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Short Communications

New macaque fossil remains from Morocco

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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;

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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. *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., 2000) 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 archaeological sites and establishing their geochronological and paleontological context (Aouraghe et al., 2016; Chacón et al., 2016). Systematic surveys led to the discovery of Pleistocene archaeological 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-Ramos 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., 20192019). 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., 2019).

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 permanently housed in the Faculty of Science, Mohammed I University in Oujda, Morocco. Three-dimensional 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 (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 and Tukey's pairwise post hoc tests, while the studied specimens were compared with these taxa using z-scores ($z = [\text{measurement} - \text{mean}]/\text{SD}$). Statistical computations and plots were performed using 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 can be 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 edges that converge toward the base), which is slightly asymmetrical (somewhat tilted mesially). The incisal edge is horizontal except on the distalmost 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

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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*.

[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.

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

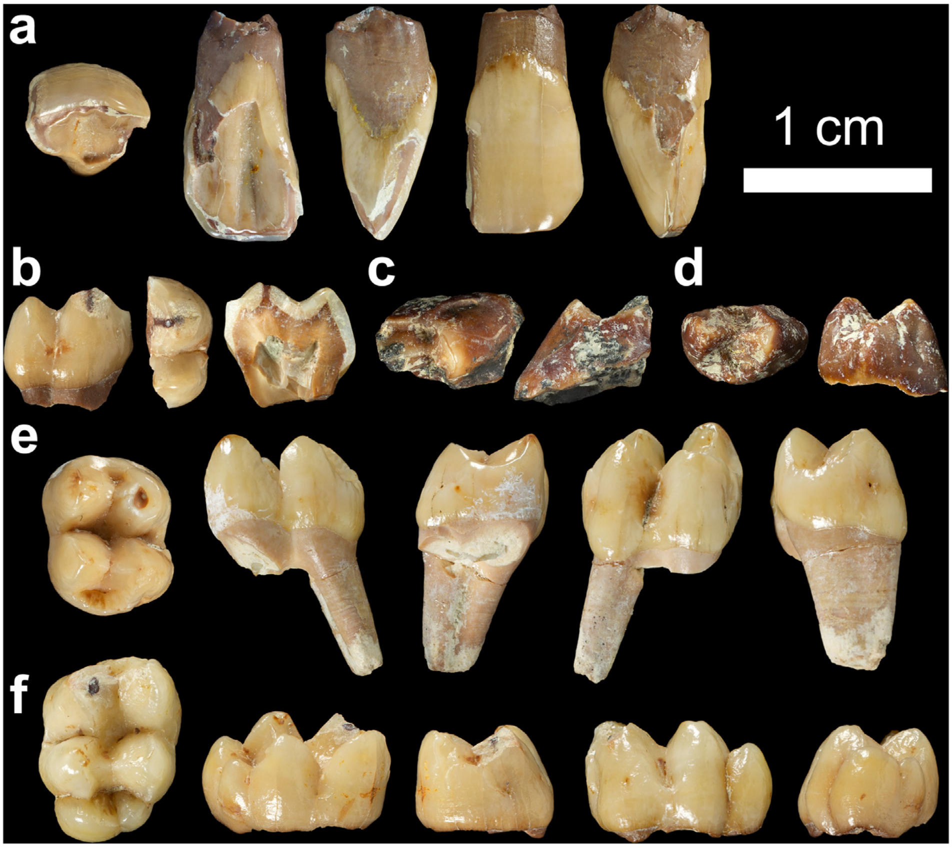

Figure 1. Teeth of *Macaca* cf. *sylvanus* from Guefaït-4.2 (views from left to right for each specimen): a) GFT4.2′18-1-Q14-70, left I^1 crown in occlusal, occusal, lingual, mesial, labial, and distal views; b) GFT4.2′18-1-Q14-13, right M_1 lingual crown fragment in occlusal, buccal, and lingual (cross-sectional) 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 occlusal, lingual, mesial, buccal, and distal views. Three-dimensional virtual models are available from MorphoSource (see SOM Files S1–S6).

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 because 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 a greater occlusal relief (with deeper foveae and notches), obliquely oriented lophids and trigonid, a 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, as well as 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

The 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 (Fig. 2A, B and 3A–C; SOM Table S2). In turn, the Guefaït-4.2 M (Fig. 2C, D and 3D–I; SOM Table S2) fits well in size with *M. s. sylvanus*, *Macaca majori*, '*P.*' *lothagamensis*, and *Pl. alemui*, but appears 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 also 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 owing 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 (Szalay and Delson, 1979; Swindler, 1983, 2002) but is almost invariably present in papionins, wherein 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 with that of *M. sylvanus* (SOM Fig. S3). Furthermore, its overall proportions fit well within the variation of extant *M. sylvanus* from northern Africa, whereas 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

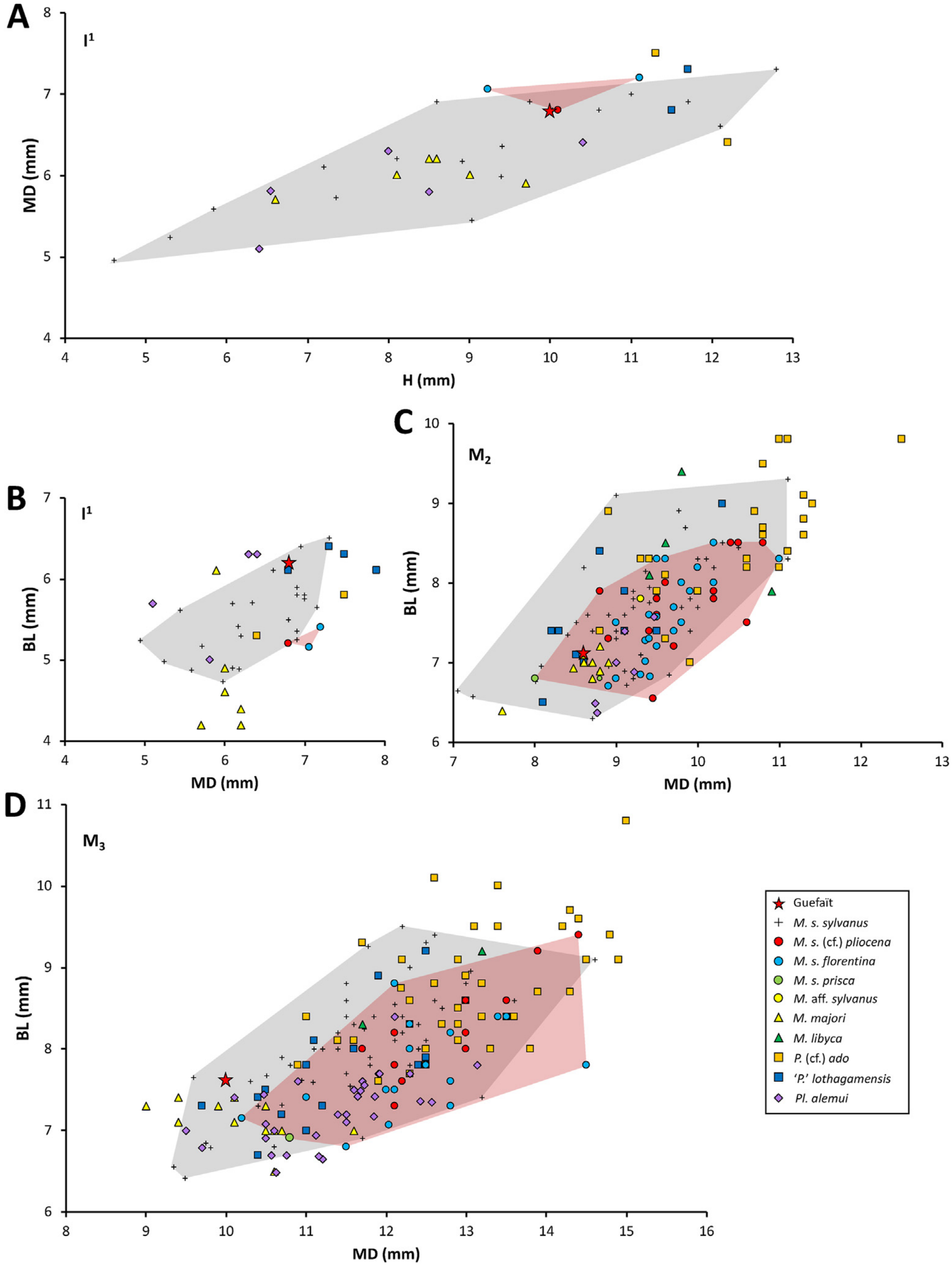

Figure 2. Bivariate plots of dental proportions in *Macaca* cf. *sylvanus* from Guefaït-4.2 (star) compared with extant Barbary macaques (*Macaca sylvanus sylvanus*), fossil macaques from the Plio-Pleistocene of Europe (*Macaca sylvanus* subspp. and *Macaca majori*), fossil *Macaca libyca* and *Macaca* 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, whereas 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). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

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

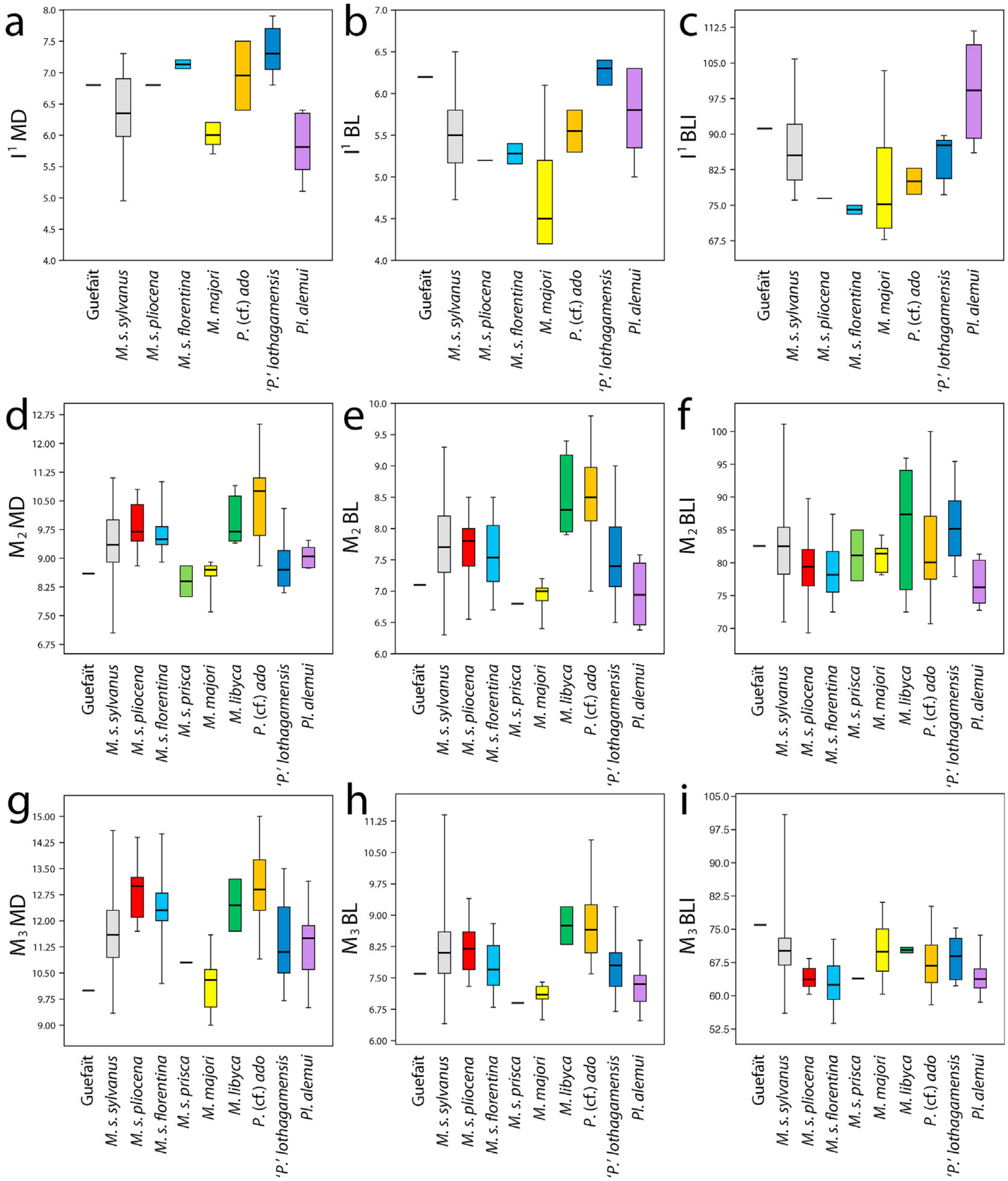

Figure 3. Box-and-whisker plots of MD (a, d, g), BL (b, e, h), and BLI (c, f, i) in extant macaques and some fossil papionins compared with *Macaca* cf. *sylvanus* from Guefaït: a–c) I^1; d–f) M_2; g–i) M_3. Vertical lines denote the median; boxes denote the 25 and 75 percentiles (Q1 and Q3), i.e., the 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 = breadth-length index (%); MD = mesiodistal length (mm).

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.

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Supplementary Online Material

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