	extant	M_2	M	9.35	8.15	6.85	87.2	PRIMO
MNHN-ZM-MO 1945.173	*Macaca sylvanus sylvanus*	extant	M_2	F	10.0	7.7	7.1	77.0	PRIMO

MNHN-ZM-MO 1962.1473	*Macaca sylvanus sylvanus*	extant	M_2	M	8.9	7.6	6.6	85.4	PRIMO
MNHN-ZM-MO 1962.1470	*Macaca sylvanus sylvanus*	extant	M_2	F	9.85	8.7	7.0	88.3	PRIMO
MNHN-ZM-MO 1931.835	*Macaca sylvanus sylvanus*	extant	M_2	M	9.5	7.85	6.6	82.6	PRIMO
MNHN-ZM-MO 1940.1201	*Macaca sylvanus sylvanus*	extant	M_2	M	9.4	7.95	6.7	84.6	PRIMO
MNHN-ZM-MO 1962.1469	*Macaca sylvanus sylvanus*	extant	M_2	M	10.0	7.9	6.9	79.0	PRIMO
MNHN-ZM-MO 1926.299	*Macaca sylvanus sylvanus*	extant	M_2	M	10.0	7.7	7.2	77.0	PRIMO
MNHN-ZM-MO 1942.180	*Macaca sylvanus sylvanus*	extant	M_2	F	8.5	7.5	6.7	88.2	PRIMO
MNHN-ZM-AC 1907.59	*Macaca sylvanus sylvanus*	extant	M_2	M	10.5	8.45	7.35	80.5	PRIMO
MNHN-ZM-AC A1415	*Macaca sylvanus sylvanus*	extant	M_2	M	9.0	7.3	6.25	81.1	PRIMO
MNHN-ZM-AC 1892.78	*Macaca sylvanus sylvanus*	extant	M_2	F	9.0	9.1	7.15	101.1	PRIMO
MNHN-ZM-AC 1876.286	*Macaca sylvanus sylvanus*	extant	M_2	M	9.8	7.5	7.0	76.5	PRIMO
MNHN-ZM-AC 1879.133	*Macaca sylvanus sylvanus*	extant	M_2	M	9.5	7.9	6.85	83.2	PRIMO
MNHG 446.36	*Macaca sylvanus sylvanus*	extant	M_2	F	9.2	7.9	7.0	85.9	PRIMO
MAC 283/4	*Macaca sylvanus sylvanus*	extant	M_2	M	11.1	9.3	7.7	83.8	PRIMO
NHMW 32990	*Macaca sylvanus sylvanus*	extant	M_2	M	8.9	6.95	6.15	78.1	PRIMO
NHMW 2614/B3976	*Macaca sylvanus sylvanus*	extant	M_2	M	10.2	8.2	7.4	80.4	PRIMO
NHMW B 3849	*Macaca sylvanus sylvanus*	extant	M_2	F	9.5	7.4	6.6	77.9	PRIMO
NHMW 4408	*Macaca sylvanus sylvanus*	extant	M_2	M	10.3	8.5	7.3	82.5	PRIMO
NHMW 2616	*Macaca sylvanus sylvanus*	extant	M_2	F	9.2	7.7	6.9	83.7	PRIMO
NHMW 2615	*Macaca sylvanus sylvanus*	extant	M_2	F	9.1	7.6	6.4	83.5	PRIMO
NHMW 4407	*Macaca sylvanus sylvanus*	extant	M_2	F	9.2	7.8	6.6	84.8	PRIMO
NHMW 34222	*Macaca sylvanus sylvanus*	extant	M_2	F	8.7	7.4	6.6	85.1	PRIMO
MAU-T no number	*Macaca sylvanus sylvanus*	extant	M_2	F	8.4	7.35	7.45	87.5	PRIMO
NHMUK-Z ZD.1984.1734	*Macaca sylvanus sylvanus*	extant	M_2	M	8.7	6.3	6.1	72.4	PRIMO
NHMUK-Z ZD.1858.5.4.247	*Macaca sylvanus sylvanus*	extant	M_2	M	9.8	7.7	6.7	78.6	PRIMO
NHMUK-Z ZD.1975.569	*Macaca sylvanus sylvanus*	extant	M_2	M	9.9	7.4	6.5	74.7	PRIMO
NHMUK-Z ZD.1977.3119	*Macaca sylvanus sylvanus*	extant	M_2	M	9.9	7.8	7.0	78.8	PRIMO
Bonifay UNCAT	*Macaca sylvanus pliocena*	St. Estève Janson	M_2	M	10.5	8.5	8.2	81.0	PRIMO

NMP UNCAT	*Macaca sylvanus pliocena*	Zlaty Kun C718	M_2	?	9.5	7.6	7.3	80.0	PRIMO
NMP UNCAT	*Macaca sylvanus pliocena*	Zlaty Kun C718	M_2	M	10.2	7.8	7.3	76.5	PRIMO
ORGNAC 353	*Macaca sylvanus pliocena*	Orgnac-3	M_2	?	8.8	7.9	7.6	89.8	PRIMO
NMP UNCAT	*Macaca sylvanus pliocena*	Gombasek	M_2	M	10.4	8.5	8.0	81.7	PRIMO
IG-R UNCAT	*Macaca sylvanus pliocena*	Monte Sacro, Rome	M_2	M	9.7	7.7	6.9	79.4	PRIMO
Harlé UNCAT	*Macaca sylvanus pliocena*	Montsaunès	M_2	?	9.7	7.2	6.9	74.2	PRIMO
IPH UNCAT	*Macaca sylvanus pliocena*	Vallonnet	M_2	?	10.2	7.9	6.9	77.5	PRIMO
IAPU-P UNCAT	*Macaca sylvanus pliocena*	Valdemino	M_2	M?	9.4	7.4	6.9	78.7	PRIMO
LPHP-S 777/G1 & 771	*Macaca sylvanus pliocena*	Gajtan	M_2	F?	8.9	7.3	7.3	82.0	PRIMO
LPHP-S 775	*Macaca sylvanus pliocena*	Gajtan	M_2	?	10.6	7.5	7.2	70.8	PRIMO
SIP-V unknown	*Macaca sylvanus pliocena*	Cova Negra	M_2	?	10.8	8.5	—	(78.7)	PRIMO
BGDG LzII.M15.-271.300	*Macaca sylvanus* cf. *pliocena*	Lezetxiki II	M_2	F	9.6	8.0	7.8	83.3	Castaños et al. (2011)
MCSNBS PA11136	*Macaca sylvanus* cf. *pliocena*	Quecchia Quarry	M_2	?	9.5	7.8	7.0	82.1	Bona et al. (2016)
UNIARQ ARO17-J8-Xa-934	*Macaca sylvanus* cf. *pliocena*	Gruta da Aroeira	M_2	?	9.45	6.55	6.5	69.3	Alba et al. (2019)
HUJ-ESE UB 314	*Macaca sylvanus florentina*	'Ubeidiya	M_2	F	9.41	6.82	6.34	72.5	PRIMO
HUJ-ESE UB 331	*Macaca sylvanus florentina*	'Ubeidiya	M_2	F?	9.36	7.01	6.85	74.9	PRIMO
HUJ-ESE UB 334	*Macaca sylvanus florentina*	'Ubeidiya	M_2	?	9.35	7.28	6.82	77.9	PRIMO
HUJ-ESE UB 347	*Macaca sylvanus florentina*	'Ubeidiya	M_2	?	9.49	7.57	6.79	79.8	PRIMO
HUJ-ESE UB 346	*Macaca sylvanus florentina*	'Ubeidiya	M_2	?	8.9	6.7	6.54	75.3	PRIMO
IGF 10034	*Macaca sylvanus florentina*	Upper Valdarno	M_2	M	9.8	8.0	7.3	81.6	PRIMO
IGF 10035	*Macaca sylvanus florentina*	Upper Valdarno	M_2	M	10.2	8.0	7.5	78.4	PRIMO
IGF 12868	*Macaca sylvanus florentina*	Upper Valdarno	M_2	F	9.6	8.3	7.5	86.5	PRIMO
IGF 13084	*Macaca sylvanus florentina*	Upper Valdarno	M_2	?	9.7	7.7	6.7	79.4	PRIMO
IGF 13087	*Macaca sylvanus florentina*	Upper Valdarno	M_2	?	9.0	6.8	6.6	75.6	PRIMO
NMB VA 352	*Macaca sylvanus florentina*	Upper Valdarno	M_2	M	9.0	7.5	7.1	83.3	PRIMO
NMB VA 1088	*Macaca sylvanus florentina*	Upper Valdarno	M_2	?	9.4	7.3	7.4	77.7	PRIMO
NMB VA 1415	*Macaca sylvanus florentina*	Upper Valdarno	M_2	M?	9.7	7.4	7.2	76.3	PRIMO
NMB VA 2058	*Macaca sylvanus florentina*	Upper Valdarno	M_2	M	9.5	7.2	6.7	75.8	PRIMO

MAP 10	*Macaca sylvanus florentina*	Upper Valdarno	M_2	M	9.9	7.9	7.4	79.8	PRIMO
RGM-L 47424	*Macaca sylvanus florentina*	Tegelen	M_2	M	11.0	8.3	7.9	75.5	PRIMO
RGM-L 53158	*Macaca sylvanus florentina*	Tegelen	M_2	?	9.5	8.3	7.8	87.4	PRIMO
ZMA 12717	*Macaca sylvanus florentina*	Tegelen	M_2	?	9.8	7.5	7	76.5	PRIMO
MUPE GCP-CV4062	*Macaca sylvanus florentina*	Quibas	M_2	?	10.2	8.5	7.6	83.3	Alba et al. (2011)
MUPE GCP-CV4060	*Macaca sylvanus florentina*	Quibas	M_2	?	9.4	(7.6)	7.2	(80.9)	Alba et al. (2011)
UM Q03-E-4a	*Macaca sylvanus florentina*	Quibas	M_2	?	10.0	8.2	6.8	82.0	Alba et al. (2011)
MSNC Mugello B	*Macaca sylvanus florentina*	Mugello	M_2	?	9.3	6.85	6.7	73.7	Zanaga (1998)
MNHN-F UNCAT	*Macaca sylvanus prisca*	Montpellier	M_2	M	8.8	6.8	6.8	77.3	PRIMO
FSL 40191	*Macaca sylvanus prisca*	Montpellier	M_2	?	8.0	6.8	6.0	85.0	PRIMO
MPC 8116	*Macaca majori*	Is Oreris	M_2	?	8.47	6.93	5.96	81.8	Zoboli et al. (2016)
IGF 2035	*Macaca majori*	Capo Figari	M_2	M	8.9	7.0	6.9	78.7	PRIMO
IGF 2036	*Macaca majori*	Capo Figari	M_2	M	8.7	6.8	6.5	78.2	PRIMO
NMB TY 5202	*Macaca majori*	Capo Figari	M_2	F	7.6	6.4	6.5	84.2	PRIMO
NMB TY 5209	*Macaca majori*	Capo Figari	M_2	?	8.8	7.2	7.0	81.8	PRIMO
NMB TY 5210	*Macaca majori*	Capo Figari	M_2	?	8.7	7.0	6.8	80.5	PRIMO
NMB TY 12454	*Macaca majori*	Capo Figari	M_2	?	8.6	7.0	6.6	81.4	PRIMO
NMB TY 12460	*Macaca majori*	Capo Figari	M_2	M	8.6	7.1	6.9	82.6	PRIMO
NMB TY 12475	*Macaca majori*	Capo Figari	M_2	?	8.8	6.9	6.3	78.4	PRIMO
GPI-F 1652	*Macaca libyca*	Wadi Natrun	M_2	?	9.6	8.5	8.6	88.5	PRIMO
YPM 21551	*Macaca libyca*	Wadi Natrun	M_2	F	9.4	8.1	7.8	86.2	PRIMO
YPM 21552	*Macaca libyca*	Wadi Natrun	M_2	?	9.8	9.4	—	(95.9)	PRIMO
BSPG 1920 I 505	*Macaca libyca*	Wadi Natrun	M_2	?	10.9	7.9	7.3	72.5	PRIMO
MB Ma 42444	*Parapapio ado*	Laetoli	M_2	M	11.4	9.0	8.0	78.9	PRIMO
MB Ma 42445	*Parapapio ado*	Laetoli	M_2	?	11.3	8.6	8.1	76.1	PRIMO
MB Ma 42451	*Parapapio ado*	Laetoli	M_2	?	10.0	7.9	7.1	79.0	PRIMO
MB Ma 42452	*Parapapio ado*	Laetoli	M_2	?	9.6	7.3	7.5	76.0	PRIMO
MB Ma 42453	*Parapapio ado*	Laetoli	M_2	?	10.8	8.6	8.0	79.6	PRIMO

MB Ma 42442 (& 42446)	*Parapapio ado*	Laetoli	M_2	M	11.0	9.8	9.2	89.1	PRIMO
NMT LAET 74-223	*Parapapio ado*	Laetoli	M_2	F	10.8	8.7	8.8	80.6	PRIMO
NMT LAET 74-243-4	*Parapapio ado*	Laetoli	M_2	F	10.6	8.3	7.8	78.3	PRIMO
NMT LAET 75-483	*Parapapio ado*	Laetoli	M_2	?	11.3	8.8	7.9	77.9	PRIMO
NMT LAET 75-812	*Parapapio ado*	Laetoli	M_2	?	12.5	9.8	8.8	78.4	PRIMO
NMT LAET 75-3035	*Parapapio ado*	Laetoli	M_2	F	10.6	8.2	8.9	77.4	PRIMO
NMT LAET 77-4595	*Parapapio ado*	Laetoli	M_2	F	11.3	9.1	9.4	80.5	PRIMO
KNM-KP 26942	*Parapapio* cf. *ado*	Kanapoi	M_2	?	11.1	9.8	8.7	88.3	Frost et al. (2020a)
KNM-KP 29306	*Parapapio* cf. *ado*	Kanapoi	M_2	M	9.3	8.3	7.9	89.2	Frost et al. (2020a)
KNM-KP 29312	*Parapapio* cf. *ado*	Kanapoi	M_2	?	10.8	9.5	8.7	88.0	Frost et al. (2020a)
KNM-KP 30538	*Parapapio* cf. *ado*	Kanapoi	M_2	F	9.5	7.9	7.2	83.2	Frost et al. (2020a)
KNM-KP 53085	*Parapapio* cf. *ado*	Kanapoi	M_2	M	10.7	8.9	8.6	83.2	Frost et al. (2020a)
KNM-ER 3122	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	8.8	7.4	6.7	84.1	Jablonski et al. (2008)
KNM-ER 17587	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	8.9	8.9	7.9	100.0	Jablonski et al. (2008)
KNM-ER 18881	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	9.4	8.3	8.1	88.3	Jablonski et al. (2008)
KNM-ER 36983	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	11.0	8.2	8	74.5	Jablonski et al. (2008)
KNM-ER 36998	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	11.1	8.4	7.9	75.7	Jablonski et al. (2008)
KNM-ER 37093	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	9.6	8.1	7.9	84.4	Jablonski et al. (2008)
KNM-ER 37128	*Parapapio* cf. *ado*	Koobi Fora	M_2	?	9.9	7.0	7.1	70.7	Jablonski et al. (2008)
KNM-LT 415	*Parapapio lothagamensis*	Lothagam	M_2	?	8.2	7.4	6.9	90.2	Leakey et al. (2003)
KNM-LT 22971	*Parapapio lothagamensis*	Lothagam	M_2	?	8.8	8.4	7.8	95.5	Leakey et al. (2003)
KNM-LT 23091	*Parapapio lothagamensis*	Lothagam	M_2	M	9.1	7.9	7.8	86.8	Leakey et al. (2003)
KNM-LT 24094	*Parapapio lothagamensis*	Lothagam	M_2	?	8.1	6.5	5.9	80.2	Leakey et al. (2003)
KNM-LT 24095	*Parapapio lothagamensis*	Lothagam	M_2	?	9.1	7.4	7.7	81.3	Leakey et al. (2003)
KNM-LT 24122	*Parapapio lothagamensis*	Lothagam	M_2	?	9.5	7.4	6.6	77.9	Leakey et al. (2003)
KNM-LT 24135	*Parapapio lothagamensis*	Lothagam	M_2	?	8.3	7.4	7.2	89.2	Leakey et al. (2003)
KNM-LT 24140	*Parapapio lothagamensis*	Lothagam	M_2	?	(8.6)	(7.0)	(7.2)	(81.4)	Leakey et al. (2003)
KNM-LT 26395	*Parapapio lothagamensis*	Lothagam	M_2	?	8.5	7.1	6.9	83.5	Leakey et al. (2003)

KNM-LT 28728	*Parapapio lothagamensis*	Lothagam	M_2	?	10.3	9.0	8.4	87.4	Leakey et al. (2003)
NME GWM-3/P84	*Pliopapio alemui*	Gona	M_2	F	9.0	7.0	7.4	77.8	Frost et al. (2020b)
NME GWMS-11/P65	cf. *Pliopapio alemui*	Gona	M_2	?	9.1	7.4	7.0	81.3	Frost et al. (2020b)
NME ARA-VP 1/816	*Pliopapio alemui*	Aramis	M_2	F	9.47	7.58	7.6	80.1	PRIMO
NME ARA-VP 1/1006	*Pliopapio alemui*	Aramis	M_2	F	9.22	6.88	7.05	74.7	PRIMO
NME ARA-VP 1/1349	*Pliopapio alemui*	Aramis	M_2	F	8.74	6.49	6.67	74.2	PRIMO
NME ARA-VP 6/8	*Pliopapio alemui*	Aramis	M_2	?	8.76	6.38	6.82	72.8	PRIMO
GFT4.2’19-1-R13-63	*Macaca* cf. *sylvanus*	Guefaït-4.2	M_3	?	10.0	7.6	7.5	76.0	This study
AMNH-M 202286	*Macaca sylvanus sylvanus*	extant	M_3	M	12.2	8.2	7.6	67.2	PRIMO
MNHN-ZM-AC 1910.166	*Macaca sylvanus sylvanus*	extant	M_3	M	12.5	9.3	7.5	74.4	PRIMO
MNHN-ZM-AC 1900.244	*Macaca sylvanus sylvanus*	extant	M_3	F	11.1	8.0	6.7	72.1	PRIMO
MNHN-ZM-AC 1874.343	*Macaca sylvanus sylvanus*	extant	M_3	M	12.2	8.4	6.3	68.9	PRIMO
MNHN-ZM-AC A-1376	*Macaca sylvanus sylvanus*	extant	M_3	F	11.6	8.3	6.4	71.6	PRIMO
NHMUK-Z ZD.1843.5.27.1	*Macaca sylvanus sylvanus*	extant	M_3	M	11.5	7.7	6.6	67.0	PRIMO
NHMUK-Z ZD.1911.11.4.1	*Macaca sylvanus sylvanus*	extant	M_3	F	11.5	8.6	6.9	74.8	PRIMO
NHMUK-Z ZD.1919.8.19.1	*Macaca sylvanus sylvanus*	extant	M_3	M	10.6	6.8	6.0	64.2	PRIMO
AMNH-M 185277	*Macaca sylvanus sylvanus*	extant	M_3	F	10.7	7.89	6.44	73.7	PRIMO
AMNH-M 19014	*Macaca sylvanus sylvanus*	extant	M_3	F	10.51	7.67	6.19	73.0	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_3	?	12.6	9.4	7.6	74.6	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_3	?	11.4	8.0	6.5	70.2	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_3	?	13.2	7.4	6.8	56.1	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_3	?	12.4	8.3	7.2	66.9	PRIMO
MNHN-F UNCAT	*Macaca sylvanus sylvanus*	extant	M_3	M	11.8	7.9	6.4	66.9	PRIMO
NMNH 196984	*Macaca sylvanus sylvanus*	extant	M_3	F	11.09	7.59	6.44	68.4	PRIMO
NMNH 476782	*Macaca sylvanus sylvanus*	extant	M_3	F	10.7	7.31	6.79	68.3	PRIMO
NMNH 476786	*Macaca sylvanus sylvanus*	extant	M_3	F	11.73	8.24	7.16	70.2	PRIMO
NMNH 341870	*Macaca sylvanus sylvanus*	extant	M_3	F	9.34	6.56	5.67	70.2	PRIMO
NMNH 341872	*Macaca sylvanus sylvanus*	extant	M_3	F	9.49	6.41	5.9	67.5	PRIMO

NMNH 476783	*Macaca sylvanus sylvanus*	extant	M_3	F	9.81	6.79	6.67	69.2	PRIMO
NMNH 476784	*Macaca sylvanus sylvanus*	extant	M_3	M	10.95	7.61	6.77	69.5	PRIMO
NMNH 255979	*Macaca sylvanus sylvanus*	extant	M_3	M	11.77	9.26	7.92	78.7	PRIMO
AMNH-M 2060/5484	*Macaca sylvanus sylvanus*	extant	M_3	F	12.1	8.55	7.05	70.7	D.M.A.
AMNH-M 19178	*Macaca sylvanus sylvanus*	extant	M_3	F	13.05	8.95	7.55	68.6	D.M.A.
MCZ 7098	*Macaca sylvanus sylvanus*	extant	M_3	M	10.3	(7.6)	>6.5	(73.8)	D.M.A.
MNHN-ZM-MO 1939.1118	*Macaca sylvanus sylvanus*	extant	M_3	M	12.2	9.5	7.45	77.9	PRIMO
MNHN-ZM-MO 1945.173	*Macaca sylvanus sylvanus*	extant	M_3	F	12.4	8.0	6.75	64.5	PRIMO
MNHN-ZM-MO 1962.1473	*Macaca sylvanus sylvanus*	extant	M_3	M	11.85	8.4	6.9	70.9	PRIMO
MNHN-ZM-MO 1931.835	*Macaca sylvanus sylvanus*	extant	M_3	M	12.3	9.0	7.0	73.2	PRIMO
MNHN-ZM-MO 1940.1201	*Macaca sylvanus sylvanus*	extant	M_3	M	12.7	8.5	6.7	66.9	PRIMO
MNHN-ZM-MO 1926.299	*Macaca sylvanus sylvanus*	extant	M_3	M	11.3	11.4	7.9	100.9	PRIMO
MNHN-ZM-MO 1942.180	*Macaca sylvanus sylvanus*	extant	M_3	F	9.6	7.65	6.4	79.7	PRIMO
MNHN-ZM-AC 1907.59	*Macaca sylvanus sylvanus*	extant	M_3	M	14.6	9.1	7.8	62.3	PRIMO
MNHN-ZM-AC A1415	*Macaca sylvanus sylvanus*	extant	M_3	M	11.4	8.2	6.2	71.9	PRIMO
MNHN-ZM-AC 1879.133	*Macaca sylvanus sylvanus*	extant	M_3	M	12.6	8.6	6.7	68.3	PRIMO
MNHG 446.36	*Macaca sylvanus sylvanus*	extant	M_3	F	11.5	8.8	6.7	76.5	PRIMO
NHMW 32990	*Macaca sylvanus sylvanus*	extant	M_3	M	11.55	7.55	6.45	65.4	PRIMO
NHMW 2614/B3976	*Macaca sylvanus sylvanus*	extant	M_3	M	13.6	8.6	7.6	63.2	PRIMO
NHMW B 3849	*Macaca sylvanus sylvanus*	extant	M_3	F	11.8	7.8	6.6	66.1	PRIMO
NHMW 4408	*Macaca sylvanus sylvanus*	extant	M_3	M	13.0	8.8	7.4	67.7	PRIMO
NHMW 2616	*Macaca sylvanus sylvanus*	extant	M_3	F	11.2	8.0	6.7	71.4	PRIMO
NHMW 2615	*Macaca sylvanus sylvanus*	extant	M_3	F	12.1	8.1	6.6	66.9	PRIMO
NHMW 4407	*Macaca sylvanus sylvanus*	extant	M_3	F	11.5	8.4	6.8	73.0	PRIMO
NHMW 34222	*Macaca sylvanus sylvanus*	extant	M_3	F	10.8	7.8	7.0	72.2	PRIMO
MAU-T no number	*Macaca sylvanus sylvanus*	extant	M_3	F	9.75	6.85	6.85	70.3	PRIMO
NHMUK-Z ZD.1939.3470	*Macaca sylvanus sylvanus*	extant	M_3	F	10.4	7.3	6.1	70.2	PRIMO
NHMUK-Z ZD.1984.1734	*Macaca sylvanus sylvanus*	extant	M_3	M	11.7	6.9	6.2	59.0	PRIMO

NHMUK-Z ZD.1858.5.4.247	*Macaca sylvanus sylvanus*	extant	M_3	M	11.4	8.2	7.1	71.9	PRIMO
NHMUK-Z ZD.1975.569	*Macaca sylvanus sylvanus*	extant	M_3	M	12.3	7.8	6.8	63.4	PRIMO
NHMUK-Z ZD.1977.3119	*Macaca sylvanus sylvanus*	extant	M_3	M	12.5	8.1	7.3	64.8	PRIMO
SMF 71-1301	*Macaca sylvanus pliocena*	Hohensülzen	M_3	?	12.1	7.3	6.7	60.3	PRIMO
Bonifay UNCAT	*Macaca sylvanus pliocena*	St. Estève Janson	M_3	M	14.4	9.4	8.4	65.3	PRIMO
NMP UNCAT	*Macaca sylvanus pliocena*	Zlaty Kun C718	M_3	?	11.7	8.0	7.5	68.4	PRIMO
NMP UNCAT	*Macaca sylvanus pliocena*	Zlaty Kun C718	M_3	M	13.0	8.0	7.9	61.5	PRIMO
ORGNAC 723	*Macaca sylvanus pliocena*	Orgnac-3	M_3	?	13.0	8.2	8.0	63.1	PRIMO
NMP UNCAT	*Macaca sylvanus pliocena*	Gombasek	M_3	M	13.5	8.6	7.7	63.7	PRIMO
IG-R UNCAT	*Macaca sylvanus pliocena*	Monte Sacro, Rome	M_3	M	13.0	8.2	7.2	63.1	PRIMO
LPHP-S 777/G1 & 771	*Macaca sylvanus pliocena*	Gajtan	M_3	F?	12.2	7.6	7.1	62.3	PRIMO
SIP-V unknown	*Macaca sylvanus pliocena*	Cova Negra	M_3	?	13.9	9.2	—	66.2	PRIMO
UG unknown	*Macaca sylvanus pliocena*	Solana de Zamborino	M_3	?	12.1	7.5	7.1	62.0	PRIMO
BGDG LzII.M15.-271.300	*Macaca sylvanus* cf. *pliocena*	Lezetxiki II	M_3	F	13.0	8.6	7.4	66.2	Castaños et al. (2011)
NMR 999100010537	*Macaca sylvanus* cf. *pliocena*	North Sea	M_3	?	12.1	7.8	7.5	64.5	Reumer et al. (2018)
MCSNBS PA11136	*Macaca sylvanus* cf. *pliocena*	Quecchia Quarry	M_3	?	12.1	8.2	—	67.8	Bona et al. (2016)
HUJ-ESE UB 314	*Macaca sylvanus florentina*	'Ubeidiya	M_3	F	12.03	7.07	6.73	58.8	PRIMO
HUJ-ESE UB 329	*Macaca sylvanus florentina*	'Ubeidiya	M_3	?	10.2	7.15	6.0	70.1	PRIMO
IGF 10034	*Macaca sylvanus florentina*	Upper Valdarno	M_3	M	12.3	8.3	7.4	67.5	PRIMO
IGF 10035	*Macaca sylvanus florentina*	Upper Valdarno	M_3	M	12.8	8.2	7.9	64.1	PRIMO
IGF 12868	*Macaca sylvanus florentina*	Upper Valdarno	M_3	F	13.5	8.4	7.8	62.2	PRIMO
IGF 13084	*Macaca sylvanus florentina*	Upper Valdarno	M_3	?	12.8	7.6	7.1	59.4	PRIMO
IGF 13087	*Macaca sylvanus florentina*	Upper Valdarno	M_3	?	11.5	6.8	6.4	59.1	PRIMO
NMB VA 352	*Macaca sylvanus florentina*	Upper Valdarno	M_3	M	12.3	8.0	7.2	65.0	PRIMO
NMB VA 2058	*Macaca sylvanus florentina*	Upper Valdarno	M_3	M	12.1	7.5	6.8	62.0	PRIMO
MAP 10	*Macaca sylvanus florentina*	Upper Valdarno	M_3	M	14.5	7.8	7.2	53.8	PRIMO
IQW 1980/16566 (Mei. 16087)	*Macaca sylvanus florentina*	Untermassfeld	M_3	F	11.0	7.4	7.0	67.3	Zapfe (2001)
IQW 1984/20021 (Mei. 16541)	*Macaca sylvanus florentina*	Untermassfeld	M_3	M	13.4	8.4	7.4	62.7	Zapfe (2001)

MUPE GCP-CV4063	*Macaca sylvanus florentina*	Quibas	M_3	?	12.1	8.8	7.6	72.7	Alba et al. (2011)
UM Q03-Ec-1	*Macaca sylvanus florentina*	Quibas	M_3	?	12.0	7.5	6.6	62.5	Alba et al. (2011)
MUPE GCP-CV4060	*Macaca sylvanus florentina*	Quibas	M_3	?	(12.5)	7.8	6.7	62.4	Alba et al. (2011)
MSNC Mugello A	*Macaca sylvanus florentina*	Mugello	M_3	?	12.8	7.3	6.7	57.0	Zanaga (1998)
FSL 40137	*Macaca sylvanus prisca*	Montpellier	M_3	?	10.8	6.9	6.1	63.9	PRIMO
NHMUK-P M11713	*Macaca majori*	Capo Figari	M_3	?	10.6	6.5	6.2	61.3	PRIMO
IGF 2035	*Macaca majori*	Capo Figari	M_3	M	10.6	7.0	6.5	66.0	PRIMO
NMB TY 5209	*Macaca majori*	Capo Figari	M_3	?	9.4	7.1	6.5	75.5	PRIMO
NMB TY 5210	*Macaca majori*	Capo Figari	M_3	?	10.5	7.0	6.2	66.7	PRIMO
NMB TY 5211	*Macaca majori*	Capo Figari	M_3	?	11.6	7.0	6.4	60.3	PRIMO
NMB TY 5214	*Macaca majori*	Capo Figari	M_3	?	9.9	7.3	6.0	73.7	PRIMO
NMB TY 5304	*Macaca majori*	Capo Figari	M_3	?	9.4	7.4	6.5	78.7	PRIMO
NMB TY 12454	*Macaca majori*	Capo Figari	M_3	?	10.1	7.4	6.6	73.3	PRIMO
NMB TY 12460	*Macaca majori*	Capo Figari	M_3	M	10.1	7.1	6.7	70.3	PRIMO
NMB TY 12469	*Macaca majori*	Capo Figari	M_3	?	10.7	7.0	6.7	65.4	PRIMO
NMB TY 12470	*Macaca majori*	Capo Figari	M_3	?	9.0	7.3	6.2	81.1	PRIMO
NMB TY 12514	*Macaca majori*	Capo Figari	M_3	?	10.5	7.3	—	69.5	PRIMO
GPI-F 1652	*Macaca libyca*	Wadi Natrun	M_3	?	11.7	8.3	7.6	70.9	PRIMO
YPM 21552	*Macaca libyca*	Wadi Natrun	M_3	?	13.2	9.2	8.1	69.7	PRIMO
MB Ma 42445	*Parapapio ado*	Laetoli	M_3	?	14.9	9.1	8.1	61.1	PRIMO
MB Ma 42441	*Parapapio ado*	Laetoli	M_3	F	14.3	8.7	8.2	60.8	PRIMO
MB Ma 42442 (& 42446)	*Parapapio ado*	Laetoli	M_3	M	15.0	10.8	8.9	72.0	PRIMO
NHMUK-P M14940	*Parapapio ado*	Laetoli	M_3	F	12.9	8.1	7.7	62.8	PRIMO
NMT LAET 64	*Parapapio ado*	Laetoli	M_3	?	13.6	8.4	7.2	61.8	PRIMO
NMT LAET 74-223	*Parapapio ado*	Laetoli	M_3	F	12.9	9.1	8.6	70.5	PRIMO
NMT LAET 74-243-4	*Parapapio ado*	Laetoli	M_3	F	13.9	8.7	8.1	62.6	PRIMO
NMT LAET 75-483	*Parapapio ado*	Laetoli	M_3	?	14.5	9.1	8.1	62.8	PRIMO
NMT LAET 75-1209	*Parapapio ado*	Laetoli	M_3	F	12.5	7.8	6.5	62.4	PRIMO

NMT LAET 75-1390	*Parapapio ado*	Laetoli	M_3	?	14.4	9.6	8.2	66.7	PRIMO
NMT LAET 75-3035	*Parapapio ado*	Laetoli	M_3	F	12.9	8.3	8.0	64.3	PRIMO
NMT LAET 77-4568	*Parapapio ado*	Laetoli	M_3	?	12.6	8.8	8.5	69.8	PRIMO
NMT LAET 77-4595	*Parapapio ado*	Laetoli	M_3	F	14.2	9.5	8.7	66.9	PRIMO
KNM-KP 286	*Parapapio* cf. *ado*	Kanapoi	M_3	M	12.6	10.1	8.6	80.2	Frost et al. (2020a)
KNM-KP 26942	*Parapapio* cf. *ado*	Kanapoi	M_3	?	14.3	9.7	8.1	67.8	Frost et al. (2020a)
KNM-KP 29305	*Parapapio* cf. *ado*	Kanapoi	M_3	?	11.0	8.4	7.1	76.4	Frost et al. (2020a)
KNM-KP 29306	*Parapapio* cf. *ado*	Kanapoi	M_3	?	12.3	8.6	8.2	69.9	Frost et al. (2020a)
KNM-KP 29312	*Parapapio* cf. *ado*	Kanapoi	M_3	?	12.2	9.1	8.5	74.6	Frost et al. (2020a)
KNM-KP 30230	*Parapapio* cf. *ado*	Kanapoi	M_3	F	12.3	8.3	7.3	67.5	Frost et al. (2020a)
KNM-KP 30233	*Parapapio* cf. *ado*	Kanapoi	M_3	M	13.0	8.9	8.1	68.5	Frost et al. (2020a)
KNM-KP 30399	*Parapapio* cf. *ado*	Kanapoi	M_3	?	13.4	9.5	8.5	70.9	Frost et al. (2020a)
KNM-KP 30483	*Parapapio* cf. *ado*	Kanapoi	M_3	?	13.1	9.5	8.4	72.5	Frost et al. (2020a)
KNM-KP 30535	*Parapapio* cf. *ado*	Kanapoi	M_3	?	13.4	10.0	8.2	74.6	Frost et al. (2020a)
KNM-KP 30538	*Parapapio* cf. *ado*	Kanapoi	M_3	F	11.7	9.3	8.4	79.5	Frost et al. (2020a)
KNM-KP 32806	*Parapapio* cf. *ado*	Kanapoi	M_3	?	10.9	7.8	7.1	71.6	Frost et al. (2020a)
KNM-KP 32817	*Parapapio* cf. *ado*	Kanapoi	M_3	?	11.1	8.1	6.9	73.0	Frost et al. (2020a)
KNM-KP 32869	*Parapapio* cf. *ado*	Kanapoi	M_3	M	(12.19)	(8.75)	8.1	(71.8)	Frost et al. (2020a)
KNM-KP 59889	*Parapapio* cf. *ado*	Kanapoi	M_3	?	12.9	8.5	7.8	65.9	Frost et al. (2020a)
KNM-KP 59899	*Parapapio* cf. *ado*	Kanapoi	M_3	?	11.4	8.1	6.7	71.1	Frost et al. (2020a)
KNM-ER 3122	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	12.3	7.7	6.9	62.6	Jablonski et al. (2008)
KNM-ER 19539	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	11.6	8.1	6.6	69.8	Jablonski et al. (2008)
KNM-ER 20437	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	13.3	8.0	7.2	60.2	Jablonski et al. (2008)
KNM-ER 36915	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	12.7	8.3	7.6	65.4	Jablonski et al. (2008)
KNM-ER 36921	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	12.5	8.0	7.3	64.0	Jablonski et al. (2008)
KNM-ER 36970	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	13.2	8.4	7.2	63.6	Jablonski et al. (2008)
KNM-ER 36972	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	14.8	9.4	8.4	63.5	Jablonski et al. (2008)
KNM-ER 36973	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	13.8	8.0	7.2	58.0	Jablonski et al. (2008)

KNM-ER 36987	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	13.2	8.8	7.6	66.7	Jablonski et al. (2008)
KNM-ER 37013	*Parapapio* cf. *ado*	Koobi Fora	M_3	?	13.0	8.6	7.6	66.2	Jablonski et al. (2008)
KNM-ER 39518	*Parapapio* cf. ado	Koobi Fora	M_3	?	11.9	7.6	7.3	63.9	Jablonski et al. (2008)
KNM-LT 415	*Parapapio lothagamensis*	Lothagam	M_3	?	11.0	7.8	7.0	70.9	Leakey et al. (2003)
KNM-LT 23066	*Parapapio lothagamensis*	Lothagam	M_3	?	12.5	7.9	7.7	63.2	Leakey et al. (2003)
KNM-LT 23090	*Parapapio lothagamensis*	Lothagam	M_3	F	10.5	7.5	6.6	71.4	Leakey et al. (2003)
KNM-LT 23091	*Parapapio lothagamensis*	Lothagam	M_3	M	11.5	8.0	7.4	69.0	Leakey et al. (2003)
KNM-LT 24094	*Parapapio lothagamensis*	Lothagam	M_3	?	10.4	6.7	5.9	64.4	Leakey et al. (2003)
KNM-LT 24105	*Parapapio lothagamensis*	Lothagam	M_3	?	12.5	9.2	7.6	73.6	Leakey et al. (2003)
KNM-LT 24117	*Parapapio lothagamensis*	Lothagam	M_3	?	13.5	8.4	7.9	62.2	Leakey et al. (2003)
KNM-LT 24122	*Parapapio lothagamensis*	Lothagam	M_3	?	11.0	7.0	6.0	63.6	Leakey et al. (2003)
KNM-LT 24133	*Parapapio lothagamensis*	Lothagam	M_3	?	11.9	8.9	7.6	74.8	Leakey et al. (2003)
KNM-LT 24135	*Parapapio lothagamensis*	Lothagam	M_3	?	10.4	7.4	—	71.2	Leakey et al. (2003)
KNM-LT 24136	*Parapapio lothagamensis*	Lothagam	M_3	M	12.4	7.8	6.8	62.9	Leakey et al. (2003)
KNM-LT 24139	*Parapapio lothagamensis*	Lothagam	M_3	?	11.1	8.1	7.1	73.0	Leakey et al. (2003)
KNM-LT 26391	*Parapapio lothagamensis*	Lothagam	M_3	?	10.7	7.2	6.4	67.3	Leakey et al. (2003)
KNM-LT 26409	*Parapapio lothagamensis*	Lothagam	M_3	?	11.2	7.3	6.4	65.2	Leakey et al. (2003)
KNM-LT 28755	*Parapapio lothagamensis*	Lothagam	M_3	?	9.7	7.3	6.3	75.3	Leakey et al. (2003)
NME GWM-3/P84	*Pliopapio alemui*	Gona	M_3	F	11.5	7.1	—	61.7	Frost et al. (2020b)
NME GWM-3/P164	*Pliopapio alemui*	Gona	M_3	?	10.9	7.6	6.0	69.7	Frost et al. (2020b)
NME GWM-3w/P183	*Pliopapio alemui*	Gona	M_3	?	10.6	7.0	5,9	66.0	Frost et al. (2020b)
NME GWM-5m/P125	*Pliopapio alemui*	Gona	M_3	?	10.5	6.9	6.2	65.7	Frost et al. (2020b)
NME GWM-5sw/P153	*Pliopapio alemui*	Gona	M_3	?	11.7	7.6	7.5	65.0	Frost et al. (2020b)
NME GWM-5m/P281	*Pliopapio alemui*	Gona	M_3	?	10.1	7.4	6.8	73.3	Frost et al. (2020b)
NME GWM-5sw/P296	*Pliopapio alemui*	Gona	M_3	?	9.5	7.0	6.7	73.7	Frost et al. (2020b)
NME GWM-5m/P514	*Pliopapio alemui*	Gona	M_3	?	11.9	7.7	6.8	64.7	Frost et al. (2020b)
NME GWM-9n/P89	*Pliopapio alemui*	Gona	M_3	?	11.5	7.2	6.5	62.6	Frost et al. (2020b)
NME GWM-9m/P256	*Pliopapio alemui*	Gona	M_3	?	12.1	8.4	7.9	69.4	Frost et al. (2020b)

NME GWM-25/27/P100	*Pliopapio alemui*	Gona	M_3	?	12.3	7.7	7.0	62.6	Frost et al. (2020b)
NME GWM-45/P46	*Pliopapio alemui*	Gona	M_3	?	11.6	7.5	6.8	64.7	Frost et al. (2020b)
NME GWMS-11/P65	cf. *Pliopapio alemui*	Gona	M_3	?	11.4	7.2	7.2	63.2	Frost et al. (2020b)
NME ARA-VP 1/816	*Pliopapio alemui*	Aramis	M_3	F	11.92	7.70	7.00	64.6	PRIMO
NME ARA-VP 1/1006	*Pliopapio alemui*	Aramis	M_3	F	10.47	7.44	6.42	71.0	PRIMO
NME ARA-VP 1/1349	*Pliopapio alemui*	Aramis	M_3	F	9.70	6.79	6.36	70.0	PRIMO
NME ARA-VP 1/744	*Pliopapio alemui*	Aramis	M_3	M	10.75	6.70	6.14	62.3	PRIMO
NME ARA-VP 1/1571	*Pliopapio alemui*	Aramis	M_3	?	11.20	6.65	6.18	59.3	PRIMO
NME ARA-VP 1/1859	*Pliopapio alemui*	Aramis	M_3	?	13.14	7.80	7.43	59.4	PRIMO
NME ARA-VP 1/190	*Pliopapio alemui*	Aramis	M_3	?	11.12	6.94	6.65	62.4	PRIMO
NME ARA-VP 1/8	*Pliopapio alemui*	Aramis	M_3	?	10.57	6.70	5.88	63.4	PRIMO
NME ARA-VP 1/1377	*Pliopapio alemui*	Aramis	M_3	?	11.86	7.42	6.76	62.6	PRIMO
NME ARA-VP 1/1574	*Pliopapio alemui*	Aramis	M_3	?	11.16	6.68	6.75	59.9	PRIMO
NME ARA-VP 1/289	*Pliopapio alemui*	Aramis	M_3	?	11.73	7.56	7.59	64.5	PRIMO
NME ARA-VP 1/1615	*Pliopapio alemui*	Aramis	M_3	?	11.68	7.49	6.80	64.1	PRIMO
NME ARA-VP 1/9	*Pliopapio alemui*	Aramis	M_3	?	11.85	7.17	6.71	60.5	PRIMO
NME ARA-VP 1/492	*Pliopapio alemui*	Aramis	M_3	?	12.57	7.35	6.92	58.5	PRIMO
NME ARA-VP 1/1573	*Pliopapio alemui*	Aramis	M_3	?	12.42	7.36	6.68	59.3	PRIMO
NME ARA-VP 1/12	*Pliopapio alemui*	Aramis	M_3	?	10.49	7.08	6.43	67.5	PRIMO
NME ARA-VP 6/8	*Pliopapio alemui*	Aramis	M_3	?	10.62	6.48	6.84	61.0	PRIMO
NME ARA-VP 6/659	cf. *Pliopapio alemui*	Aramis	M_3	?	11.64	7.42	6.12	63.7	PRIMO

Abbreviations: F = female; M = male; ? = unknown sex.

Institutional acronyms: AMNH-M = American Museum of Natural History (Mammalogy), New York, USA; BGDG = Basque Government official repository institution for the District of Guipúzcoa, San Sebastián, Spain; UNIARQ = Centro de Arqueologia da Universidade de Lisboa, Lisbon, Portugal; Bonifay = Research collection of Dr. Marie-Francoise Bonifay, Marseille, France; BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; FSL = Dept. Sciences de la Terre, Faculté des Sciences, Université Claude-Bernard Lyon I, Lyon, France; GOV =

Soprintendenza dell'Abruzzo, Chieti, Italy; GPI = Geologisches-Paläontologisches Institut, Universität Freiburg im Breisgau, Freiburg, Germany; Harlé = Collection of M. Édouard Harlé (not located), Toulouse, France; HUJ-ESE = Hebrew University (Ecology, Systematics & Evolution), Jerusalem, Israel; IAPU-P = Istituto di Antropologia e Paleontologia Umana, Università di Pisa, Italy; IG-R = Istututo di Geologia, Universita di Roma, Italy; IGF = Museo di Storia Naturale (Sezione di Paleontologia e Geologia), Florence, Italy—formerly Istituto di Geologia e Paleontologia, Università di Firenze); IPH = Institut de Paléontologie Humaine, Paris, France; IQW = Senckenberg Research Station of Quaternary Paleontology, Weimar, Germany; KNM = National Museums of Kenya, Kenya; LPHP-S = Laboratori i Paleontologjise Humane Prehistorise, ILP "Luigi Gurakuqi", Shkoder, Albania; MAP = Museo dell'Accademia del Poggio, Montevarchi, Italy; MB = Paläontologisches Museum der Humboldt-Universität, Berlin, Germany; MAC = Museo Anatomia Comparata, Modena, Italy; MAU-T = Museo di Anatomia Umana "Luigi Rolando", Università di Torino, Turin, Italy; MCSNBS = Museo Civico di Scienze Naturali di Brescia, Italy; MCZ = Museum of Comparative Zoology, Harvard, USA; MHNL = Musée des Confluences (formerly Musée d'Histoire Naturelle de Lyon), Lyon, France; MNHN-F = Muséum National d'Histoire Naturelle (Paleontology), Paris, France; MNHN-ZM-AC = Muséum National d'Histoire Naturelle (Zoologie Mammifères – Anatomie Comparée), Paris, France; MNHN-ZM-MO = Muséum National d'Histoire Naturelle (Zoologie Mammifères – Mammifères et Oiseaux), Paris, France; MPC = Museo dei Paleoambienti Sulcitani – E.A. Martel, Carbonia, Sardinia, Italy; MSNC = Museo di Storia naturale e del Calci, Pisa, Italy; MUPE = Museu Paleontològic d'Elx, Elche, Spain; NHMUK-Z = Natural History Museum (Zoology), London, United Kingdom—formerly British Museum (Natural History) [BM(NH)-Z]; NHMUK-P = Natural History Museum (Paleontology), London, United Kingdom—formerly British Museum (Natural History) [BM(NH)-P]; NMB = Naturhistorisches Museum Basel, Switzerland; NME = National Museum of Ethiopia, Addis Ababa, Ethiopia; NMNH = National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; NMP = Národní Muzeum, Prague, Czech Republic; NMR = Natural History Museum Rotterdam, The Netherlands; NMT = National Museum of Tanzania, Dar es Salaam, Tanzania; ORGNAC = Orgnac faunal collection, details uncertain; RGM-L = Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands; SIP-V = Servicio de Investigaciones Prehistorica, Diputación Provincial de Valencia, Spain; SMF = Senckenberg

Forschungsinstitut und Naturmuseum (Terrestrische Zoologie), Frankfurt am Mein, Germany (formerly Senckenberg Museum Forschungstinstitut); UG = Universidad de Granada, Granada, Spain; UM = Universidad de Murcia, Spain; ZMA = Zoologisch Museum, Universiteit van Amsterdam, The Netherlands.

[a] Data taken from the PRIMO (PRImate Morphometrics Online) database (http://primo.nycep.org), measured by one of the authors (D.M.A.), or available from the literature.

SOM Table S2

Descriptive statistics for the various measurements investigated in the tooth loci preserved at Guefaït-4.2, and the z-scores computed for the latter (bolded when significant at $p < 0.05$, i.e., z >|1.96|) based on the mean and SD of each sample.[a]

I^1 H	*n*	Mean	SD	Minimum	Maximum	z-score
Guefaït	1	10.00	—	—	—	—
Macaca s. sylvanus	18	8.90	2.29	4.60	12.80	0.48
Macaca s. pliocena	1	10.10	—	—	—	—
Macaca s. florentina	2	10.17	1.32	9.23	11.10	—
Macaca majori	6	8.42	1.04	6.60	9.70	—
Parapapio (cf.) *ado*	2	11.75	0.64	11.30	12.20	—
Pliopapio alemui	6	8.19	1.56	6.40	10.40	—
I^1 MD	***n***	**Mean**	**SD**	**Minimum**	**Maximum**	**z-score**
Guefaït	1	6.80	—	—	—	—
Macaca s. sylvanus	23	6.37	0.66	4.95	7.30	0.66
Macaca s. pliocena	1	6.08	—	—	—	—
Macaca s. florentina	2	7.13	0.10	7.06	7.20	—
Macaca majori	6	6.00	0.19	5.70	6.20	—
Parapapio (cf.) *ado*	2	6.95	0.78	6.40	7.50	—
'Parapapio' lothagamensis	5	7.36	0.40	6.80	7.90	—
Pliopapio alemui	5	5.88	0.52	5.10	6.40	—
I^1 BL	***n***	**Mean**	**SD**	**Minimum**	**Maximum**	**z-score**
Guefaït	1	6.20	—	—	—	—
Macaca s. sylvanus	23	5.50	0.48	4.73	6.50	1.47
Macaca s. pliocena	1	5.20	—	—	—	—
Macaca s. florentina	2	5.28	0.17	5.16	5.40	—
Macaca majori	6	4.73	0.72	4.20	6.10	—
Parapapio (cf.) *ado*	2	5.55	0.35	5.30	5.80	—
'Parapapio' lothagamensis	5	6.26	0.15	6.10	6.40	—
Pliopapio alemui	5	5.82	0.54	5.00	6.30	—
I^1 BLI	***n***	**Mean**	**SD**	**Minimum**	**Maximum**	**z-score**

Guefaït	1	91.18	—	—	—	—
Macaca s. sylvanus	23	86.90	7.78	76.09	105.86	0.55
Macaca s. pliocena	1	76.47	—	—	—	—
Macaca s. florentina	2	74.05	1.35	73.09	75.00	—
Macaca majori	6	79.02	12.86	67.74	103.39	—
Parapapio (cf.) *ado*	2	80.07	3.87	77.33	82.81	—
'Parapapio' lothagamensis	5	85.25	4.94	77.22	89.71	—
Pliopapio alemui	4	99.07	10.51	86.06	111.76	—
M_2 MD	*n*	Mean	SD	Minimum	Maximum	z-score
Guefaït	1	8.60	—	—	—	—
Macaca s. sylvanus	55	9.35	0.80	7.05	11.10	-0.94
Macaca s. (cf.) *pliocena*	15	9.82	0.61	8.80	10.80	**-2.01**
Macaca s. florentina	22	9.61	0.47	8.90	11.00	**-2.17**
Macaca s. prisca	2	8.4	0.57	8.00	8.80	—
Macaca majori	9	8.57	0.39	7.60	8.90	0.07
Macaca libyca	4	9.93	0.67	9.40	10.90	—
Parapapio (cf.) *ado*	24	10.47	0.92	8.80	12.50	**-2.03**
'Parapapio' lothagamensis	10	8.85	0.68	8.10	10.30	-0.37
Pliopapio alemui	6	9.05	0.28	8.74	9.47	—
M_2 BLm	*n*	Mean	SD	Minimum	Maximum	z-score
Guefaït	1	7.10	—	—	—	—
Macaca s. sylvanus	55	7.69	0.66	6.30	9.30	-0.90
Macaca s. (cf.) *pliocena*	15	7.74	0.53	6.55	8.50	-1.21
Macaca s. florentina	22	7.58	0.55	6.70	8.50	-0.86
Macaca s. prisca	2	6.80	0	6.80	6.80	—
Macaca majori	9	6.93	0.23	6.40	7.20	0.77
Macaca libyca	4	8.48	0.67	7.90	9.40	—
Parapapio (cf.) *ado*	24	8.53	0.76	7.00	9.80	-1.89
'Parapapio' lothagamensis	10	7.55	0.72	6.50	9.00	-0.63
Pliopapio alemui	6	6.96	0.48	6.38	7.58	—
M_2 BLl	*n*	Mean	SD	Minimum	Maximum	z-score

Guefaït	1	82.56	—	—	—	—
Macaca s. sylvanus	55	82.55	6.07	70.98	101.11	<0.01
Macaca s. (cf.) *pliocena*	15	78.99	5.07	69.31	89.77	0.70
Macaca s. florentina	22	78.81	4.00	72.48	87.37	0.94
Macaca s. prisca	2	81.14	5.47	77.27	85.00	—
Macaca majori	9	80.83	2.08	78.16	84.21	0.84
Macaca libyca	4	85.78	9.79	72.48	95.92	—
Parapapio (cf.) *ado*	24	81.73	6.39	70.71	100.00	0.13
‘Parapapio' lothagamensis	10	85.34	5.41	77.89	95.45	-0.51
Pliopapio alemui	6	76.80	3.45	72.77	81.30	—

M_3 MD	*n*	Mean	SD	Minimum	Maximum	z-score
Guefaït	1	10.00	—	—	—	—
Macaca s. sylvanus	51	11.61	1.07	9.34	14.60	-1.50
Macaca s. (cf.) *pliocena*	13	12.78	0.81	11.70	14.40	**-3.41**
Macaca s. florentina	16	12.36	1.01	10.20	14.50	**-2.35**
Macaca s. prisca	1	10.80	—	—	—	—
Macaca majori	12	10.20	0.71	9.00	11.60	-0.28
Macaca libyca	2	12.45	1.06	11.70	13.20	—
Parapapio (cf.) *ado*	40	12.97	1.08	10.90	15.00	**-2.75**
‘Parapapio’ lothagamensis	15	11.36	1.03	9.70	13.50	-1.33
Pliopapio aleumi	31	11.31	0.84	9.50	13.14	-1.56

M_3 BLm	*n*	Mean	SD	Minimum	Maximum	z-score
Guefaït	1	7.60	—	—	—	—
Macaca s. sylvanus	51	8.12	0.87	6.41	11.40	-0.60
Macaca s. (cf.) *pliocena*	13	8.20	0.62	7.30	9.40	-0.96
Macaca s. florentina	16	7.75	0.56	6.80	8.80	-0.27
Macaca s. prisca	1	6.90	—	—	—	—
Macaca majori	12	7.12	0.25	6.50	7.40	1.92
Macaca libyca	2	8.75	0.64	8.30	9.20	—
Parapapio (cf.) *ado*	40	8.74	0.73	7.60	10.80	-1.56
‘Parapapio’ lothagamensis	15	7.77	0.69	6.70	9.20	-0.24

Pliopapio alemui	31	7.26	0.42	6.48	8.40	0.81
M_3 BLI	*n*	Mean	SD	Minimum	Maximum	z-score
Guefaït	1	76.00	—	—	—	—
Macaca s. sylvanus	51	70.11	6.39	56.06	100.88	0.92
Macaca s. (cf.) *pliocena*	13	64.17	2.46	60.33	68.38	**4.81**
Macaca s. florentina	16	62.91	4.88	53.79	72.73	**2.68**
Macaca s. prisca	1	63.89	—	—	—	—
Macaca majori	12	70.17	6.54	60.34	81.11	0.89
Macaca libyca	2	70.32	0.88	69.70	70.94	—
Parapapio (cf.) *ado*	40	67.60	5.32	57.97	80.16	1.58
‘*Parapapio’ lothagamensis*	15	68.53	4.66	62.22	75.26	1.60
Pliopapio alemui	31	64.40	4.06	58.50	73.68	**2.86**

Abbreviations: H = maximum recorded crown height (mm); BL = buccolingual (or labiolingual) breadth (mm); BLm = buccolingual breadth across the mesial lophid (mm); BLI = breadth/length index (%; using BLm for molars); MD = mesiodistal length (mm).

[a] z-scores for I^1 measurements are only provided based on *M. s. sylvanus*, as the small samples available for the remaining taxa would make render them unreliable. For the same reason, z-scores for the molars are not provided based on *M. libyca*, *M. s. prisca*, or *Pl. alemui* M_2, while those for *M. majori* and ‘*P.*’ *lothagamensis* should be interpreted with care.

SOM Table S3

ANOVA results for the metrical comparisons of taxa included in the comparative sample (see SOM Tables S1 and S2)[a]. Significant results at $p < 0.05$ are bolded. See SOM Table S4 for the results of pairwise comparisons.

Variable	F	*p*
I^1 H	1.59	0.203
I^1 MD	5.25	**0.001**
I^1 BL	5.80	**<0.001**
I^1 BLI	3.74	**0.008**
M_2 MD	10.82	**<0.001**
M_2 BL	9.94	**<0.001**
M_2 BLI	3.08	**0.005**
M_3 MD	16.58	**<0.001**
M_3 BL	15.90	**<0.001**
M_3 BLI	6.20	**<0.001**

Abbreviations: H = maximum recorded crown height (mm); BL = buccolingual (or labiolingual) breadth (mm); BLI = breadth/length index (%); MD = mesiodistal length (mm).

[a] *Macaca s. prisca* was excluded due to insufficient sample size.

SOM Table S4

Tukey's pairwise post hoc tests among the comparative sample (see SOM Tables S1 and S2)[a]. The Studentized range statistic Q is given below the diagonal, whereas *p*-values are given above. Significant differences at $p < 0.05$ are bolded.

I^1 H	*M. s. sylvanus*	*M. s. florentina*	*M. majori*	*P.* (cf.) *ado*	*Pl. alemui*
M. s. sylvanus	—	0.902	0.984	0.302	0.936
M. s. florentina	1.243	—	0.802	0.923	0.723
M. majori	0.746	1.565	—	0.243	1.000
P. (cf.) *ado*	2.797	1.159	2.984	—	0.189
Pl. alemui	1.097	1.768	0.287		—

I^1 MD	*M. s. sylvanus*	*M. s. florentina*	*M. majori*	*P.* (cf.) *ado*	*'P.' lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	0.469	0.721	0.734	**0.013**	0.528
M. s. florentina	2.568	—	0.174	1.000	0.997	0.119
M. majori	1.979	3.430	—	0.341	**0.004**	0.999
P. (cf.) *ado*	1.963	0.446	2.883	—	0.954	0.246
'P.' lothagamensis	4.992	0.681	5.566	1.214	—	**0.003**
Pl. alemui	2.431	3.696	0.483	3.163	5.791	—

I^1 BL	*M. s. sylvanus*	*M. s. florentina*	*M. majori*	*P.* (cf.) *ado*	*'P.' lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	0.990	**0.018**	1.000	**0.038**	0.774
M. s. florentina	0.864	—	0.750	0.994	0.190	0.777
M. majori	4.816	1.924	—	0.344	**0.001**	**0.010**
P. (cf.) *ado*	0.188	0.776	2.874	—	0.525	0.986

‘P.' lothagamensis	4.415	3.366	7.244	2.438	—	0.719
Pl. alemui	1.853	1.855	5.156	0.927	1.999	—
I^1 BLI	*M. s. sylvanus*	*M. s. florentina*	*M. majori*	*P.* (cf.) *ado*	*‘P.’ lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	0.335	0.351	0.882	0.999	0.114
M. s. florentina	2.899	—	0.979	0.980	0.620	**0.019**
M. majori	2.859	1.013	—	1.000	0.830	**0.010**
P. (cf.) *ado*	1.541	1.002	0.214	—	0.977	0.129
‘P.' lothagamensis	0.555	2.227	1.712	1.030	—	0.176
Pl. alemui	3.733	4.803	5.163	3.647	3.423	—

M_2 MD	*M. s. sylvanus*	*M. s.* (cf.) *pliocena*	*M. s. florentina*	*M. majori*	*M. libyca*	*P.* (cf.) *ado*	*‘P.’ lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	0.346	0.834	0.061	0.785	**<0.001**	0.468	0.977
M. s. (cf.) *pliocena*	3.139	—	0.990	**0.002**	1.000	0.114	**0.027**	0.352
M. s. florentina	2.046	1.189	—	**0.009**	0.993	**0.002**	0.108	0.683
M. majori	4.247	5.790	5.164	—	**0.044**	**<0.001**	0.991	0.915
M. libyca	2.177	0.378	1.124	4.417	—	0.854	0.194	0.562
P. (cf.) *ado*	8.993	3.906	5.705	9.535	1.987	—	**<0.001**	**<0.001**
‘P.' lothagamensis	2.867	4.654	3.937	1.179	3.571	8.463	—	1.000
Pl. alemui	1.386	3.126	2.414	1.767	2.669	6.125	0.755	—
M_2 BLm	*M. s. sylvanus*	*M. s.* (cf.) *pliocena*	*M. s. florentina*	*M. majori*	*M. libyca*	*P.* (cf.) *ado*	*‘P.’ lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	1.000	0.995	**0.020**	0.267	**<0.001**	0.997	0.122
M. s. (cf.) *pliocena*	0.341	—	0.994	0.052	0.451	**0.005**	0.995	0.174
M. s. florentina	1.065	1.098	—	0.163	0.164	**<0.001**	1.000	0.396

M. majori	4.802	4.331	3.685	—	**0.002**	**<0.001**	0.391	1
M. libyca	3.346	2.903	3.682	5.757	—	1.000	0.218	**0.007**
P. (cf.) *ado*	7.616	5.359	7.222	9.185	0.241	—	**0.002**	**<0.001**
'P.' lothagamensis	0.967	1.057	0.168	3.035	3.491	5.833	—	0.608
Pl. alemui	3.863	3.644	3.023	0.125	5.258	7.721	2.573	—

M_2 BLI	*M. s. sylvanus*	*M. s.* (cf.) *pliocena*	*M. s. florentina*	*M. majori*	*M. libyca*	*P.* (cf.) *ado*	*'P.' lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	0.367	0.146	0.989	0.952	0.999	0.828	0.253
M. s. (cf.) *pliocena*	3.090	—	1.000	0.994	0.383	0.814	0.107	0.992
M. s. florentina	3.754	0.140	—	0.984	0.303	0.641	0.051	0.994
M. majori	1.208	1.104	1.296	—	0.820	1.000	0.649	0.869
M. libyca	1.581	3.054	3.249	2.085	—	0.880	1.000	0.208
P. (cf.) *ado*	0.851	2.102	2.503	0.579	1.901	—	0.623	0.531
'P.' lothagamensis	2.061	3.940	4.341	2.488	0.186	2.436	—	0.068
Pl. alemui	3.386	1.150	1.104	1.938	3.524	2.733	4.191	—

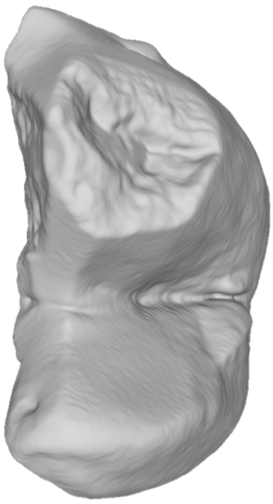
M_3 MD	*M. s. sylvanus*	*M. s.* (cf.) *pliocena*	*M. s. florentina*	*M. majori*	*M. libyca*	*P.* (cf.) *ado*	*'P.' lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	**0.005**	0.149	**<0.001**	0.938	**<0.001**	0.989	0.876
M. s. (cf.) *pliocena*	5.356	—	0.953	**<0.001**	1.000	0.999	**0.005**	**<0.001**
M. s. florentina	3.751	1.578	—	**<0.001**	1.000	0.447	0.096	**0.015**
M. majori	6.282	9.192	8.093	—	0.065	**<0.001**	0.057	**0.027**
M. libyca	1.661	0.615	0.163	4.207	—	0.996	0.826	0.760
P. (cf.) *ado*	9.166	0.851	2.910	12.010	1.019	—	**<0.001**	**<0.001**
'P.' lothagamensis	1.223	5.339	3.991	4.277	2.068	7.580	—	1.000

Pl. alemui	1.915	6.356	4.909	4.646	2.239	9.913	0.245	—
M_3 BLm	*M. s. sylvanus*	*M. s.* (cf.) *pliocena*	*M. s. florentina*	*M. majori*	*M. libyca*	*P.* (cf.) *ado*	*'P.' lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	1.000	0.572	**0.001**	0.907	**0.001**	0.655	**<0.001**
M. s. (cf.) *pliocena*	0.536	—	0.653	**0.003**	0.965	0.220	0.709	**0.001**
M. s. florentina	2.647	2.477	—	0.238	0.525	**<0.001**	1.000	0.283
M. majori	6.441	5.578	3.425	—	**0.044**	**<0.001**	0.226	0.999
M. libyca	1.804	1.493	2.745	4.408	—	1.000	0.550	0.064
P. (cf.) *ado*	6.046	3.478	6.881	10.459	0.032	—	**<0.001**	**<0.001**
'P.' lothagamensis	2.474	2.357	0.088	3.459	2.692	6.618	—	0.272
Pl. alemui	7.785	5.870	3.296	0.863	4.212	12.750	3.327	—
M_3 BLI	*M. s. sylvanus*	*M. s.* (cf.) *pliocena*	*M. s. florentina*	*M. majori*	*M. libyca*	*P.* (cf.) *ado*	*'P.' lothagamensis*	*Pl. alemui*
M. s. sylvanus	—	**0.009**	**<0.001**	1.000	1.000	0.336	0.973	**<0.001**
M. s. (cf.) *pliocena*	5.085	—	0.998	0.097	0.793	0.471	0.378	1.000
M. s. florentina	6.687	0.900	—	**0.010**	0.579	0.063	0.070	0.985
M. majori	0.052	3.989	5.062	—	1.000	0.822	0.993	**0.035**
M. libyca	0.081	2.157	2.632	0.054	—	0.997	1.000	0.790
P. (cf.) *ado*	3.162	2.857	4.220	2.080	1.002	—	0.999	0.194
'P.' lothagamensis	1.427	3.063	4.165	1.126	0.634	0.821	—	0.213
Pl. alemui	6.676	0.180	1.286	4.522	2.164	3.563	3.501	—

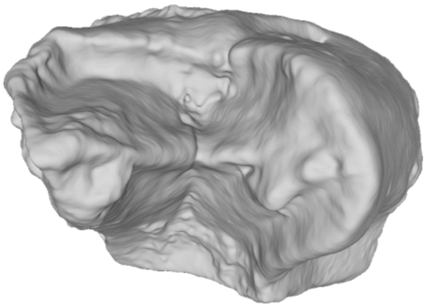
Abbreviations: BL = buccolingual (or labiolingual) breadth (mm); BLm = buccolingual breadth across the mesial lophid (mm); BLI = breadth/length index (%) (using BLm for molars); MD = mesiodistal length (mm).

[a] *Macaca s. prisca* was excluded due to insufficient sample size.

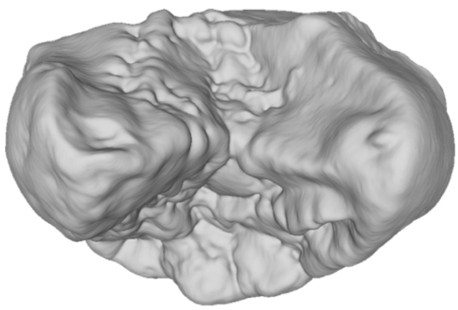
SOM File S1. Virtual model of GFT4.2'18-1-Q14-70, left I^1 crown of *Macaca* cf. *sylvanus* from Guefaït-4.2, available in PLY format from MorphoSource at https://doi.org/10.17602/M2/M158035 (unique identifier: ark:/87602/m4/M158035). A digital rendering in lingual view is depicted.



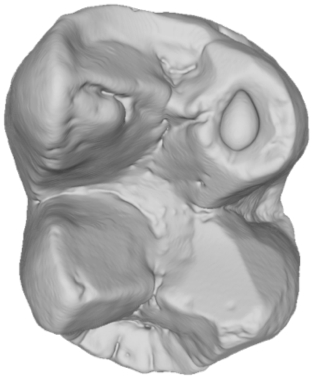
SOM File S2. Virtual model of GFT4.2'18-1-Q14-13, right M_1 lingual crown fragment of *Macaca* cf. *sylvanus* from Guefaït-4.2, available in PLY format from MorphoSource at https://doi.org/10.17602/M2/M158036 (unique identifier: ark:/87602/m4/M158036). A digital rendering in occlusal view is depicted.



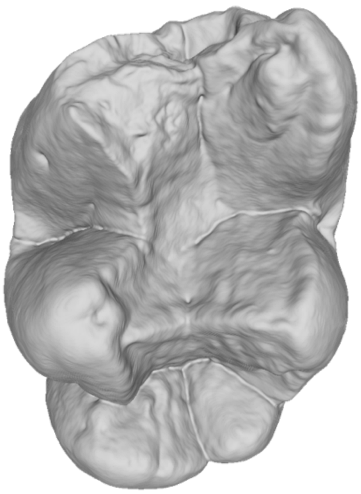
SOM File S3. Virtual model of GFT4.2’18-1-P13-191, right M_2 or M_3 mesial germ fragment of *Macaca* cf. *sylvanus* from Guefaït-4.2 available in PLY format from MorphoSource at https://doi.org/10.17602/M2/M158037 (unique identifier: ark:/87602/m4/M158037). A digital rendering in occlusal view is depicted.



SOM File S4. Virtual model of GFT4.2’19-1-R15-45, right M_2 distal germ fragment of *Macaca* cf. *sylvanus* from Guefaït-4.2 available in PLY format from MorphoSource at https://doi.org/10.17602/M2/M158038 (unique identifier: ark:/87602/m4/M158038). A digital rendering in occlusal view is depicted.



SOM File S5. Virtual model of GFT4.2’19-1-S15-65, right M_2 crown with distal root of *Macaca* cf. *sylvanus* from Guefaït-4.2 available in PLY format from MorphoSource at https://doi.org/10.17602/M2/M158291 (unique identifier: ark:/87602/m4/M158291). A digital rendering in occlusal view is depicted.



SOM File S6. Virtual model of GFT4.2’19-1-R13-63, left M_3 crown of *Macaca* cf. *sylvanus* from Guefaït-4.2 available in PLY format from MorphoSource at https://doi.org/10.17602/M2/M158292 (unique identifier: ark:/87602/m4/M158292). A digital rendering in occlusal view is depicted.

SOM References

Alba, D.M., Carlos Calero, J.A., Mancheño, M.Á., Montoya, P., Morales, J., Rook, L., 2011. Fossil remains of *Macaca sylvanus florentina* (Cocchi, 1872) (Primates, Cercopithecidae) from the Early Pleistocene of Quibas (Murcia, Spain). J. Hum. Evol. 61, 703–718.

Alba, D. M., Daura, J., Sanz, M., Santos, E., Yagüe, A. S., Delson, E., Zilhão, J., 2019. New macaque remains from the Middle Pleistocene of Gruta da Aroeira (Almonda karst system, Portugal). J. Hum. Evol. 131, 40–47.

Bona, F., Bellucci, L., Casali, D., Schirolli, P., Sardella, R., 2016. *Macaca sylvanus* Linnaeus 1758 from the Middle Pleistocene of Quecchia quarry (Brescia, Northern Italy). Hystrix 27. https://doi.org/10.4404/hystrix-27.2-11503

Castaños, P., Murelaga, X., Arrizabalaga, A., Iriarte, M.-J., 2011. First evidence of *Macaca sylvanus* (Primates, Cercopithecidae) from the Late Pleistocene of Lezetxiki II cave (Basque Country, Spain). J. Hum. Evol. 60, 816–820.

Frost, S.R., 2001a. New Early Pliocene Cercopithecidae (Mammalia: Primates) from Aramis, Middle Awash Valley, Ethiopia. Am. Mus. Nov. 3350, 1–36.

Frost, S.R., Ward, C.V., Manthi, F.K., Plavcan, J.M., 2020a. Cercopithecid fossils from Kanapoi,West Turkana, Kenya (2007-2015). J. Hum. Evol. 140, 102642.

Frost, S.R., Simpson, S.W., Levin, N.E., Quade, J., Rogers, M.J., Semaw, S., 2020b. Fossil Cercopithecidae from the Early Pliocene Sagantole Formation at Gona, Ethiopia. J. Hum. Evol. 144, 102789.

Jablonski, N.G., Leakey, M.G., Antón, M., 2008. Systematic paleontology of the cercopithecines. In: Jablonski, N.G., Leakey, M.G. (Eds.), Koobi Fora Research Project. Volume 6. The Fossil Monkeys. California Academy of Sciences, San Francisco, pp. 103–300.

Leakey, M.G., Teaford, M.F., Ward, C.V., 2003. Cercopithecidae from Lothagam. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 201–248.

Reumer, J.W.F., Mol, D., Kahlke, R.-D., 2018. First finds of Pleistocene *Macaca sylvanus* (Cercopithecidae, Primates) from the North Sea. Rev. Paléobiol. 37, 555–560.

Ruff, C.B., 2003. Long bone articular and diaphyseal structure in Old World monkeys and apes. II: Estimation of body mass. Am. J. Phys. Anthropol. 120, 16–37.

Zanaga, M., 1998. *Macaca majori* Azzaroli 1946, Primate endemico del Pleistocene della Sardegna. Bachelor Thesis, Università degli Studi di Firenze.

Zoboli, D., Pillola, G.L., Rook, L., 2016. New remains of *Macaca majori* Azzaroli, 1946 (Primates, Cercopithecidae) from Is Oreris (Fluminimaggiore, southwestern Sardinia). Boll. Soc. Paleontol. Ital. 55, 227–230.