Reassessment of Olduvai Bed I cercopithecoids: a new biochronological and biogeographical link to the South African fossil record

Christopher C. Gilbert^{a,b,c,d*}, Stephen R. Frost^e, and Eric Delson^{b,d,f,g,h}

^aDepartment of Anthropology, Hunter College of the City University of New York, 695 Park Avenue, New York, NY 10065, USA

^bPhD Program in Anthropology, Graduate Center of the City University of New York, 365 Fifth Avenue, NY 10016, USA

^cPhD Program in Biology, Graduate Center of the City University of New York, 365 Fifth Avenue, NY 10016, USA

^dNew York Consortium in Evolutionary Primatology

^eDepartment of Anthropology, University of Oregon, Eugene, Oregon, 97403, USA

^fDepartment of Anthropology, Lehman College of the City University of New York, 250 Bedford Park Boulevard West, Bronx, NY 10468, USA

^gDepartment of Vertebrate Paleontology, American Museum of Natural History, Central Park West, New York, NY 10024, USA

^hInstitut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain

* Corresponding author

E-mail address: cgilbert@hunter.cuny.edu

ABSTRACT

Fossil monkeys have long been used as important faunal elements in studies of African Plio-Pleistocene biochronology, particularly in the case of the South African karst cave sites. Cercopithecoid fossils have been known from Tanzania's Olduvai Gorge for nearly a century, with multiple taxa documented including *Theropithecus oswaldi* and *Cercopithecoides kimeui*, along with papionins and colobines less clearly attributable to species. A small number of large papionin fossils, including a partial male cranium and partial female skull, have been previously identified as an early form of *Papio*, but noted as distinct from extant baboons as well as other fossil *Papio* species. In 2013 we reviewed the Olduvai cercopithecoid material at the National Museum of Tanzania, with a particular focus on the specimens from Beds I – IV. Quantitative and qualitative comparisons of the Olduvai papionins largely confirmed previous observations, with one notable exception. The large papionin taxon from Bed I previously recognized as *Papio* sp. is more properly recognized as *Gorgopithecus major*, a taxon previously known only from South Africa. Features shared between the Olduvai specimens and *G. major* include relatively short and concavo-convex tubular nasals, antero-posteriorly curved upper incisor roots, downwardly curved brow ridges in the midline, and robust zygomatic arches. The recognition of *G. major* at Olduvai Bed I, a well-known horizon with precise radiometric dates, provides an important biochronological and biogeographical link with South African localities and suggests an age ~1.89-1.63 Ma for Kromdraai A, Swartkrans Member 1 and possibly Swartkrans Members 2-3 and Cooper's A and D.

Keywords: cercopithecoid, papionin, crania, *Gorgopithecus*, baboons, Pleistocene

Introduction

Because they are widely present and abundant members of the African Plio-Pleistocene fossil record, cercopithecoid monkeys have played an important role in African biochronology, particularly for many South African localities (e.g., Delson, 1984, 1988; McKee, 1993; McKee et al., 1995; Herries et al., 2009, 2013). Although over one-third of known Plio-Pleistocene cercopithecoid genera are shared between eastern and southern Africa, only five of approximately 45 described species are found in both geographic regions: *Parapapio jonesi*, *Soromandrillus quadratiostris*, *Papio hamadryas*, *Cercopithecoides williamsi*, and *Theropithecus oswaldi*¹ (e.g., Delson, 1984; Benefit, 1999; Frost, 2007; Jablonski and Frost, 2010; Gilbert, 2013). Among these, only *T. oswaldi* is widely distributed in both regions, leading to a relative dearth of biochronologically significant species aiding in age estimation across Plio-Pleistocene African sites (Delson, 1984; Frost, 2007; Jablonski and Frost, 2010). Here we provide evidence that *Gorgopithecus major*, a genus and species assumed, for the past half-century, to be endemic to South Africa (e.g., Freedman, 1957; Szalay and Delson, 1979; Delson, 1984, 1988; Jablonski, 2002; Jablonski and Frost, 2010), is also present at Bed I Olduvai Gorge, thereby providing an additional time-sensitive link between eastern and southern African hominin-bearing localities.

Brief background of fossil monkeys at Olduvai

¹Harris et al. (1988) recognized cf. *Parapapio whitei* from fragmentary remains that we consider undiagnostic (Frost 2001, 2007). *S. quadratiostris* is found in Angola, not South Africa proper. In this paper, we recognize *T. oswaldi* as an evolving lineage with at least three time-successive chronosubspecies: *T. o. darti*, *T. o. oswaldi*, and *T. o. leakeyi*. See also Leakey (1993), Delson (1993), Frost and Delson (2002), Jablonski (2002), Jablonski and Frost (2010), and Frost et al. (2014).

Fossil cercopithecoids have been known from Olduvai Gorge since the early 20th Century, including well-documented taxa such as *Theropithecus oswaldi* and *Cercopithecoides kimeui* (e.g., Remane, 1925²; Hopwood, 1934; Leakey and Whitworth, 1958; Jolly, 1972; Leakey and Leakey, 1973a,b; 1976; Leakey, 1982). A number of other cercopithecoid specimens are less clearly attributable to specific taxa, but several craniodental fossils from Bed I (male partial cranium OLD/69 S.196, female partial skull FLK NNI 1011, maxillary fragment OLD/69 S.193, and mandibular fragment OLD/61 2968) representing a large papionin taxon were described by Leakey and Leakey (1976) as cf. *Papio* sp. nov., suggesting a new species similar to *Papio* but distinct from other known extant and fossil baboon populations. In general agreement with Leakey and Leakey (1976), Delson (1984) referred to these perplexing Bed I papionin specimens as ?*Papio* sp. indet., again indicating that the specimens seemed similar to *Papio*, yet slightly different. A contrasting opinion was expressed by Eck and Jablonski (1984), who attributed the large papionin specimens to *T. oswaldi*, which is common at Olduvai, although the morphological justifications for their reassignments were not specified and the specimens do not display the distinctive *Theropithecus* tooth enamel pattern. Most recently, Frost (2007) linked OLD/69 S.196 to *Papio* as “*Papio (Papio)* sp. Olduvai”, but did not comment on the other specimens.

In 2013 we reviewed the Olduvai cercopithecoid collection at the National Museum of Tanzania (NMT) as a part of a larger project on African Plio-Pleistocene

²Remane (1925) reported a well-preserved partial cranium of a juvenile papionin that seems to represent an extant subspecies of *Papio hamadryas*, although its exact identity has never been determined. The specimen was said to derive from Bed IV, which has since been subdivided. Thus its precise horizon and taxonomy are both unclear at this time.

cercopithecoid systematics and biochronology. While our observations largely corroborated previous studies, particularly in the overwhelming abundance of *T. oswaldi* and presence of *C. kimeui*, we noted a number of shared derived characters uniting the disputed large papionin specimens from Olduvai with *G. major*. In this study, we document these similarities in a series of qualitative and quantitative comparisons and conduct a phylogenetic analysis based on our observations. Because the geological age of Olduvai Bed I is tightly constrained by radiometric dates to between 1.79 and 2.03 millions of years ago (Ma; Deino, 2012; McHenry, 2012), any taxonomic link between Olduvai Bed I and the South African karsts is biochronologically significant and may help refine age estimates for any site where *G. major* is positively identified.

Materials and methods

Fossil specimens examined in this study derive from collections at the Ditsong National Museum, Pretoria (formerly Transvaal Museum), University of the Witwatersrand Anatomy Department, Johannesburg (UW-AD), and NMT, Dar es Salaam. Digital calipers were used to collect standard craniometric measurements, and qualitative characters were scored according to the criteria described in Gilbert (2013). Comparative measurements were also taken from the PRIMO online database (<http://primo.nycep.org>) and Gilbert (2013). For taxonomic comparison, 10 measurements available on a large number of extant and fossil taxa, including the Olduvai Bed I specimens, were collected: minimum frontal breadth, biporion, bizygion, bizygomaxillare, maximum orbit height, malar height, zygomaxillare-porion, nasion-rhinion, nasion-prosthion, and biectomolare. A geometric mean of these 10

measurements was then calculated for each specimen as a representation of cranial size. Bivariate regressions plotting distinctive *G. major* male cranial measurements versus size were created to evaluate the Olduvai male OLD/69 S.196 relative to other papionin males and *G. major* from South Africa. To consider all of the available cranial shape data simultaneously, a number of cranial shape indices were created by dividing raw cranial measurements by the geometric mean (GM; i.e, Mosimann shape variables) or another variable for each specimen, and a principal components analysis was conducted on the resulting 11 cranial shape variables: relative postorbital constriction (minimum frontal breadth/GM), relative calvarial width (biporion/GM), relative zygomatic width (bizygion/GM), relative facial breadth (bizygomaxillare/GM), relative orbit size (maximum orbit height/GM), relative malar height (malar height/GM), relative calvarial length (zygomaxillare-porion/GM), relative nasal length (nasion-rhinion/nasion-prosthion), relative sagittal nasal length (nasion-rhinion/GM), relative snout/muzzle length (nasion-prosthion/GM), and relative palate breadth (biectomolare/GM). The bivariate regressions and principal components analysis (PCA) were performed in PAST 3.07 (Hammer et al., 2001).

In addition to craniometric comparisons, a 362 character phylogenetic analysis, including 24 extant and fossil cercopithecoid taxa plus the Olduvai large papionin as a distinct operational taxonomic unit (OTU), was conducted in PAUP* 4.10b. A 1,000 replication heuristic search was employed using the random addition sequence option with *Victoriapithecus*, *Allenopithecus*, *Parapapio lothagamensis*, and *Macaca* constrained as successive outgroups to find the most parsimonious tree (MPT). In addition to the 318 craniodental characters listed in Gilbert (2013), 44 postcranial

characters (22 for each sex) previously noted to be phylogenetically informative were also added to the current matrix (see Pugh and Gilbert, 2015; Gilbert et al., 2016). These additional characters are listed in Table S1 of the Supplementary Online Material (SOM) and were scored for males and females separately, as previously described for craniodental data in Gilbert (2013). For clade support, a 1,000 replication bootstrap procedure with replacement was conducted, and decay indices (Bremer support values) were calculated. The matrix used in this study is provided as a nexus file in the SOM.

Results

Qualitatively, the Olduvai papionin specimens in question possess a number of features that, in combination, are shared only with *G. major* among known living and extinct taxa (Table 1). Many of these features were previously noted in the original descriptions by Leakey and Leakey (1976; pp. 128-129), such as “marked” maxillary fossae extending into the infraorbital plate, “wide” and “robust” zygomatic arches, male supraorbital tori more anteriorly and inferiorly oriented in the midline, and a “bulbous” muzzle dorsum that is not flat or slightly rounded, as typically seen in *Papio* ssp. We confirm these observations and note that they are also present and distinctive in *Gorgopithecus major* (Freedman, 1957; Szalay and Delson, 1979; Jablonski and Frost, 2010). In addition, we note that the two partial crania from Olduvai share narrow muzzles with little to no development of the maxillary ridges in males, relatively short nasals, peaked (i.e., tube-shaped) and concavo-convex nasal bones, antero-posteriorly curved upper incisor roots, and overall large size (see Table 1; Fig. 1).

Unfortunately, many craniodental measurements are unavailable for the fragmentary large Olduvai papionin specimens, but those that can be measured are provided in Table 2 (dentition) and Table 3 (face, snout, and palate). The best cranial specimens of *G. major* from South Africa are also fragmentary or, in the case of the adult male cranium from Kromdraai A (KA 192), heavily crushed and distorted. Thus, while quantitative comparisons are limited, measurements of the Olduvai specimens are either within the range of known *G. major* values or only slightly beyond it (Tables 2-3). Three other distinctive features described in Freedman's (1957) diagnosis of *G. major* include relatively short nasals, a relatively short muzzle, and an "exceptionally" narrow muzzle; we observe that this last point applies to the dorsal surface of the rostrum, in particular. Quantitative comparisons in Figures 2-4 relating to nasal length and muzzle length confirm Freedman's (1957) observations and demonstrate that OLD/69 S.196 shares these distinctive features with KA 192.

The shared distinctiveness of OLD/69 S.196 and KA 192 compared to other extant and fossil male papionin specimens is also revealed by a PCA of cranial shape variables (Fig. 5). In this analysis, PC 1 represents 69.9% of the variance and loads highest on snout length (0.60) and sagittal nasal length (0.59), and it is also strongly correlated with size as represented by the GM ($r=0.855$). PC 2 (15.6% of the variance) loads highest on zygomatic width (0.58) and postorbital constriction (-0.46). In PCA space, OLD/69 S.196 plots closest to KA 192, and both specimens are noticeably separated in the upper left quadrant from all other adult male papionin crania (Fig. 5). In particular, other large papionins plot on the positive end of PC 1, highlighting the positions for OLD/69 S.196 and KA 192 as clear outliers for their size.

Finally, a phylogenetic analysis was conducted using craniodental and postcranial characters, considering the Olduvai specimens as a separate OTU. Four MPTs were recovered, all of which supported the Olduvai specimens as the sister taxon to *G. major* with relatively high bootstrap values and Bremer support (Fig. 6).

Discussion

Shared features between the unusual Olduvai large papionin specimens, particularly the male partial cranium OLD/69 S.196 and female partial skull FLK NNI 1011, and *G. major* include antero-inferiorly oriented brow ridges in the midline, robust and flaring zygomatics, deep maxillary fossae invading the infraorbital plate, relatively short and narrow muzzles with little to no development of the maxillary ridges even in males, relatively short, peaked (tube-shaped) and concavo-convex nasal bones, antero-posteriorly curved upper incisor roots, and overall large size (Figs. 1-5). In all four MPTs of the phylogenetic analysis, the Olduvai specimens grouped with *G. major* (Fig. 6), and we therefore reassign the specimens to *G. major* pending additional data. The only obvious difference between the Olduvai *Gorgopithecus* specimens and the classic South African *G. major* specimens is that the maxillary fossae present in the Olduvai male are noticeably shallower than those typically seen in South African *G. major*. However, since there is only one male specimen at Olduvai, and because the female appears to demonstrate deep fossae (although filled with matrix, which could perhaps be virtually removed if the specimen were CT scanned), it is difficult to judge the range of variation in this feature within the Olduvai population. Other minor differences between the Olduvai cranium and the few South African specimens preserving cranial anatomy

include the presence of slight maxillary ridges in OLD/69 S.196 vs. little to no maxillary ridges present in KA 192, a post-orbital depression present in OLD/69 S.196 vs. more of a sulcus present in KA 192, and a few minor differences in quantitative character values that result in different codings due to the small sample sizes involved ($n=1$ for both populations in most cases) and the blunt nature of the general allometric coding method (see Gilbert et al., 2009). Because modern papionin species vary in all of these features, it seems reasonable at this time to assume that the Olduvai and South African specimens fit comfortably within the range of variation expected for a single species. If additional specimens confirm that the Olduvai series consistently have shallower fossae, more developed male maxillary ridges, and less developed post-orbital sulci than South African *G. major*, specific status for the Olduvai population may be necessary.

All of the specimens recognized here as *G. major* derive from Bed I. Most are from DK I and thus below Tuff IB, while FLK NNI 1011 is from FLK NNI which is between Tuffs IB and IC (Hay, 1976). These specimens therefore date to approximately 1.85 Ma (Deino, 2012). Leakey and Leakey (1976) also mentioned an additional large papionin specimen, OLD/69 S.61, a right M³ from surface of TK II in Bed II. This specimen is not included in *G. major* here. While OLD/69 S.61 may also be *G. major*, we have decided not to refer it at this time given the difficulty of diagnosing papionins based solely on teeth and the presence of other, similar-sized papionins known from eastern Africa at this time, such as *Papio* and *Soromandrillus* (Delson and Dean, 1993; Frost, 2001; 2007; Jablonski et al., 2008; Jablonski and Frost, 2010; Gilbert, 2013).

Due to the small number of shared cercopithecoid species between eastern and southern Africa during the Plio-Pleistocene, the recognition of *G. major* at Olduvai is

significant in that it provides a rare definitive link between a well-dated East African horizon and a number of South African fossil karsts, including Kromdraai A, Swartkrans Member 1, and possibly Swartkrans Members 2 – 3, Cooper’s A, and Cooper’s D, suggesting that some of these localities may be closer to ~1.85 Ma than recently argued (e.g., see Curnoe et al., 2001; Balter et al., 2008; DeRuiter et al., 2009; Herries et al., 2009, 2010, 2013). While African cercopithecoid and other large mammal species may typically persist for anywhere between ~0.5 – 2.3 million years according to one recent analysis (Bibi and Kiessling, 2015), and there is always some error associated with biochronological age estimates, cercopithecoids are common throughout the East African Plio-Pleistocene and yet *G. major* is found only at Bed I of Olduvai Gorge. This limited distribution in space and time does indeed suggest that its longevity was probably brief, making it a good species to use in biochronological analyses.

Recent biochronological analyses of Swartkrans Member 1 and Kromdraai A (and by extension Kromdraai B Members 1 – 3) have suggested age ranges of 2.36-1.65 Ma and 1.89-1.63 Ma, respectively (Herries et al., 2009). The presence of *G. major* at Olduvai Bed I provides another link and may help refine these estimates, suggesting that a more limited correlation with Bed I, Lower-Middle Bed II, Omo Shungura Members H-J, and Koobi Fora just above the KBS tuff, is most likely (based on shared monkeys, bovids, and suids: see Herries et al., 2009). In total, this suggests an age closer to the ~1.89-1.63 Ma estimate for both hominin sites. The fact that Swartkrans Member 1 and Kromdraai A share *G. major* also points to their similar age.

In addition to Swartkrans Member 1 and Kromdraai A, limited dental material consistent with *G. major* is present at Swartkrans Members 2 – 3, Coopers A, and

Coopers D; if diagnostic cranial material of *G. major* can be documented, an age between ~1.9-1.6 Ma becomes more likely for these sites as well, in contrast to suggestions of significant time depth on the basis of previous faunal, ESR, and U-PB analyses (e.g., Vrba, 1995; Curnoe et al., 2001; DeRuiter, 2003; Albarède et al., 2006; Balter et al., 2008). Finally, the results of this study demonstrate that faunal analysis continues to be an important tool in assessing the age of African Plio-Pleistocene sites, and additional biogeographic and biochronological links between East and South Africa (such as *G. major*) will be crucial in helping to further refine the chronology of many South African hominin localities moving forward (e.g., Gilbert and Frost, in prep).

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Figure Captions

Figure 1. Comparison of *Gorgopithecus major* (left) and large papionin specimens from Olduvai Bed I (OLD/69 S.196, right). a) *G. major* male KA 192 (left), Olduvai papionin male OLD/69 S.196 (right) in frontal view (scale bar = 1 cm). b) *G. major* male KA 192 (left), Olduvai papionin male OLD/69 S.196 (right) in lateral view (scale bar = 1 cm.) c) *G. major* presumed male KA 605 (left), Olduvai papionin female FLK NNI 1011 (right) in lateral view (not to scale). d) *G. major* presumed female KA 944 (left), Olduvai papionin female FLK NNI 1011 (right) in lateral view (not to scale). Arrows indicate: 1. brow ridge inferiorly curved in the midline; 2. lateral orbital margin flared infero-laterally; 3. nasals short relative to rostrum (nasals damaged in OLD/69 S.196, but length can be accurately estimated); 4. suborbital fossa extensive, deep, and invades anterior zygoma; 5. zygomatic arch robust; 6. concavo-convex, tubular nasals; 7. upper incisor roots antero-posteriorly curved. These features are not found in combination in any known papionin taxon except *Gorgopithecus*.

Figure 2. Regression plot illustrating snout length relative to cranial size in adult male papionins. Red stars = *G. major* and Olduvai S.196, blue open squares = *Cercocebus*, blue closed squares = *Mandrillus*, blue open diamond = *Procercocobus*, blue closed diamond = *Soromandrillus*, green open triangles = *Lophocebus*, green closed triangles = *Papio*, green inverted open triangles = *Theropithecus gelada*, green inverted closed triangles = fossil *Theropithecus*, yellow/gold circles = *Macaca*, green cross = *Pliopapio*, and black circles = *Parapapio* specimens. Regression line: $y=1.571x - 0.792$, $r^2=0.967$, $r=0.983$, $p < 0.001$.

Figure 3. Regression plot illustrating sagittal nasal length relative to cranial size in adult male papionins. Key = same as Fig. 2. Regression line: $y=1.930x - 1.677$, $r^2=0.925$, $r=0.962$, $p < 0.001$.

Figure 4. Regression plot illustrating relative nasal length relative to cranial size in adult male papionins. Key = same as Fig. 2. Regression line: $y=0.356x - 0.881$, $r^2=0.365$, $r=0.604$, $p < 0.001$.

Figure 5. Principal components analysis of adult male papionin cranial shape as represented by 11 relative cranial shape indices. Key = same as Fig. 2.

Figure 6. Results of phylogenetic analysis including the large Olduvai papionin as a distinct OTU. a) Strict consensus tree of four MPTs; Length=1496, CI=0.4024, HI=0.5976, RI=0.4522, RC=0.1820. Numbers above branches represent bootstrap support values and numbers in parentheses below branches represent decay indices (Bremer support values). b) Majority-rule consensus tree of four MPTs. Numbers above branches represent the percentage of MPTs in which that particular clade is found. For individual MPTs, see SOM.

Table 1. Qualitative craniodental features found in papionin taxa compared to the Olduvai Bed I large papionin specimens.^a

Taxon	Maxillary fossae	Maxillary ridges in males	Supraorbital tori in males	Muzzle dorsum shape	Nasal bone shape and orientation	Incisor root orientation	Molar enamel
<i>Cercocebus</i>	Present, up to the infrorbital plate to invading the infraorbital plate	Variably present	Not prominent	Flat to rounded	Flat to rounded, no anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
<i>Dinopithecus</i>	Absent to variably present, very shallow and not clearly defined	-	Prominent, horizontally oriented	Flat to rounded?	Flat to rounded, anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
<i>Gorgopithecus</i>	Present, deeply invading the infraorbital plate	Absent	Prominent, anteroinferiorly oriented	Peaked	Rounded/tube-shaped, anteorbital drop, slightly upturned to upturned and concavo-convex	Horizontal	Non-elevated enamel folding
<i>Lophocebus</i>	Present, invading the infraorbital plate to deeply invading the infraorbital plate	Variably present	Polymorphic	Flat to rounded	Flat to rounded, no anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
<i>Macaca</i>	Absent	Absent	Polymorphic	Flat to rounded	Flat to rounded, no anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
<i>Mandrillus</i>	Present, superior to alveoli	Present	Prominent, horizontally oriented	Flat	Flat, anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
<i>Papio</i>	Present, up to the infrorbital plate to invading the infraorbital plate	Present	Prominent, horizontally oriented	Flat	Flat, anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
<i>Parapapio</i>	Absent to variably present, very shallow and not clearly defined to up to infraorbital plate	Variably present	Not prominent	Flat to rounded to peaked	Flat to rounded, no anteorbital drop, slightly upturned to upturned and sometimes concavo-convex	Vertical	Non-elevated enamel folding
<i>Pliopapio</i>	Variably present, very shallow and not clearly defined	Absent	Not prominent	Rounded	Rounded, anteorbital drop, upturned	Vertical	Non-elevated enamel folding
<i>Procercopithecus</i>	Present, up to the infrorbital plate to invading the infraorbital plate	Present	Not prominent	Flat to rounded	Flat to rounded, no anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
<i>Soromandrillus</i>	Present, superior to alveoli	Present	Prominent, horizontally oriented	Flat	Flat, anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
<i>Theropithecus</i>	Present to variably present, very shallow and not clearly defined to invading the infraorbital plate	Present to variably present	Prominent, horizontally oriented	Flat to rounded	Flat, anteorbital drop, slightly upturned to upturned	Vertical	Elevated and complex enamel folding

Oludvai papionin	Present, invading the infraorbital plate to deeply invading the infraorbital plate?	Absent	Prominent, anteroinferiorly oriented	Peaked	Rounded/tube-shaped, anteorbital drop, slightly upturned to upturned and concavo-convex	Horizontal	Non-elevated enamel folding
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^aDash (-) = State unknown due to lack of preservation. See also Figure 1 and nexus file in Supplementary Online Material for coded character states expressed by each taxon.

Table 2. Measurements (mm) of the dentition comparing South African *Gorgopithecus major* with Olduvai Bed I papionin specimens.^a

Upper Dentition																		
Taxon	Specimen #	Sex	I ¹ MD	I ¹ BL	P ³ MD	P ³ BL	P ⁴ MD	P ⁴ BL	M ¹ MD	M ¹ MBL	M ¹ DBL	M ² MD	M ² MBL	M ² DBL	M ³ MD	M ³ MBL	M ³ DBL	SOURCE
<i>G. major</i>	KA 153	F	-	-	6.8	8.4	8.0	11.1	11.8	11.5	10.8	14.7	14.3	13.3	13.0	13.8	11.0	PRIMO
<i>G. major</i>	KA 154	F?	-	-	7.8		8.3	9.8	13.4	11.4	10.4	15.8	14.4	12.3	14.1	12.9	10.7	PRIMO
<i>G. major</i>	KA 169	?	10.1	8.5	-	-	-	-	13.6	11.2	10.7	15.0	-	-	-	-	-	PRIMO
<i>G. major</i>	KA 170	?	-	-	-	-	8.2	9.3	-	-	10.4	13.7	12.5	11.1	-	-	-	PRIMO
<i>G. major</i>	KA 171	?	-	-	-	-	8.1	8.8	-	-	-	-	-	-	-	-	-	PRIMO
<i>G. major</i>	KA 178	?	-	-	-	-	-	-	13.0	11.3	10.3	-	-	-	-	-	-	PRIMO
<i>G. major</i>	KA 182	?	-	-	-	-	-	-	-	-	-	-	-	-	13.8	13.8	10.2	PRIMO
<i>G. major</i>	KA 183	?	10.1	8.4	-	-	-	-	-	-	-	-	-	-	-	-	-	PRIMO
<i>G. major</i>	KA 192	M	-	8.0	7.2	8.7	7.7	10.0	12.9	11.8	11.0	15.5	14.1	13.1	14.7	14.4	11.5	PRIMO
<i>G. major</i>	KA 193	?	-	-	-	-	-	-	-	-	-	14.7	13.6	13.1	14.5	14.0	11.0	PRIMO
<i>G. major</i>	KA 524/676	M	-	-	7.5	9.8	7.5	-	-	-	-	-	-	-	-	-	-	PRIMO
<i>G. major</i>	KA 944	F?	8.7	8.0	7.2	9.3	8.7	11.0	13.7	-	-	15.4	14.9	13.3	13.7	14.0	10.6	PRIMO
<i>G. major</i>	KA (2348)	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	PRIMO
<i>G. major</i>	KA 605	M?	-	6.0	7.5		8.1	11.1	13.6	11.9	11.0	15.6	14.4	12.5	13.6	14.1	10.7	PRIMO
<i>G. major</i>	SK 604A	?	10.6	9.5	7.4	9.4	8.5	11.4	13.0	12.5	11.5	16.7	15.3	13.9	14.5	16.7	13.9	PRIMO
<i>G. major</i>	Mean	-	9.9	8.1	7.3	9.1	8.1	10.3	13.1	11.7	10.8	15.2	14.2	12.8	14.0	14.2	11.2	-
<i>G. major</i>	Range	-	8.7-10.6	6.0-9.5	6.8-7.5	8.4-9.8	7.5-8.7	8.8-11.4	11.8-13.7	11.2-12.5	10.3-11.5	13.7-16.7	12.5-15.3	11.1-13.9	13.0-14.7	12.9-16.7	10.2-13.9	-
Olduvai papionin	FLK NNI 1011	F	9.5	8.5	-	-	-	-	-	-	-	-	-	-	(14.0)	-	-	Leakey and Leakey (1976)
Olduvai papionin	OLD/69 S.196	M	-	-	-	(9.5)	(7.7)	(10.2)	(11.5)	-	-	(16.1)	-	-	16.3	(14.5)	-	Leakey and Leakey (1976), PRIMO
Olduvai papionin	OLD/69 S.193	?	-	-	-	-	8.6	9.3	-	-	-	15.3	12.7	11.8	-	-	-	PRIMO
Lower Dentition																		
Taxon	Specimen #	Sex	I ₁ MD	I ₁ BL	P ₃ MD	P ₃ BL	P ₄ MD	P ₄ BL	M ₁ MD	M ₁ MBL	M ₁ DBL	M ₂ MD	M ₂ MBL	M ₂ DBL	M ₃ MD	M ₃ MBL	M ₃ DBL	SOURCE
<i>G. major</i>	KA 150	M	-	-	17.0	6.3	9.3	8.3	11.8	9.5	9.8	14.8	11.3	11.3	20.0	12.7	11.9	PRIMO

<i>G. major</i>	KA 152	?	-	-	-	-	9.0	8.0	12.6	9.1	9.2	14.8	10.9	11.4	18.7	11.7	11.5	PRIMO
<i>G. major</i>	KA 198	?	-	-	-	-	-	-	-	-	-	-	-	-	18.6	12.1	10.8	PRIMO
<i>G. major</i>	KA 1148	M	-	-	18.2	6.8	10.0	8.7	-	-	-	-	-	-	-	-	-	PRIMO
cf. <i>G. major</i>	CO 114/119	F?	-	-	-	6.7	9.2	8.2	11.1	-	-	13.1	-	11.1	18.1	12.0	11.0	PRIMO
cf. <i>G. major</i>	CO 104AB	?	-	-	-	-	10.0	9.0	11.0	9.5	10.0	14.7	12.7	12.1	18.5	12.5	11.5	PRIMO
<i>G. major</i>	SK 423	M	-	-	-	7.6	9.3	8.5	9.9	8.7	8.7	14.6	12.3	11.8	19.5	12.9	11.7	PRIMO
<i>G. major</i>	Mean	-	-	-	17.6	6.9	9.5	8.5	11.3	9.2	9.4	14.4	11.8	11.5	18.9	12.3	11.4	-
<i>G. major</i>	Range	-	-	-	17.0-18.2	6.3-7.6	9.0-10.0	8.0-9.0	9.9-12.6	8.7-9.5	8.7-10.0	13.1-14.8	10.9-12.7	11.1-12.1	18.1-20.0	11.7-12.9	10.8-11.9	-
Olduvai papionin	FLK NNI 1011	F	-	-	-	-	-	-	-	-	-	13.7	11.8	10.9	17.3	11.8	9.9	PRIMO
Olduvai papionin	OLD/61 2968	?	-	-	-	-	-	-	-	-	7.6	12.3	9.8	-	-	-	-	PRIMO

^a: MD = maximum mesiodistal length, BL = maximum buccolingual width, MBL = maximum buccolingual width across the mesial loph(id), DBL = maximum buccolingual width across the distal loph(id). In the case of the incisors, MD = maximum length in the coronal plane and BL = maximum labiolingual depth. - = unavailable measurement. F=Female, M=Male, ?=Unknown. Numbers in parentheses represent estimates. The arithmetic Mean and Range were calculated for each tooth position of the South African *G. major* and cf. *G. major* specimens and highlighted in bold. SOURCE column refers to the source of the measurements, which were taken from a combination of Leakey and Leakey (1976) and the online PRIMO database (<http://primo.nycep.org>).

Table 3. Measurements (mm) of the cranium comparing South African male *G. major* with Olduvai Bed I male papionin specimen.^a

Taxon	Specimen #	Sex	Min Frontal Breadth	Biporionic Breadth	Max Biorbital Breadth	Nasion-Prosthion	Nasospinale-Prosthion	Bizygomatic Breadth (Zygion-Zygion)	Bimaxillary Breadth (Zygomaxillare-Zygomaxillare)	Max Orbit Height	SOURCE
<i>G. major</i>	KA 192	M	67.0	(101.0)	91.0	89.5	17.0	141.0	83.0	23.0	Freedman (1957), this study
Olduvai papionin	OLD/69 S.196	M	(58.0)	(115.0)	104.0	(92.5)	(16.0)	(148.0)	(94.0)	19.0	this study

			Malar Height	Max Nasal Aperture Width	Nasion-Rhinion	Zygomaxillare-Porion	Biectomolare	Upper Incisor Alveolar Length (Prosthion-I ² /C ¹)	Upper Premolar Alveolar Length (C ¹ /P ³ -P ⁴ /M ⁴)	Upper Molar Length (P ⁴ /M ⁴ -post M ³)	SOURCE
<i>G. major</i>	KA 192	M	(30.0)	20.0	(36.0)	75.0	58.0	83.0	16.0	47.0	Freedman (1957), this study
Olduvai papionin	OLD/69 S.196	M	30.0	(16.5)	(40.0)	(76.5)	(59.5)	94.0	14.0	45.0	this study

^aMin = Minimum, Max = Maximum. M=Male. Numbers in parentheses represent estimates. SOURCE column refers to the source of the measurements, which were taken during the course of this study as well as from Freedman (1957). See also Gilbert et al. (2009), Gilbert (2013) and Supplementary Online Material for corresponding character numbers and definitions.

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FIGURES

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