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A new cercopithecoid dentognathic specimen attributed to *Theropithecus* from the late Early Pleistocene (c. 1 Ma) deposits of Simbiro, at Melka Kunture, Ethiopian highlands

Un nouveau spécimen dentognathique de cercopithécoïde attribué à Theropithecus, *provenant des dépôts du Pléistocène inférieur final (c. 1 Ma) de Simbiro, à Melka Kunture, plateaux d'Éthiopie*

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ABSTRACT

The archeological and paleontological area of Melka Kunture, in the Ethiopian highlands, has yielded particularly rich mammal fossil assemblages, including a few human and nonhuman primate remains. The cercopithecoid specimens reported so far consist of a fragmentary lower third molar crown and of a maxillary fragment, coming from the Early Pleistocene sites of Garba IV and Garba XII, respectively. In this study we describe an additional dentognathic specimen, labelled SIM III-13-1, collected in 2013 in the c. 1 Ma sedimentary deposits of Simbiro. In addition to classical descriptions and measurements, this specimen was detailed by X-ray tomography (CT) and two-three dimensional (2–3D) quantitative analyses were performed on the virtual reconstruction to assess its taxonomic assignment. Comparison with a number of fossil and extant cercopithecoid specimens/samples suggests that SIM III-13-1 belongs to the genus *Theropithecus*, more likely to *Theropithecus* sp. cf. *oswaldi*.

RÉSUMÉ

L'aire archéologique et paléontologique de Melka-Kunture, sur les plateaux d'Éthiopie, a délivré des assemblages de mammifères particulièrement riches, incluant quelques restes de primates humains et non humains. Les spécimens de cercopithécoïdes rapportés jusqu'ici consistent en un fragment de couronne de troisième molaire inférieure et en un fragment de maxillaire, provenant respectivement des sites du Pléistocène inférieur de Garba IV et Garba XII. Dans cette étude, nous décrivons un spécimen dentognathique supplémentaire, catalogué SIM III-13-1, collecté en 2013 dans les dépôts sédimentaires de

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c. 1 Ma de Simbiro. En plus des descriptions et mesures classiques, ce spécimen a été détaillé par tomographie à rayons X (CT), et des analyses quantitatives bi-/tridimensionnelles (2–3D) ont été réalisées à partir de la reconstruction virtuelle afin de proposer une attribution taxinomique. La comparaison avec un certain nombre de spécimens/échantillons cercopithécoïdes fossiles et actuels suggère que SIM III-13-1 appartient au genre *Theropithecus*, plus probablement à *Theropithecus* sp. cf. *oswaldi*.

1. Introduction

Melka Kunture is an archaeological and paleontological area of the Ethiopian highlands located on the western shoulder of the Rift Valley, at c. 2000 m asl. This complex of sites extends over some 100 km^2 along the upper Awash valley, 50 km south of Addis Ababa. The deposits, produced by fluvial-lacustrine sedimentation and by volcanic activity, accumulated and eroded in a semi-graben depression during most of the Pleistocene (Chavaillon and Piperno, 2004a; Gallotti, 2013; Morgan et al., 2012; Piperno et al., 2009). After the discovery of the area, in 1963, archaeological surveys and excavations were undertaken by G. Bailloud (Bailloud, 1965), then by J. Chavaillon, who directed the French Archaeological Mission from 1965 to 1998. Since 1999, the research has been under the responsibility of the Italian Archaeological Mission (Chavaillon and Piperno, 2004b; Mussi et al., 2014).

The many sites of Melka Kunture are named after the gullies where they have been discovered, i.e., after the seasonal tributaries of the Awash River that drain the area (Fig. 1A–B). The presence of volcanic deposits allowed ^{40}Ar/^{39}Ar dating (Morgan et al., 2012; for magnetostratigraphy, see Tamrat et al., 2014). The archaeological record starts at c. 1.7 Ma with the Oldowan of Karre I, Gombore I, Gombore Iγ and Garba IV E (Gallotti, 2013; Morgan et al., 2012; Piperno et al., 2009), while the first evidence of Acheulean dates back to 1.5 Ma at Garba IV D (Gallotti, 2013). The occurrence of the Acheulean lasts c. one million years (Chavaillon and Berthelet, 2004; Gallotti et al., 2010, 2014). Notably, the early Middle Stone Age is represented at Garba III (Mussi et al., 2014), while Late Stone Age sites are less substantial and still lack any geochronological resolution (Chavaillon and Berthelet, 2004; Hivernel-Guerre, 1976; Mussi et al., 2014).

Seven human fossil remains have been discovered so far in the area of Melka Kunture (Coppens, 2004; rev. and updating in Mussi et al., 2014). They consist of an immature partial mandible (the specimen Garba IV E) from Garba IV (Condemi, 2004; Zanolli et al., 2014; Zilberman et al., 2004a, b) and a distal humerus (MK 76 GOM IB 7594) from Gombore I (Chavaillon et al., 1977; Puymerail et al., 2014; Senut, 1979), both associated with Oldowan industries; two cranial portions (MK 73 GOM II 6169 and MK 76 GOM II 576) from Gombore II (Chavaillon and Coppens, 1986; Chavaillon et al., 1974), associated with a Middle Acheulean industry; and three cranial fragments (MK 78 GAR III A4-W9 n. 1918, MK 78 GAR III B3-A13 n. 1656–1919, and MK 78 GAR III A4-W9 n. 1917) from Garba III (Chavaillon et al., 1987; Mussi et al., 2014), associated with an early Middle Stone Age industry (Mussi et al., 2014).

Besides the paleoanthropological findings, the large mammal fossil assemblage, particularly rich at the localities of Garba and Gombore, includes bovids (notably, Alcelaphini and some Antilopini and Reduncini, while Tragelaphini are absent), hippopotamids, equids, suids, giraffids, and a few specimens/fragments representing proboscideans, rhinocerontids, carnivores and nonhuman primates (Chavaillon and Berthelet, 2004; Gallotti et al., 2010; Geraads, 1979, 1985; Geraads et al., 2004a; Oussedik, 1976; rev. in Morgan et al., 2012; Tamrat et al., 2014). As a whole, this assemblage associates *Hippopotamus* sp. (cf. *amphibious* and cf. *aethiopicus*) and other artiodactyls indicative of relatively wet grasslands (*Kobus*) along with grazer taxa (e.g., *Connochaetes*, *Damaliscus*) more commonly found in drier open savannah environments (Geraads et al., 2004a, b). While the latter scenario is also consistent with information from the microfauna (Gallotti et al., 2010; Geraads et al., 2004b; Sabatier, 1980-82) and with some biogeochemical (Bocherens et al., 1996) and palynological data (Bonnefille, 1976) supporting the presence of open C4 grasslands across most Early to early Middle Pleistocene (in Morgan et al., 2012), conclusive paleoecological interpretations at Melka Kunture should be drawn with caution, as strong taphonomic biases have affected the faunal assemblage as a whole, notably the proportions of ungulate remains (Gallotti et al., 2010: 298).

The nonhuman primate fossil record reported so far from this site complex consists of a fragmentary lower M3 crown (GAR IV D-74-7596) and a maxillary fragment bearing both premolars and the M1 (GAR XII J-78-1952) from the Early Pleistocene levels of Garba IV D and Garba XII J, respectively, both attributed to *Theropithecus* sp. cf. *oswaldi* (Geraads, 1979; Geraads et al., 2004a).

Here we report an additional dentognathic cercopithecoid specimen collected in 2013 in the late Early Pleistocene sedimentary deposits outcropping in the vicinity of the locality of Simbiro.

2. The site of Simbiro III

The deposits of the Simbiro gully, a feeder of the Awash river (Fig. 1A–B), were first identified by Taieb (1967) and the archaeological sequence of the Simbiro III site excavated from 1973 to 1976 (Chavaillon and Berthelet, 2004; Oussedik, 1976), and again in 2005 (in Gallotti et al., 2010). The fluviatile and associated floodplain depositional environments of the creek are mostly made up of pebbles, sandy gravels and sandy clays. Groundwater washing carried the ash and pumice from the surrounding volcanic deposits down into the valley mixing them with the alluvial deposits (Chavaillon and Berthelet, 2004; Kieffer et al., 2004; Raynal

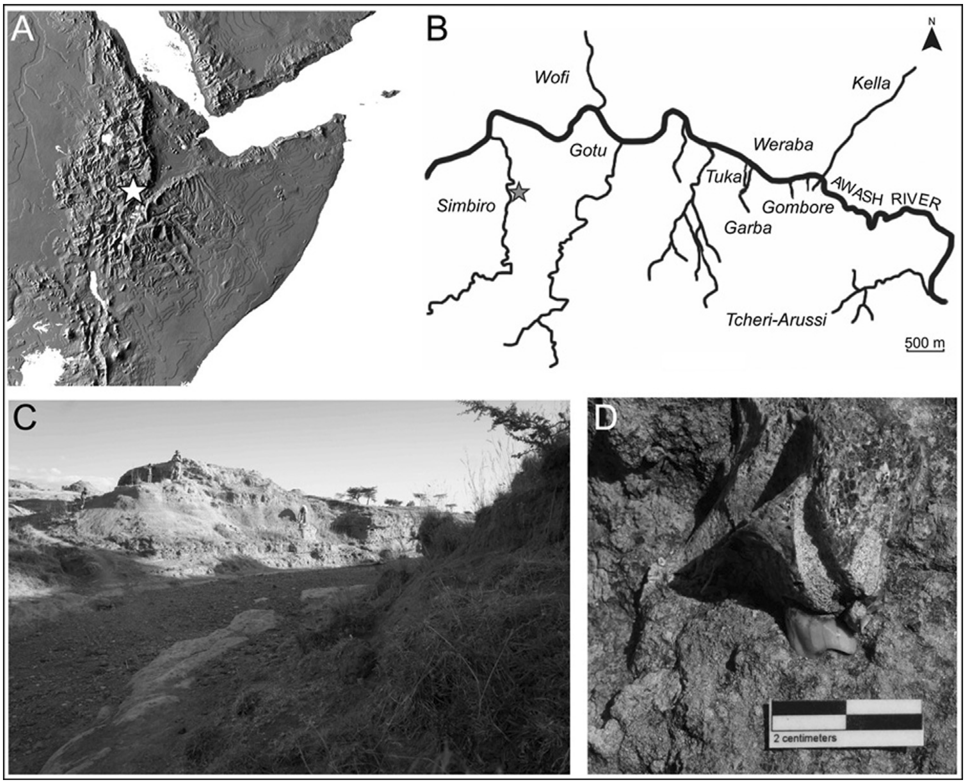

Fig. 1. Location of Melka Kunture (white star) on the shoulder of the Main Ethiopian Rift (A); map of the Melka Kunture area with location of the major archaeological and paleontological sites, including Simbiro (grey star); the deposits outcropping at Simbiro III (C); the specimen SIM III-13-1 (posterior aspect of the right maxillary fragment) still embedded in the sediments.

Fig. 1. Localisation de Melka Kunture (étoile blanche) sur les hauteurs du rift principal d'Éthiopie (A) ; carte de la région de Melka Kunture, avec la position des sites archéologiques et paléontologiques majeurs, incluant Simbiro (étoile grise) ; les dépôts affleurant à Simbiro III (C) ; le spécimen SIM III-13-1 (aspect postérieur du fragment maxillaire droit), encore en place dans le sédiment.

et al., 2004). At Simbiro III (Fig. 1 C), the upper part of the c. 15 m thick litho-stratigraphic sequence of unconsolidated sediments is composed of clays, tuffs, sandy-clay and gravels, while the middle part consists predominantly of sandy-clay layers interbedded with fine sands, thin volcanic ash and conglomerates (Tamrat et al., 2014).

Published and unpublished evidence (F. Altamura, R. Melis and M. Mussi, pers. comm.) points to a minimum of seven archaeological levels, which yielded abundant Early Acheulean industry and some faunal remains (Chavaillon and Berthelet, 2004; Geraads et al., 2004a; Oussedik, 1976). Importantly, the sequence is capped by a volcanic deposit, the so-called tuff 'B' (Kieffer et al., 2004; Morgan et al., 2012), dating back to 0.878 ± 0.014 Ma (Morgan et al., 2012; Tamrat et al., 2014).

Below the tuff 'B' and the underlying 20–60 cm thick sandy level bearing sporadic bone remains (unit A), the 20 to 50 cm thick level B, considered as the most significant of the entire archaeological sequence of the Simbiro creek formation, consists of yellowish gravel-sand deposits bearing the highest number of lithic artefacts, mostly manufactured from fine-grained lavas (Chavaillon and Berthelet, 2004; Gallotti et al., 2010; Piperno et al., 2009). Below, the 5 to 20 cm thick archaeostratigraphic unit C of coarse channel-lag deposits represents the Acheulean accumulation level remarkably rich of obsidian flakes, handaxes, cleavers and other tools embedded in a greyish sandy matrix preserving some macrofaunal remains (Chavaillon and Berthelet, 2004). Regional lithostratigraphic correlations place Simbiro III B and C units approximately at the same age as Gombore II (Gallotti et al., 2010), thus slightly earlier 0.878 ± 0.014 Ma, likely around 1.0 Ma (Morgan et al., 2012). At its bottom, just below the unit C, the sequence starts with a fine-grained light grey tuffaceous silty-sandy deposit, the so-called level D (in Chavaillon and Berthelet, 2004).

Following the discovery, in 1973, of a *Pelorovis* skull embedded in level B (Oussedik, 1976), nearly 300 bony, horny, and tooth remains representing bovids (e.g., *Pelorovis turkanensis*, *Damaliscus* cf. *lunatus*, cf. *Connochaetes gentryi*), hippos (*Hippopotamus* cf. *amphibius*) and other large mammals have been reported from the A–D archaeological sequence at Simbiro III (Chavaillon and Berthelet, 2004; Geraads et al., 2004a) (Fig. 1 C).

The cercopithecoid dentognathic specimen considered in the present study, consisting of a partial maxilla bearing two premolars preliminarily labelled SIM III-13-1, has been found on 18th November 2013 during a survey of the eastern river bank of the creek performed by three among us (B.E.R., R.M. and C.Z.). The fossil (Fig. 1D) was found still embedded in the sediments along the section outcropping at Simbiro III (8°42′ 34.56″ N, 38°34′ 1.79″ E), c. 50 m N to the accumulation of obsidian tools of level C described and imaged as "locality 2b" by Chavaillon and Berthelet (2004: 46). More precisely, SIM III-13-1 was collected in situ in a variably thickened (5–50 cm) whitish/slightly yellow level of consolidated fine silty sands sandwiched between level C and B, intermittently exposed along the section and immediately overlying level C, c. 15–20 cm above its top. Accordingly, its chronological age nears 1 Ma.

3. Materials and methods of analysis

The morphodimensional description of the outer aspect of SIM III-13-1 was performed in November 2013 at the Dept. of Paleoanthropology of the National Museum of Ethiopia, Addis Ababa, where the specimen is permanently stored, using traditional analytical methods supported by observations realized by a Nikon SMZ645 stereomicroscope (magnification from 0.8 × to 5 ×) and a Keyence VHX-600 digital microscope equipped by a 2.11 Mp CCD camera (zoom up to 10x). Descriptions of the dental features basically follow Swindler (2002). The specimen was also detailed by X-ray tomography (CT) at the Wudassie Diagnostic Centre of Addis Ababa. The acquisitions have been realized with a Philips Brilliance16 equipment according to the following parameters: 140 kV voltage, 100 μA current, 1.76 s exposition time per projection. Its final volume was reconstructed with a voxel size of 130 × 130 × 300 μm. All two-three dimensional (2–3D) elaborations (quantitative virtual imaging and morphometrics) were performed at the ICTP of Trieste and at the laboratory AMIS (University of Toulouse).

To comparatively characterize the internal morphology of SIM III-13-1, for the purposes of this study we used the high-resolution microtomographic (μCT) record of a number of fossil and extant cercopithecoid crania virtually stored at the laboratory AMIS of the University of Toulouse (Beaudet et al., 2014). More specifically, we used the original record of the following Plio-Pleistocene South African specimens: STS 394A, a complete *Cercopithecoides williamsi* adult female face from Sterkfontein Member 4 (Eisenhart, 1974); SK 561, a well-preserved adult female cranium of *Theropithecus oswaldi oswaldi* from Swartkrans Member 1 (Freedman, 1957); and M 3073, a subadult *Theropithecus oswaldi darti* female cranium from Makapansgat Member 4 (Maier, 1972). The specimens STS 394A and SK 561, permanently stored at the Ditsong National Museum of Natural History, Pretoria, were detailed (by A.B.) using the X-Tek (Metris) XT H225L industrial CT system available at the South African Nuclear Energy Corporation (Necsa). The specimen M 3073, stored at the University of the Witwatersrand, Johannesburg, was scanned (by A.B.) with the Nikon Metrology XTH 225/320 LC dual source industrial CT system set at the Wits Palaeosciences Centre In order to document the extant variation, several crania of *Theropithecus gelada*, *Papio cynocephalus*, *P. anubis, Colobus guereza, Chlorocebus aethiops* and *Lophocebus albigena* from the primate skeletal collections of the Muséum national d'Histoire naturelle (MNHN) of Paris, the Muséum d'Histoire naturelle of Toulouse and the Musée royal de l'Afrique centrale of Tervuren were scanned (by A.B.) for comparison at different resolutions at the AST-RX imagery platform set at the MNHN Paris using the v|tome|x L 240-180 model from GE Sensing & Inspection Technologies, and at the French Research Federation FERMaT (FR3089) of Toulouse by means of a Phoenix/GE Nanotom 180 system. Additional CT-scans of *Macaca fascicularis* were obtained from the Digital Morphology Museum of the Kyoto University Primate Research Institute (KUPRI; www.pri.kyoto-u.ac.jp).

We comparatively assessed topographic enamel thickness variation on the P4 crown. For SIM III-13-1, we used the microscopic image of the naturally fractured mesiodistal section through the paracone (see infra) while, in the case of the specimens selected for comparisons (representing two fossil and five extant taxa), we used a homologous μCT-based virtual section. The linear and surface variables measured to assess enamel thickness include: the area of the sectioned enamel cap (a, mm^2); the area of the dentine (and pulp) enclosed by the enamel-dentine junction (EDJ) and a straight line connecting the mesial and the distal cervical margins (b, mm^2); the enamel-dentine junction length (EDJL, mm); the maximum linear thickness perpendicular to the EDJ (ET max., mm) (Grine et al., 2005). We thus calculated the average enamel thickness (AET, mm), corresponding to the ratio a/EDJL, and the scale-free relative enamel thickness (RET), obtained through the ratio $(AET/b^{1/2})$*100 (Martin, 1985).

Following 3D virtual rendering using Avizo v.7.0 (Visualization Sciences Group Inc.), linear cranial and tooth measurements were taken using the software package MPSAK v.2.9 (in Dean and Wood, 2003). Intra- and interobserver tests for accuracy of the 2–3D measurements taken in this study were run by two observers (AB, CZ) and recorded differences were less than 4%, which is compatible with similar previous analyses (e.g., Macchiarelli et al., 2009).

4. Results

4.1. Description of the maxillary fragment SIM III-13-1

The right maxillary fragment SIM III-13-1 (max. length: 5.2 cm; max. height: 4.4 cm; max. thickness: 1.6 cm) is from an adult individual (Fig. 2), very likely of the female sex based on its estimated canine root size (see infra). It preserves the fully erupted third (P3) and fourth (P4) premolars and the mesial root of the first molar (M1), the latter only bearing a tiny enamel fragment. The specimen is broken anteriorly near the intermaxillary suture (still visible for 1.2 cm) and posteriorly at the level of the M1. The vertically-set posterior fracture partially exposes the cancellous network (Fig. 2B). On the lateral aspect, between the thickening of the nasal aperture and the slightly prominent canine jugum, the premaxillary suture runs along a deep subvertical groove (Fig. 2 C). Medially, the cylindrically-shaped nasal cavity, corresponding to the inferior meatus (Figs. 2D and 3A), is 3.5 mm long, with a vertical diameter ranging from 0.6 (anteriorly) to 0.9 mm. Virtual imaging reveals no trace of a maxillary sinus, even at the level of the first molar mesial root (Fig. 3B–C).

In inferior view (Fig. 2E), the empty sockets of the central and lateral incisors, both showing an ovoid outline, and that of the canine, exhibiting a C-shaped outline, are

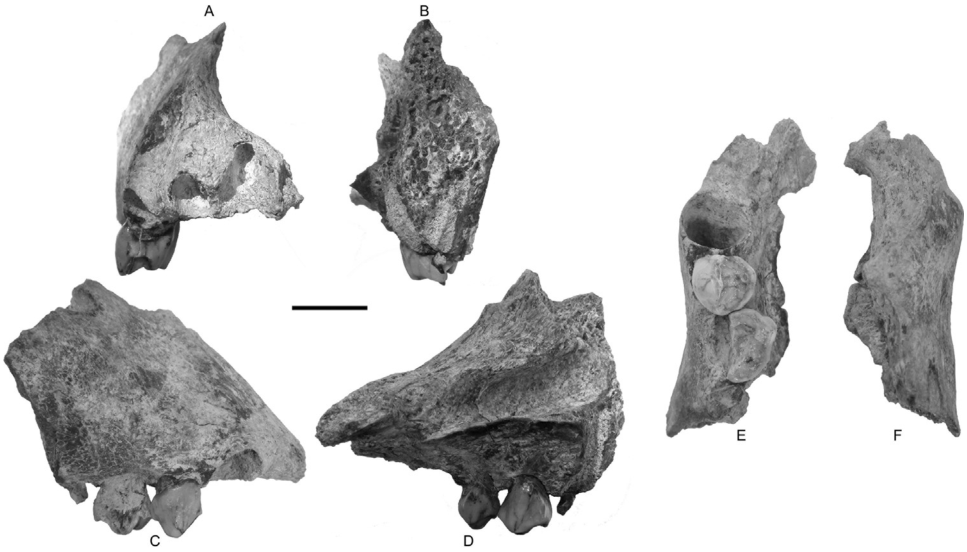

Fig. 2. The right partial maxilla SIM III-13-1 in anterior (A), posterior (B), lateral (C), medial (D), inferior (E) and superior (F) views. Scale bar: 1 cm.

Fig. 2. Le fragment maxillaire droit SIM III-13-1 en vues antérieure (A), postérieure (B), latérale (C), médiale (D), inférieure (E) et supérieure (F). Échelle : 1 cm.

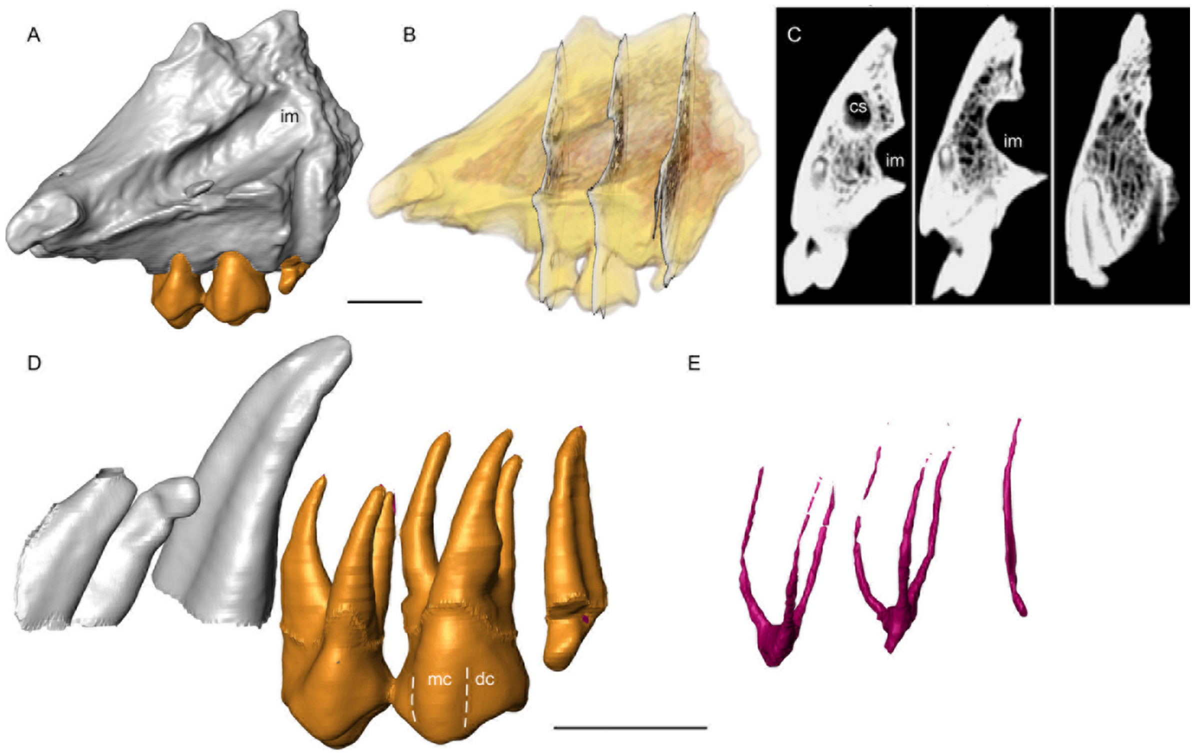

Fig. 3. (Color online). CT-based virtual rendering of SIM III-13-1. The specimen in medial view showing the inferior meatus (A); the specimen (medial view) in semi-transparency with indication of the position of the three coronal sections through the P3, the P4, and the M1 illustrated in (C); virtual filling of the sockets (from left to right) of the central and lateral incisors and the canine (in grey) and 3D rendering of the preserved P3, P4, and M1 (gold) (D); the pulp cavity (from left to right) of the two premolars and the M1 mesial root (E). cs: Canine socket; dc: distal cleft; im: inferior meatus; mc: mesial cleft. Scale bars: 1 cm.

Fig. 3. (Couleur en ligne). Rendu virtuel de SIM III-13-1 d'après les examens CT. Le spécimen en vue médiale, montrant le méat nasal inférieur (A) ; le spécimen (vue médiale) en semi-transparence, avec la position des trois sections coronales passant par la P3, la P4 et la M1, illustré en (C) ; remplissage virtuel de l'alvéole (de gauche à droite) des incisives centrale et latérale et de la canine (en gris) et le rendu 3D des P3, P4 et M1 encore présentes (doré) (D) ; la cavité pulpaire (de gauche à droite) des deux prémolaires et de la racine mésiale de la M1 (E). cs : Alvéole de la canine ; dc : fente distale ; im : méat inférieur ; mc : fente mésiale. Échelle: 1 cm.

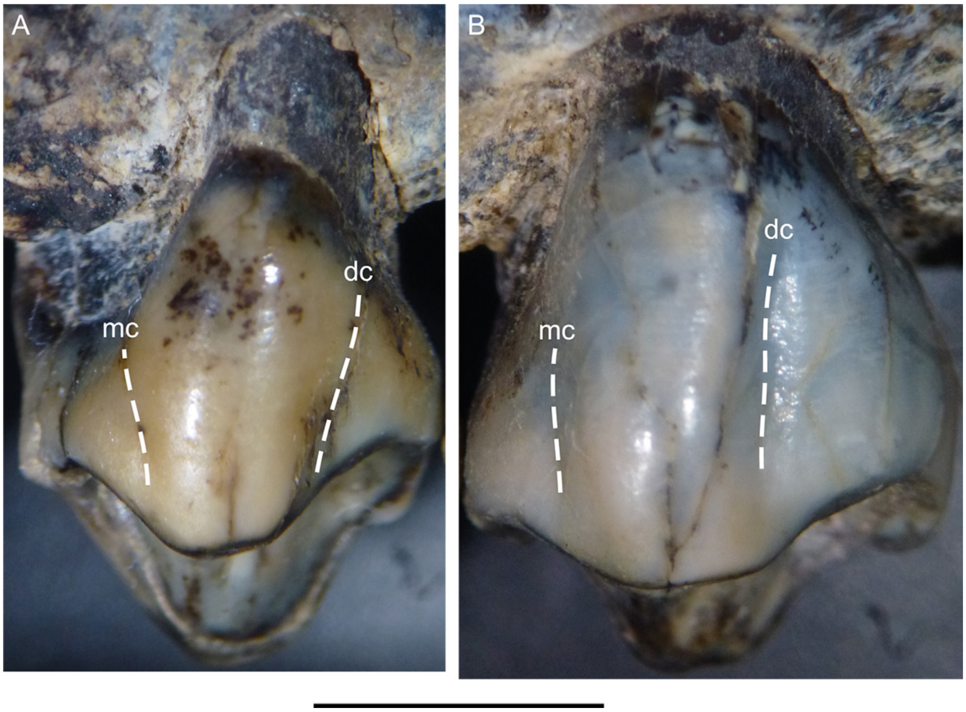

Fig. 4. (Color online). SIM III-13-1. The upper P3 (A) and P4 (B) crowns in lingual view exhibiting a distinct mesial (mc) and a distal cleft (dc). Scale bar: 5 mm.

Fig. 4. (Couleur en ligne). SIM III-13-1. Les couronnes de la P3 (A) et de la P4 (B) supérieures en vue linguale, montrant des fentes mésiale (mc) et distale (dc) distinctes. Échelle : 5 mm.

nearly complete to the alveolar level. The outlines of their roots, rendered by virtually filling the entirely preserved empty sockets (Fig. 3D), reveal a long axis bending distally, notably that of the lateral incisor. Based on the depth of its alveolus used here as a proxy, the estimated length of the canine root (20.5 mm) is compatible with the size of a female cercopithecoid individual (Swindler, 2002).

The P3 is complete and rather well preserved, even if a longitudinal breakage crossing the paracone apex runs mesiodistally through the whole crown and also affects part of the root. The enamel shows no evidence of hypoplasia or other developmental defects; some perikymata are noticeable at c. 2/3 distance from the cervix. The crown, showing an ovoid outline in occlusal view, has a mesiodistal (MD) diameter of 7.6 mm, a buccolingual (BL) diameter of 8.3 mm, and a buccal height of 8.0 mm. While moderately worn and bearing a small dentine spot (Fig. 2E), both main cusps are still high and relatively sharp (Fig. 4A), the paracone being slightly higher than the protocone. A small parastyle and a distostyle lie mesially and distally to the paracone, respectively. Together with a high, thick and slightly incised transverse crest, the lower, thinner and complete mesial marginal ridge encloses a triangular-shaped small and shallow mesial fovea. Conversely, the distal fovea is relatively large, shallow and sub-rectangular, closed by a low, moderately thick and complete distal marginal ridge. Two vertical clefts run on the mesial and distal aspects of the lingual protocone pillar (Fig. 4A). The virtually extracted roots reveal a mesiobuccal, a distobuccal, and a lingual branch (Fig. 3D). The pulp cavity bears two horns in correspondence of the paracone and the protocone and separates apically into three canals filling each root branch (Fig. 3E).

The P4 crown, whose MD diameter measures 8.8 mm, entirely lacks its buccal aspect (Fig. 2E) because of a relatively fresh mesiodistal fracture through the paracone which has exposed a nearly perfectly preserved enamel section (Fig. 5). On this section, maximal radial thickness corresponds to 0.9 mm, on the mesial, and 1.6 mm, on the distal aspect, respectively, while sub-apical radial thickness measured at the mesial aspect of the paracone equals 0.5 mm. The preserved portion of this tooth shows similar outer and inner features as seen in the P3 (Fig. 3D–E), including a developed mesial and distal cleft on the lingual aspect, a deep distal fovea and a well-developed continuous transverse crest joining the two cusps (Fig. 4B).

4.2. *Comparisons and taxonomic assessment*

We compared for its general morphology and detailed structural features the late Early Pleistocene specimen SIM III-13-1 from Simbiro with the record from a number of Plio-Pleistocene and extant cercopithecoid taxa (Table 1; Figs. 6–8). Besides the maxillary fragment of *Theropithecus* cf. *oswaldi* from Garba XII J, at Melka Kunture (Geraads, 1979; Geraads et al., 2004a), the comparative fossil record used in this study samples colobine and papionin specimens from eastern (Dechow and Singer, 1984; Delson, 1984, 1988; Frost, 2001, 2007; Frost and Alemseged, 2007;

Table 1
Crown dimensions (mesiodistal, MD, and buccolingual, BL, diameters, in mm) of the upper P3 and P4 of the specimen SIM III-13-1 from Simbiro compared to the estimates from some Plio-Pleistocene and extant cercopithecoid specimens/samples. M, male; F, female.
Tableau 1
Dimensions des couronnes (diamètres mésio-distal, MD, et bucco-lingual, BL, en mm) des P3 et P4 supérieures du spécimen SIM III-13-1 de Simbiro, comparées aux estimations pour des spécimens/échantillons cercopithécoïdes du Plio-Pléistocène et actuels. M, mâle ; F, femelle.

Specimen/taxon	Location/chronology	UP3						UP4			Source
		n	MD	sd	n	BL	sd	n	MD	sd	
SIM III-13-1	Simbiro/late Early Pleistocene		7.6			8.3			8.8		present study
Cercopithecoides kimeui	Koobi Fora/Early Pleistocene							2	7		Jablonski and Leakey, 2008
cf. *Chlorocebus* aff. *aethiops*	Afar/Middle Pleistocene	2	3.1		2	4.4		3	3.6		Frost and Alemseged, 2007
Colobus cf. *angolensis*	Afar/Middle Pleistocene	3	5.0		3	5.4		6	4.9	0.5	Frost, 2001
Lophocebus cf. *albigena*	Koobi Fora/Early Pleistocene	4	5.5		4	5.9		8	5.9	0.4	Jablonski and Leakey, 2008
Papio hamadryas ssp.	Asbole/Middle Pleistocene	2	5.9		1	7.1		2	6.3		Frost and Alemseged, 2007
Theropith. cf. *oswaldi*	Garba XII J/Early Pleistocene	1	8.7		1	10.0		1	10.0		Geraads, 1979
Theropith. oswaldi darti	Afar/Pliocene	5	7.0	0.5	5	7.8	0.5	9	7.3	0.7	Frost, 2001
Theropith. oswaldi ssp.	Swartkrans/Early Pleistocene	6	8.4	0.3	5	9.3	0.3	7	9.2	0.4	Delson, 1993
Theropith. oswaldi oswaldi	Afar/Early Pleistocene	5	7.4	0.7	5	9.1	0.8	6	7.9	0.6	Frost, 2001
Theropith. oswaldi leakeyi	Afar/Middle Pleistocene	4	8.0		4	10.6		2	9.8		Frost, 2001
Theropith. atlanticus	Ahl al Oughlam/Middle Pleistocene	1	8.6		1	9.4		2	10.3		Alemseged and Geraads, 1998
Theropith. brumpti	Koobi Fora/Plio-Pleistocene	3	6.4		3	7.1		3	7.2		Jablonski and Leakey, 2008
Chlorocebus aethiops M	extant	21	4.0	0.4	25	4.3	0.6	27	4.3	0.3	Swindler, 2002
Chlorocebus aethiops F	extant	11	3.6	0.4	20	3.9	0.5	19	3.9	0.4	Swindler, 2002
Colobus polykomos M	extant	49	5.3	0.6	48	5.6	0.5	47	5.2	0.3	Swindler, 2002
Colobus polykomos F	extant	29	5.1	0.3	29	5.4	0.5	28	5.1	0.3	Swindler, 2002
Lophocebus albigena M	extant	30	5.4	0.5	29	5.8	0.3	30	4.7	0.3	Swindler, 2002
Lophocebus albigena F	extant	28	4.9	0.3	29	5.4	0.3	29	4.5	0.3	Swindler, 2002
Papio cynocephalus M	extant	31	7.3	0.6	33	7.9	0.5	34	7.7	0.4	Swindler, 2002
Papio cynocephalus F	extant	31	6.5	0.4	32	7.2	0.5	32	7.1	0.4	Swindler, 2002
Theropith. gelada M	Ethiop. highlands/extant	25	6.8	0.7	28	7.2	0.4	12	7.2	0.4	Swindler, 2002
Theropith. gelada F	Ethiop. highlands/extant	11	6.2	0.4	24	6.7	0.4	8	7.0	0.3	Swindler, 2002

Fig. 5. SIM III-13-1. Buccal view of the naturally fractured upper P4 crown revealing the enamel thickness topographic variation. mes: mesial; dis: distal. Scale bar: 0.5 mm.
Fig. 5. SIM III-13-1. Vue buccale de la couronne de la P4 supérieure naturellement fracturée, révélant les variations topographiques d'épaisseur de l'émail. mes : mésial ; dis : distal. Échelle : 0.5 mm.

Frost and Delson, 2002; Frost et al., 2014; Gilbert and Frost, 2008; Harrison and Harris, 1996; Jablonski and Leakey, 2008; Rook et al., 2010), southern (Dechow and Singer, 1984; Delson, 1984, 1988; Delson, 1993), and northwestern Africa (Alemseged and Geraads, 1998; Dechow and Singer, 1984; Delson and Hoffstetter, 1993).

The moderately prognathic profile of SIM III-13-1 (facial angle of c. 50°) and its absolutely small and short canine alveolus are compatible with the condition seen in likely female specimens attributed to *T. o. oswaldi* (spec. SK 561 from Swartkrans) and *T. o. darti* (spec. M 3073 from Makapansgat), as well as in *Cercopithecoides williamsi* (spec. STS 394A from Sterkfontein) (Fig. 6A). Also, given its lack of maxillary fossa and ridges (relatively flat and smooth maxillary outline), SIM III-13-1 is similar to the morphology of extant *T. gelada*, *Macaca fascicularis*, *Colobus guereza*, *Chlorocebus aethiops* and *Lophocebus albigena*, but distinct from that of *Papio anubis* where, in association with a maxillary ridge running along the muzzle dorsum from the line of the canine eminence to the origin of the muzzle below the infraorbital margin, a relatively deep fossa extending just behind the canine to the level of the third molar is commonly found (Jablonski, 2002; Szalay and Delson, 1979)

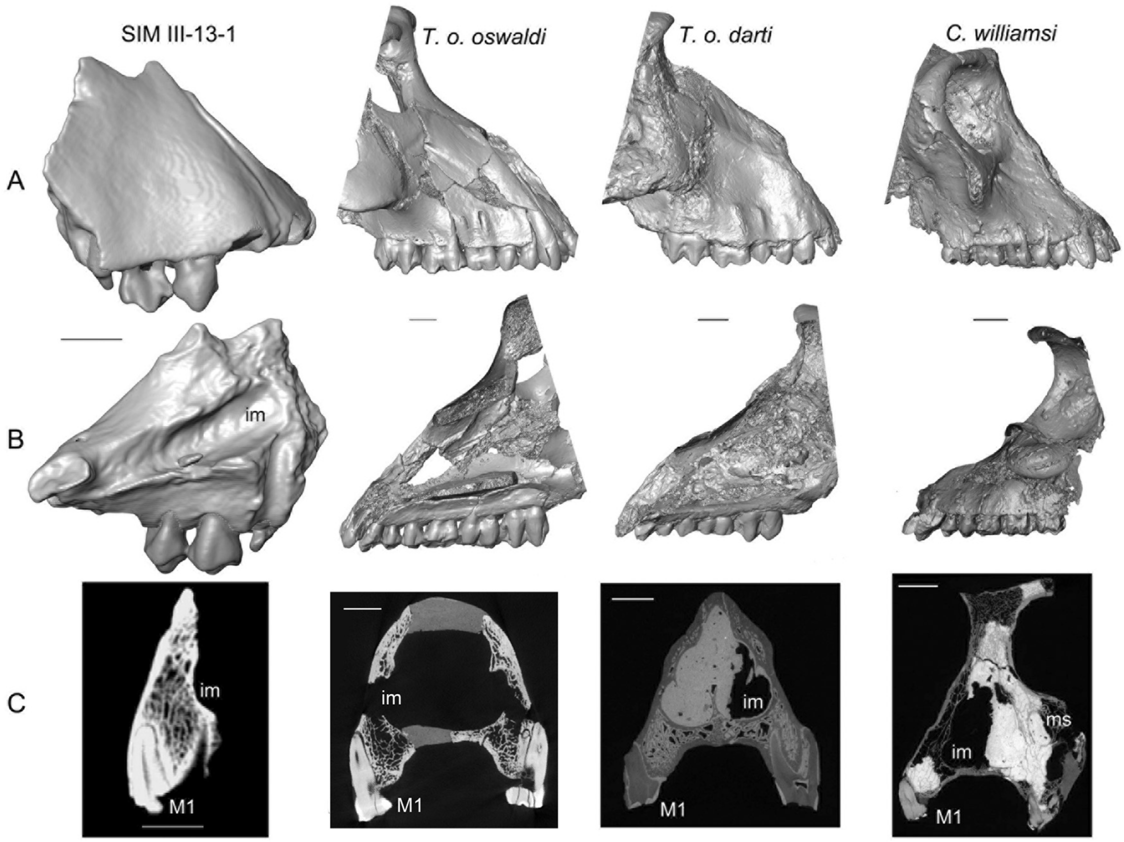

Fig. 6. (Color online). Outer and inner morphology of SIM III-13-1 compared to three South African Plio-Pleistocene specimens representing *Theropithecus oswaldi oswaldi* (SK 561 from Swartkrans), *T. o. darti* (M 3073 from Makapansgat) and *Cercopithecoides williamsi* (STS 394A from Sterkfontein). Lateral (A) and medial (B) aspects of the maxillary region; CT-based coronal section through the M1 mesial root (C). im: Inferior meatus; ms: maxillary sinus. Scale bars: 1 cm.

Fig. 6. (Couleur en ligne). Morphologies externe et interne de SIM III-13-1, comparées à celles de trois spécimens sud-africains du Plio-Pléistocène représentant *Theropithecus oswaldi oswaldi* (SK 561 de Swartkrans), *T. o. darti* (M 3073 de Makapansgat) et *Cercopithecoides williamsi* (STS 394A de Sterkfontein). Aspects latéral (A) et médial (B) de la région maxillaire; section coronale par CT passant par la racine mésiale de la M1 (C). im : Méat inférieur ; ms : sinus maxillaire. Échelles : 1 cm.

(Figs. 6A and 7A). However, because of its sex-related variable degree of expression observed in extant baboon taxa (Dechow and Singer, 1984), this feature is of only modest diagnostic value in taxonomic assessments.

The lack of a maxillary sinus in SIM III-13-1 (Fig. 6 C) is shared with fossil and extant *Theropithecus*, *Papio*, *Chlorocebus*, *Lophocebus* and *Colobus* species, whereas this structure, while variably positioned and developed, is commonly present in South and East African forms of *Cercopithecoides* and in extant *Macaca* (Kuykendall and Rae, 2008; Nishimura et al., 2007; Rae, 2008) (Figs. 6B–C and 7B–C).

The well-preserved P3 from Simbiro exhibits a proportionally large and elevated protocone, a paraloph between the two cusps separating a small mesial fovea, and a larger trigon basin, features also partially preserved on the P4. This condition, which is clearly distinct from the morphology seen in Colobinae members (Delson, 1973, 1975; Swindler, 2002), is similar to that displayed by extinct *Theropithecus* taxa, even if the columnar aspect of the protocone and the enamel infolding are usually expressed to a greater extent in this latter genus (Jablonski, 1993; Jolly, 1972). More importantly, both premolar crowns in SIM III-13-1 show a fully developed mesial and distal cleft on their lingual aspect (Fig. 4), a morphological combination typical of *Theropithecus* but absent in other papionin taxa, where only a distolingual cleft is commonly found (Delson, 1973; Swindler, 2002).

Comparative P3 and P4 crown dimensions measured in the specimen from Simbiro and in a number of extinct and extant cercopithecoids are summarized in Table 1 and the related adjusted Z-scores shown in Fig. 8. The diameters of SIM III-13-1 exceed the estimates reported for fossil *P. hamadryas* (*P. hamadryas ssp.*), extant and extinct colobine species (*Col.* cf. *angolensis* and *Col. polykomos*), and the *Lophocebus* and *Chlorocebus* specimens/samples included in this study. They also exceed the male values of some extant papionins, such as *T. gelada* and *P. cynocephalus*. Conversely, the diameters are compatible with the size variation range expressed by fossil *Theropithecus* taxa (Fig. 8), the closest fit being the Early Pleistocene *T. o. oswaldi* sample from the Afar region (Frost, 2001).

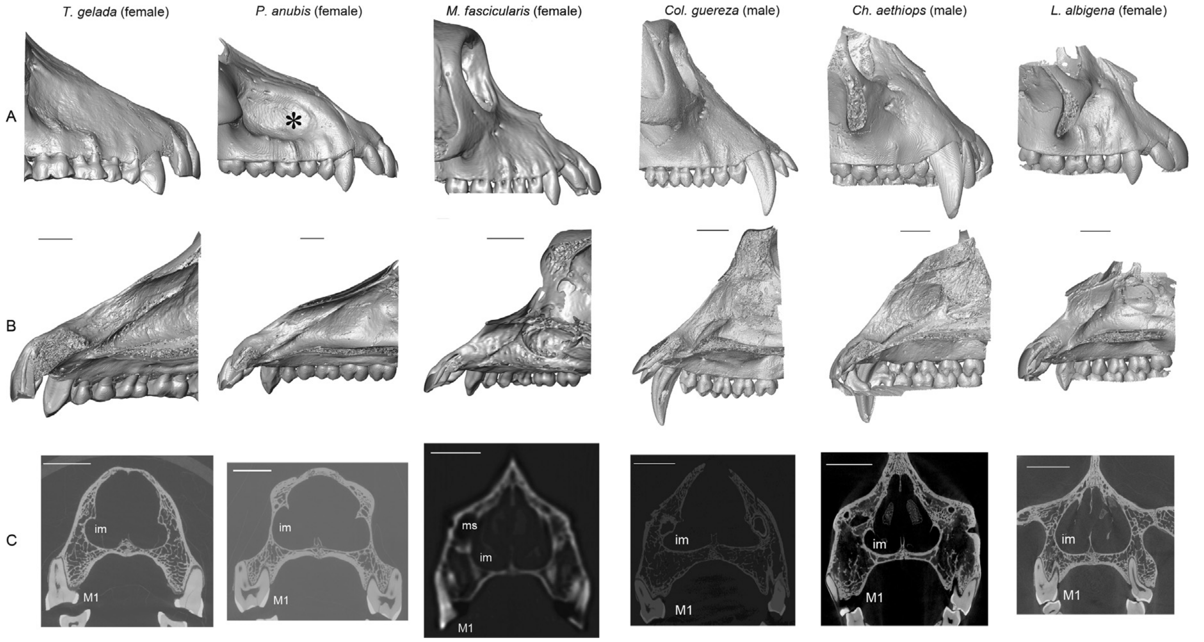

Fig. 7. Comparative outer and inner morphology of the maxillary region in six cercopithecoid specimens representing extant *Theropithecus gelada*, *Papio anubis*, *Macaca fascicularis, Colobus guereza, Chlorocebus aethiops, Lophocebus albigena*. Lateral (A) and medial (B) aspects; CT-based coronal section through the first molar (M1). In the *P. anubis* representative, the position of the maxillary fossa is indicated by a black asterisk. im: inferior meatus; ms: maxillary sinus. Scale bars: 1 cm.

Fig. 7. Morphologies comparatives externe et interne de la région maxillaire chez six spécimens cercopithécoïdes actuels, représentant *Theropithecus gelada*, *Papio anubis*, *Macaca fascicularis, Colobus guereza, Chlorocebus aethiops, Lophocebus albigena*. Aspects latéral (A) et médial (B); section coronale par CT passant par la racine mésiale de la M1 (C). Chez le représentant de *P. anubis*, la position de la fosse maxillaire est indiquée par un astérisque noir. im : méat inférieur ; ms : sinus maxillaire. Échelles: 1 cm.

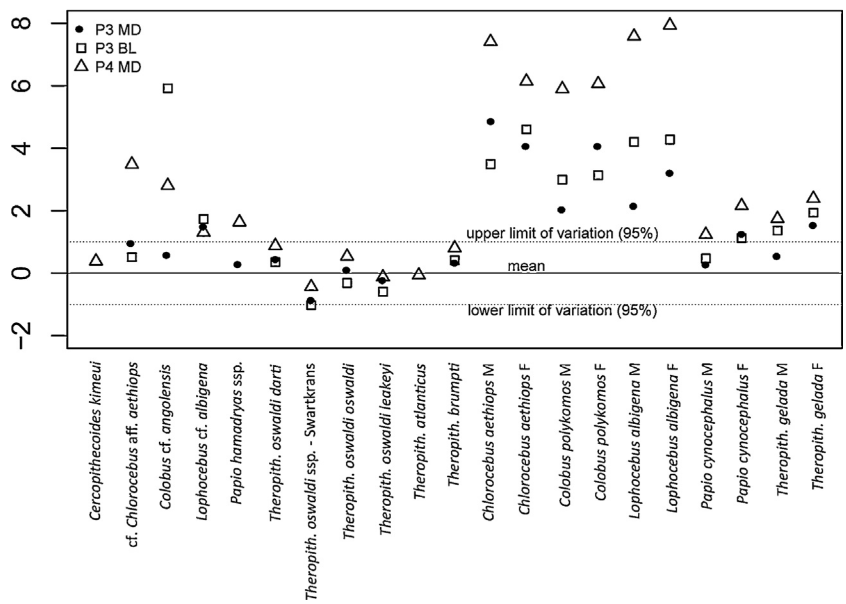

Fig. 8. Adjusted Z-scores of the upper P3 and P4 mesiodistal (MD) and buccolingual (BL) crown diameters in SIM III-13-1 compared to the figures from eleven Plio-Pleistocene and five extant cercopithecoid specimens/samples (see Table 1). M, male; F, female.

Fig. 8. Écarts réduits ajustés des diamètres mésio-distal (MD) et bucco-lingual (BL) des P3 et P4 supérieures de SIM III-13-1, comparés à ceux de onze spécimens/échantillons cercopithécoïdes du Plio-Pléistocène et actuels (voir Tableau 1). M, mâle ; F : femelle.

Table 2
Comparative estimates of crown tissue proportions (a, b, EDJL) and enamel thickness (AET, RET and maximum linear thickness) assessed in the P4 of SIM III-13-1, in two South African Plio-Pleistocene specimens and in four representatives of extant cercopithecoids. See the text (section 3) for the meaning of the variables. M, male; F, female.
Tableau 2
Estimations comparatives des proportions des tissus de la couronne (a, b, EDJL) et de l'épaisseur de l'émail (AET, RET et épaisseur linéaire maximale), évaluées pour la P4 de SIM III-13-1, chez deux spécimens sud-africains du Plio-Pléistocène et chez quatre représentants actuels de cercopithécoïdes. Voir le texte (section 3) pour la définition des variables. M, mâle ; F, femelle.

Specimen/taxon	Location/chronology	a (mm^2)	b (mm^2)	EDJL (mm)	AET (mm)	RET	ET max. (mm)
SIM III-13-1	Simbiro/late Early Pleisto.	11.3	28.5	16.4	0.7	12.9	1.6
Theropith. oswaldi oswaldi (SK 561)	Swartkrans Mem. 1/Early Pleisto.	9.5	23.9	17.7	0.5	11.0	0.9
Theropith. oswaldi darti (M 3073)	Makapansgat Mem. 4/Plio.-Pleisto.	8.6	23.0	15.6	0.6	11.5	1.0
Theropith. gelada M	Ethiop. highlands/extant	7.5	17.7	12.9	0.6	13.9	1.0
Papio cynocephalus F	Congo/extant	7.5	13.2	11.8	0.6	17.4	1.0
Colobus guereza M	Congo/extant	4.0	11.2	10.0	0.4	12.0	0.5
Chlorocebus aethiops M	Senegal/extant	3.1	8.0	8.9	0.4	12.4	0.9
Lophocebus albigena F	Cameroon/extant	5.2	10.0	9.1	0.6	18.1	1.1

Both premolars of the *T.* cf. *oswaldi* maxillary specimen collected at the site of Garba XII, few kilometres apart from Simbiro in the Melka Kunture area (Fig. 1B), exhibit larger crown dimensions than measured in SIM III-13-1 (Geraads, 1979; Geraads et al., 2004a) (Table 1), but comparable proportions and very similar occlusal morphology (Geraads, 1979: planche I, fig. 1).

To the best of our knowledge, comprehensive information on enamel thickness topographic variation assessed in the upper P4s of nonhominin primate taxa is not available. For the specific purposes of the present study, comparative estimates of crown tissue proportions and enamel thickness (AET and RET) assessed in the SIM III-13-1's P4 and in a limited number of South African fossil (*T. o. oswaldi* and *T. o. darti*) and extant African cercopithecoids (*T. gelada*, *P. cynocephalus*, *Col. guereza*, *Ch. aethiops*, *L. albigena*) are shown in Table 2. Despite our very limited comparative framework, we note that the specimen from Simbiro displays the highest value for the maximum linear enamel thickness (1.6 mm measured on the distal aspect). More interestingly, combined enamel thickness values in SIM III-13-1, including the scale-free RET, which indicates intermediate-thin enamel compared to other papionins (Kay, 1981; Swindler and Beynon, 1993), fit the estimates obtained for the two fossil *Theropithecus* and the living gelada specimen (Table 2).

5. Conclusive remarks

The absence of maxillary sinus and the presence of a well-developed protocone on both premolars exclude SIM III-13-1 from representing a fossil colobine (Kuykendall and Rae, 2008; Rae, 2008; Swindler, 2002) but rather indicate affinities with the Papionini tribe. The specimen from Simbiro also shows marked mesial and distal clefts running sub-vertically along the lingual aspect of both premolars, as typically found in the genus *Theropithecus* (Delson, 1973; Jolly, 1972). In our comparative analysis, this affinity is also supported by measures of the premolar and molar crown dimensions, as well as by the assessment of the enamel thickness of the P4 crown.

Previous research in the Melka Kunture site area provided the distal portion of a lower M3 crown (GAR IVD-74-7596) and a right maxillary fragment (GAR XIIJ-78-1952) bearing the erupting P3 and P4 and the M1 in functional occlusion (Geraads, 1979; Geraads et al., 2004a). The M3 crown comes from the D level of Garba IV (the "Garba IV excavation datum", in Morgan et al., 2012: fig. 2 C), sandwiched between the <1.719 ± 0.199 Ma *Grazia tuff* and a <1.429 ± 0.029 Ma overlying tuff, while the maxillary fragment, penecontemporaneous with SIM III-13-1, comes from a late Early Pleistocene level at Garba XII which underlies a tuff dated to 0.772 ± 0.091 Ma (Morgan et al., 2012). Both specimens were originally attributed to *Theropithecus* (*Simopithecus*) *brumpti* or *oswaldi* (Geraads, 1979). However, given that the former taxon is essentially known from deposits of the Omo Valley and the Turkana Basin (Jablonski, 2002; Leakey, 1993), while the second is widely spread in the African Early-Middle Pleistocene, a more likely attribution to *T.* cf. *oswaldi* has been proposed (Geraads et al., 2004a). Accordingly, based on the currently available evidence, we also preliminary allocate the specimen SIM III-13-1 to *Theropithecus* sp. cf. *oswaldi* Andrews, 1916.

Besides enlarging the scanty Catarrhine fossil record from the Ethiopian highlands, the interest of the cercopithecid from Simbiro is twofold: together with the late Early Pleistocene specimen from Garba XII and the c. 1 Ma old cranial fragment UA-463 from Uadi Aalad, Buia, Eritrea (Rook et al., 2010), SIM III-13-1 likely documents one of the last occurrences of *Theropithecus* cf. *oswaldi* in East Africa (Jablonski, 1993; Jablonski and Frost, 2010; Rook et al., 2010). Additionally, given that *Theropithecus* fossils in Quaternary African deposits are often associated with remains belonging to the genus *Homo* (Rook et al., 2010), the presence of spread lithic industry and of relatively well preserved mammal remains at Simbiro III strengthens the possibility of recovering in the future some human fossil specimens in this promising but still poorly explored fossiliferous area at Melka Kunture.

Besides the 1.2–1.6 Ma isolated calcaneus likely representing *Theropithecus* from Ubeidiya, Israel (Belmaker, 2010), a few late Early Pleistocene remains sampling this large-bodied cercopithecine taxon are known also from extra-African deposits. In Spain, associated to some taxonomically controversial tooth and postcranial remains

(Ferràndez-Cañadell et al., 2014; Gibert et al., 1995; Martínez-Navarro et al., 2005, 2008), a maxillary P4 of *T. oswaldi leakeyi* was recently reported from Cueva Victoria (Ferràndez-Cañadell et al., 2014). While its crown is elongated mesiodistally compared to SIM III-13-1 (9.5 vs. 8.8 mm), it is morphologically similar to the Ethiopian specimen because of the presence of two clefts on both sides of the lingual protocone pillar and of a paraloph between the two cusps. Additionally, the c. 1 Ma old *T. oswaldi delsoni* maxilla preserving two molar teeth from the Mirzapur area (Delson, 1993; Gupta, 1977) shows that, at the same time, the genus occurred also in the north-eastern part of the Indian subcontinent.

African papionins, particularly *Theropithecus*, have been historically used as reference model for assessing different aspects of early hominin biohistory. Indeed, valuable ecological, biogeographical and evolutionary information has been inferred from the cercopithecoid fossil record based on the evidence that monkey taxa underwent selection pressures and radiations similar to those associated with early hominins, thus mirroring, to some extent, the population structural patterns, migration dynamics and speciation events occurred in hominin evolution (e.g., Elton, 2006; Jolly, 1970, 2001; Kopp et al., 2014; Strait and Wood, 1999; Turner and Wood, 1993). Therefore, besides contributing to the reconstruction of catarrhine paleobiodiversity and time-related adaptive trends, the discovery and accurate identification of new cercopithecoid fossil specimens from well-constrained geo-chronological contexts also add to our comprehension of hominin evolution.

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