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Papionin Taxa: An Investigation of Possible Dental Differences
Between Parapapio and Papio**

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**Analysis of Third Premolar Flange Length in Male African Papionin Taxa: An
Investigation of Possible Dental Differences Between *Parapapio* and *Papio***

by

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Submitted in partial fulfillment
of the requirements for the degree of
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Abstract:

African papionin monkeys are abundant throughout the African Plio-Pleistocene fossil record. Because *Parapapio* and *Papio* overlap in dental size, and because no obvious dental differences have been documented between the two genera, it can be difficult to identify fragmentary material at fossil sites where both taxa occur. Based on recent anecdotal observations, this study investigates whether there is a significant difference between relative P3 flange length between *Parapapio* and *Papio* in the upper and lower dentitions. Regressions, X-Y plots, box and jitter plots, and ANOVAS, were performed using the statistics package PAST 3.14. The results demonstrated that relative P3 flange length in both *Parapapio* and fossil *Papio* are largely contained within the range of variation exhibited by extant *Papio*, but with very little overlap between the fossil taxa themselves. Results of the ANOVAs also indicate that there is a significant difference between an average *Parapapio* specimen and an average *Papio* specimen when it comes to relative P3 flange length, representing one of the only potential dental characteristics that separate the two genera. This information can be used in future studies to help identify isolated dental specimens at fossil sites where both *Papio* and *Parapapio* occur.

Keywords: *Parapapio*, *Papio*, dentition, premolars, flange length, fossil record, molars

1. Introduction:

African papionins

Cercopithecoid monkeys (Order Primates, Family Cercopithecidae) are one of the most successful groups of living primates. They inhabit a wide range of habitats that stretch throughout Africa and much of Asia as well (Fleagle, 2013). Unlike humans and apes, cercopithecoids have bilophodont teeth (anterior cusps and posterior cusps align to form two ridges) (Szalay and Delson, 1979; Fleagle, 2013). These monkeys also tend to exhibit large sharp canines in males and smaller sharp canines in females, with the level of canine dimorphism being among the highest seen across all primates (Plavcan, 2003; Fleagle, 2013). The upper canines are paired with a narrow anterior lower premolar which acts as a natural sharpener. Cranially speaking, Cercopithecids have relatively narrow nasal openings and narrow tooth rows compared with apes, and most lack maxillary sinuses (Szalay and Delson, 1979; Rae and Koppe, 2004; Fleagle, 2013).

Papionins are cercopithecines (Subfamily Cercopithecinae, Tribe Papionini), which are further characterized as having a narrow interorbital region, broad incisors, shallow jaw, low dental cusps, cheek pouches and similar length legs and arms (Szalay and Delson, 1979; Fleagle, 2013). Papionins are the best known of the cercopithecines and include the living genera *Macaca* (macaques), *Papio* (baboons), *Mandrillus* (mandrills and drills), *Theropithecus* (geladas), *Lophocebus* (crested mangabeys), *Cercocebus* (white-eyelid mangabeys), and *Rungwecebus* (kipunjis) (Gilbert et al., 2009, 2011; Fleagle, 2013; DeVreese and Gilbert, 2015). The exclusively African members of this group (i.e., all of the above minus *Macaca*) are further recognized to form their own

group, subtribe Papionina (*sensu* Strasser and Delson, 1987; Gilbert et al., 2009; Gilbert et al., 2011), here referred to simply as African papionins. These are a very successful group of monkeys that are found all throughout sub-Saharan Africa and even into the Arabian Peninsula.

In addition to their modern distribution, African papionins are found throughout the African Plio-Pleistocene fossil record (e.g., Szalay and Delson, 1979; Frost, 2001; Jablonski, 2002; Jablonski and Frost, 2010; Gilbert, 2013). The fossil record is rich with both cranio-dental specimens as well as isolated dental specimens. However, even with the abundance of dental specimens, very few if any dental characteristics have been proven to distinguish primitive fossil papionin taxa such as *Parapapio* from more derived taxa such as *Papio* (Szalay and Delson, 1979). This presents an obvious problem for determining the taxonomic identity of individual specimens in the absence of more complete craniofacial material, resulting in many specimens inconclusively attributed to various fossil taxa or simply left unassigned to any species at all. The ability to fully understand African papionin evolution hinges on being able to correctly identify taxa from the remains preserved in the fossil record; our understanding of first and last appearance dates, morphological variation, and biogeography, to name a few, all depend on accurate and, as much as possible, precise taxonomic IDs across fossil localities. Thus, being able to more precisely identify isolated dental specimens is of high importance for understanding African papionin, and more broadly, cercopithecoid monkey evolution.

2. Background:

Among Plio-Pleistocene fossil sites in South Africa, papionin monkeys are very common (e.g., Freedman, 1957; Szalay and Delson, 1979; Jablonski, 2002; Jablonski and Frost, 2010). At some sites, mostly those considered to be older in age (e.g., Makapansgat, Sterkfontein Members 2 and 4, Bolt's Farm Pit 23, etc.), the fossil papionin genus *Parapapio* is commonly recognized among the more complete maxillary and mandibular specimens (Freedman, 1957; Szalay and Delson, 1979; Jablonski, 2002; Jablonski and Frost, 2010; Gilbert, 2013). *Parapapio* is a primitive papionin from the Late Miocene to Plio-Pleistocene of eastern and southern Africa and it is generally recognized as a primitive African papionin or one of the most primitive members of the extant *Papio/Lophocebus/Rugwecebus/Theropithecus* group (Gilbert, 2013; Pugh and Gilbert, 2018). *Parapapio* specimens can be sorted into at least five probably paraphyletic species: *Pp. jonesi*, *Pp. broomi*, *Pp. whitei*, *Pp. ado* and *Pp. lothagamensis* (Gilbert, 2013), and at least some of these taxa may lie near the ancestry of all living genera (Fleagle, 2013). *Parapapio* spans a range of body sizes, from small/medium-sized to large, and is generally recognized based on craniofacial material displaying relatively weak brow ridges, no anteorbital drop, a lack of facial fossae, and a lack of maxillary ridges in males (Freedman, 1957; Szalay and Delson, 1979; Jablonski and Frost, 2010).

Extant baboons (genus *Papio*) are found all throughout sub-Saharan Africa as well as parts of the Arabian Peninsula and are currently classified into six species: *P. papio*, *P. anubis*, *P. cynocephalus*, *P. ursinus*, *P. kindae*, and *P. hamadryas* (Frost et al., 2003; Fuchs et al., 2018). They are very large monkeys and are highly sexually dimorphic. In addition, they are also found in the fossil record, with a couple of named

species/subspecies found in the Plio-Pleistocene of South Africa: *Papio robinsoni* and *Papio angusticeps* (Gilbert et al., 2018). Morphologically speaking, relative to other papionin taxa, *Papio* tends to have a long snout and mandible, pronounced brow ridges/glabella region, an anteorbital drop, pronounced facial fossae, definitive maxillary ridges in males, long molars, and broad incisors (Szalay and Delson, 1979; Jablonski and Frost, 2010; Gilbert et al., 2018). Specimens attributable to the genus *Papio* appear in the South African fossil record appear beginning somewhere between ~2.4-2.0 Ma, at sites such as Sterkfontein (Members 4-6), Swartkrans (Members 1-3), Kromdraai A, Malapa, Haasgat, Drimolen, and Bolt's Farm Pits 6 and 23 (Gilbert et al., 2018).

Because *Parapapio* and *Papio* overlap in dental size, and because no obvious dental differences have been documented between the two genera, it can be difficult to identify fragmentary material at sites where both taxa occur in the fossil record (e.g., Sterkfontein Member 4, Bolt's Farm Pit 23, etc.), particularly among maxillary and mandibular fragments preserving teeth but lacking the diagnostic regions containing facial fossae. More importantly, there are many fragmentary specimens at South African sites that may extend the temporal and/or geographical range of either genus, but cannot be allocated to either genus with confidence due to an inability to identify dental remains in the absence of more complete craniomandibular material (e.g., Kromdraai A, Swartkrans, etc.). In these cases, our understanding of the evolution of both genera may be hampered by the apparent lack of diagnostic dental features.

3. Hypothesis:

As highlighted by both Freedman (1957) and Szalay and Delson (1979) there are no clear dental features that help to distinguish between the genera *Parapapio* and *Papio* in the fossil record. However, in a recent survey of all South African fossil papionin material, Gilbert and Frost (pers. comm.) noted that the P₃ flanges in male *Parapapio* appeared to be consistently shorter than those of male *Papio*. If the P₃ flange is indeed consistently shorter in male *Parapapio* specimens compared to *Papio*, it might represent an easily observable feature useful for identifying fragmentary dental remains in the fossil record. This thesis aims to examine this issue in greater detail, looking to see if there is a consistent and significant dental difference between the two genera in not only male P₃ flange length, but also P³ flange length as well.

4. Materials and Methods:

Identifiable male fossil craniodental specimens collected from Sterkfontein, Swartkrans, Makapansgat, Kromdraai B, Coopers, Hadar, Laetoli, Bolts Farm Pit 6 and Bolts Farm Pit 23 were measured using standard calipers to the nearest tenth of a millimeter. In addition, a large sample of male extant *Papio* specimens was also collected for comparison. Specific measurements were taken on upper and lower P₃s, including flange length and maximum buccolingual breadth, as well as upper and lower M₂ maximum buccolingual breadth as a body size proxy (see Table 1 for a list of measurements with descriptions; See Appendix Tables 1-2 for a list of specimens included in this study along with their individual measurements). All data was taken from the PRIMO (PRimate MORphology) online database, access courtesy of Eric Delson.

For analysis, four size-corrected indices were created: LP_3FL/LM_2AW , LP_3FL/LP_3W , UP_3FL/UM_2AW , and UP_3FL/UP_3W . The anterior widths (i.e., breadths) of the upper and lower second molars were chosen as size corrections due to their demonstrated close correlation with body mass (see Delson et al., 2000). In addition, the breadths of the upper and lower P3s were used in an effort to keep the size-correction internal to those teeth and include as many specimens as possible. Thus, the relative lengths of the upper and lower P3s were analyzed in two slightly different ways.

ANOVAs were performed to test for significant differences between fossil *Parapapio*, fossil *Papio*, and extant *Papio*. In addition, data for each index was plotted as a regression to test for any significant allometric relationship and, if so, evaluate the data relative to the regression line. Additionally, box and jitter plots were used for visualization across taxa. All statistics were performed in the software program PAST v 3.14 (Hammer et al., 2001). Regression plots and statistics are provided in Figures 1-10 and Tables 1-2.

Table 1: Measurements collected and analyzed in this study

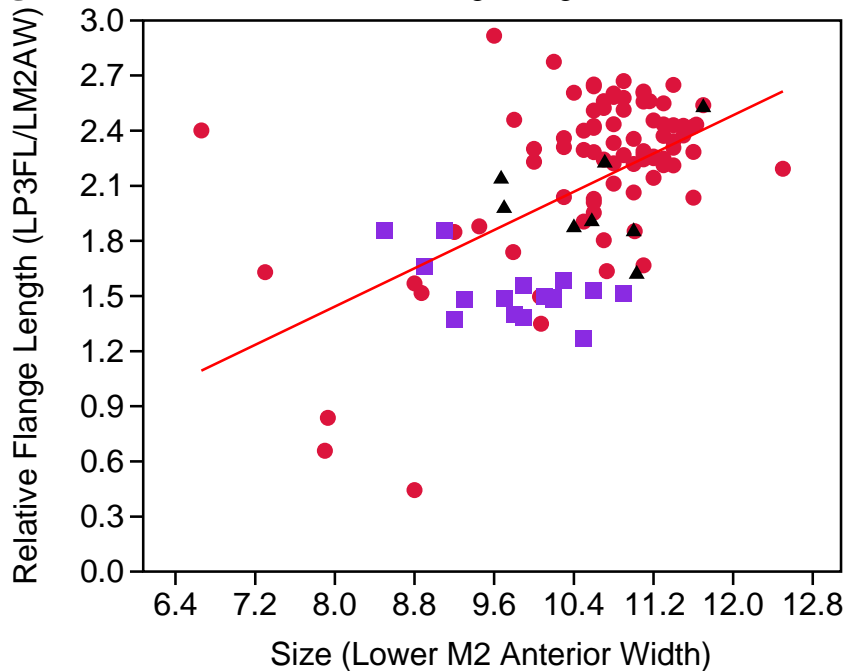
Abbreviation	Description
LM ₂ AW	Lower second molar anterior breadth across the mesial lophid
LP ₃ FL	Lower third premolar mesiodistal flange length
LP ₃ W	Lower third premolar buccolingual breadth
UM ₂ AW	Upper second molar anterior breadth across the mesial loph
UP ₃ FL	Upper third premolar mesiodistal flange length
UP ₃ W	Upper third premolar buccolingual breadth

Table 2: Key for all following figures.

Taxon	Symbol
Extant <i>Papio</i>	■
Fossil <i>Papio</i>	▲
<i>Parapapio</i>	■

5. Results:

Figure 1: Linear Fit Model of P₃ Flange Length vs. Size (M₂ Anterior Width).



A least square regression between size and relative P₃ flange length shows a slightly positive correlation with size (Fig. 1; $p < 0.0001$ and $r^2 = 0.28689$). Thus, it is most useful to evaluate the specimens on an X-Y plot (Fig. 2). An X-Y plot of relative P₃ flange length vs. size shows that both fossil *Papio* (aquablue triangles) and *Parapapio* (blueviolet squares) are contained within the range for extant *Papio* (crimson dots). However, among fossil taxa, *Parapapio* and fossil *Parapapio* do not overlap in relative flange length at any given size. Furthermore, an ANOVA between extant *Papio*, fossil *Papio*, and fossil *Parapapio* for relative P₃ flange length relative to M₂ anterior width was statistically significant ($p < 0.0001$), and when post-hoc comparisons were examined, extant and fossil *Papio* populations were both found to possess significantly longer P₃ flanges compared to *Parapapio* (Tukey's pairwise extant *Papio* vs. *Parapapio* $p < 0.001$; fossil *Papio* vs. *Parapapio* $p < 0.01$) (see also boxplots; Fig. 3).

Figure 2. X-Y plot with convex hulls for relative P₃ Flange Length vs. Size (M₂ Ant. Width)

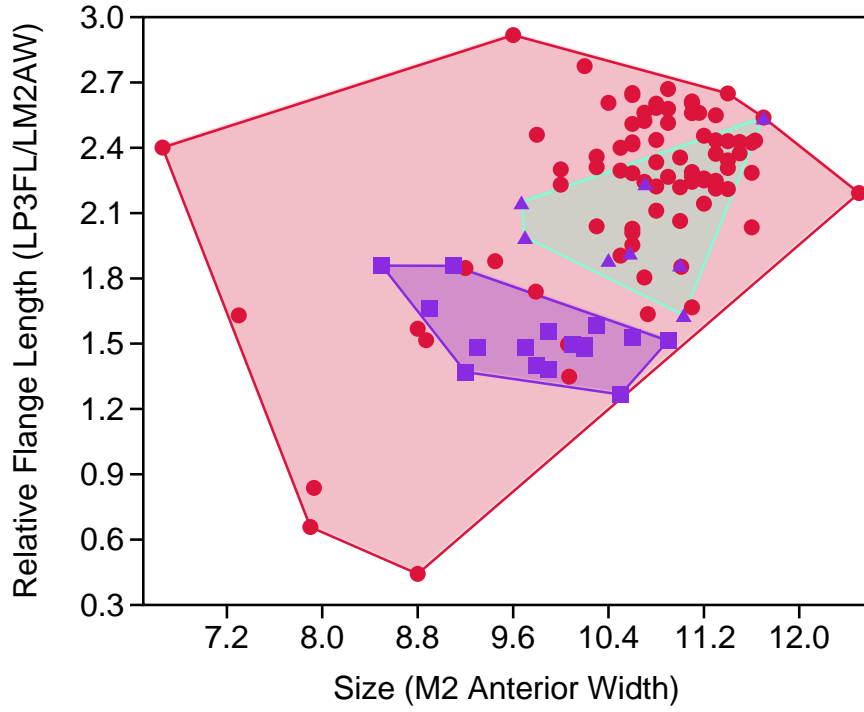
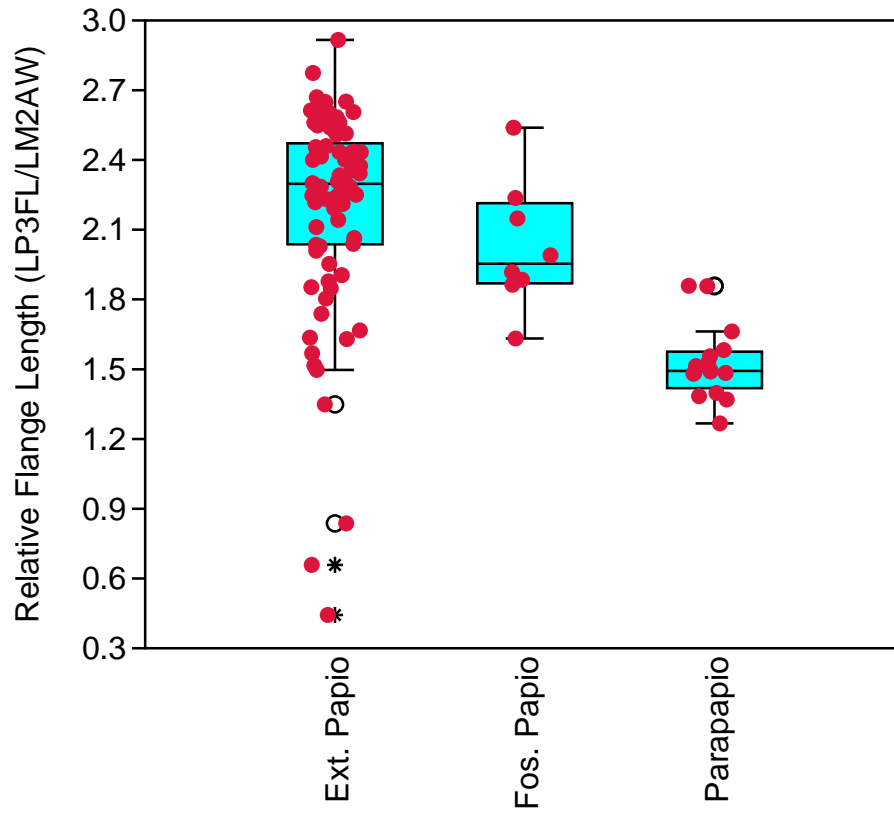
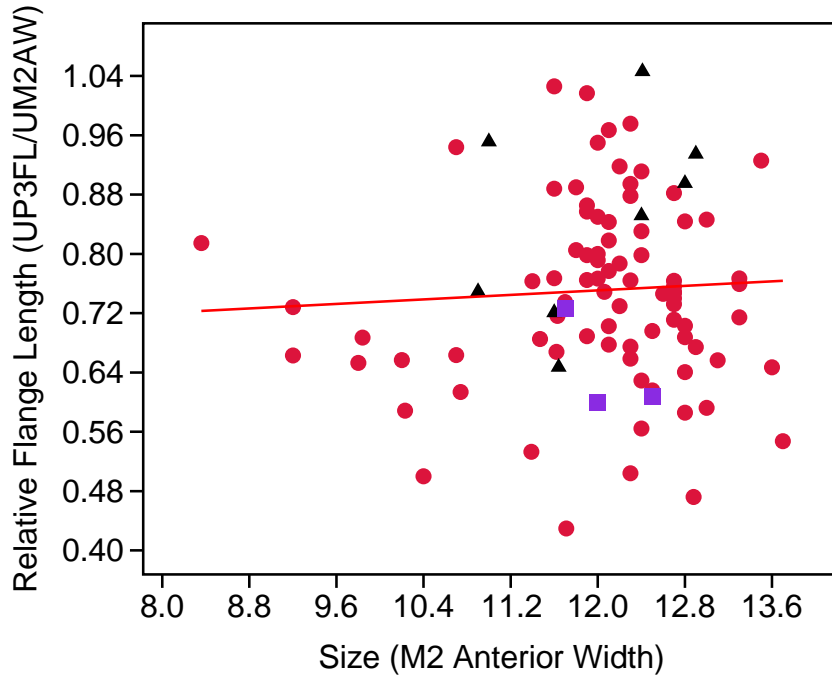


Figure 3: Relative P₃ flange length as a box and jitter plot.



Analysis of P³ relative flange length relative to M² anterior width is similar. A least square regression between size and relative P³ flange length shows no correlation with size (Fig. 4; $p=0.5844$ and $r^2=0.0032439$).

Figure 4: Linear fit model of P³ flange length vs. size (M² Ant. Width)



Similar to the situation with the lower premolar flange lengths, an X-Y plot of P³ relative flange length vs size shows that both fossil *Papio* (aquablue triangles) and *Parapapio* (blueviolet squares) are largely contained within the range for extant *Papio* (crimson dots) (Fig. 5). However, note that among fossil taxa, *Parapapio* and fossil *Parapapio* show very little overlap in relative flange length at any given size (one known *Parapapio* specimen overlaps the fossil *Papio* range). An ANOVA again detects significant differences amongst the analyzed groups ($p < 0.05$), with Tukey's post-hoc comparisons only detecting a significant difference between fossil *Papio* and *Parapapio* in this instance ($p < 0.05$), demonstrating that P³ flanges are likely different between these two fossil groups, but broadly more difficult to discern between *Papio* and *Parapapio*, particularly extant *Papio* and *Parapapio* (see also boxplots, Fig. 6).

Figure 5: X-Y plot with convex hulls for relative P³ Flange Length vs. Size (M₂ Ant. Width)

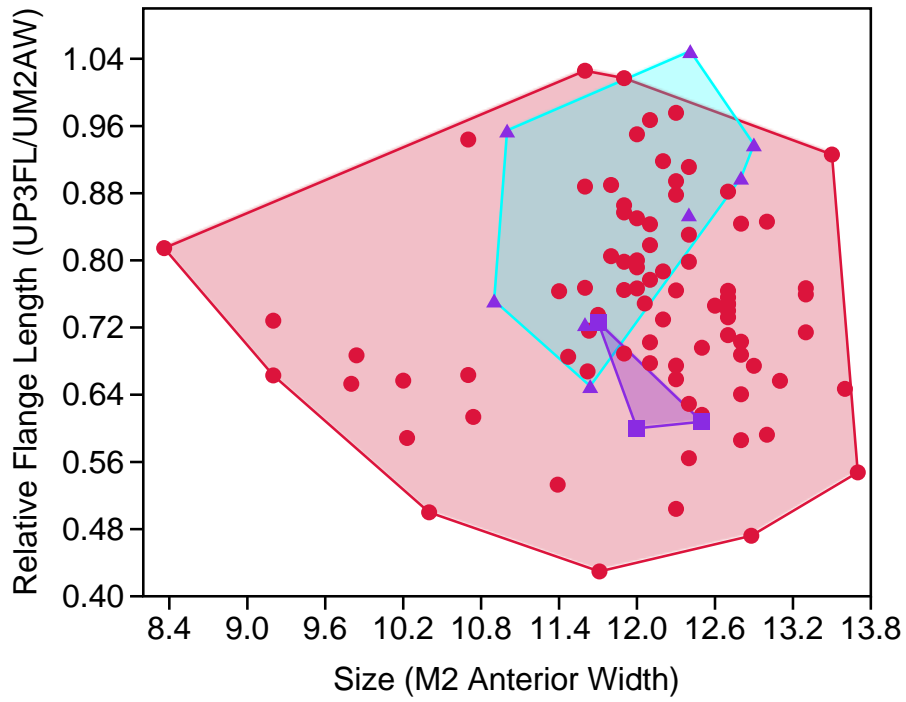
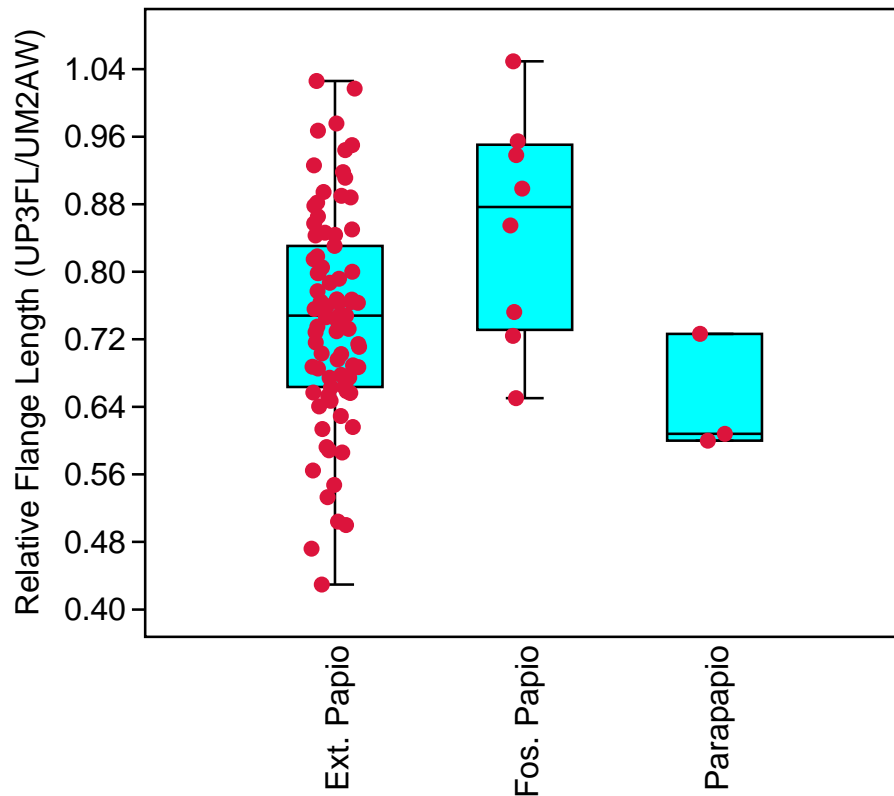
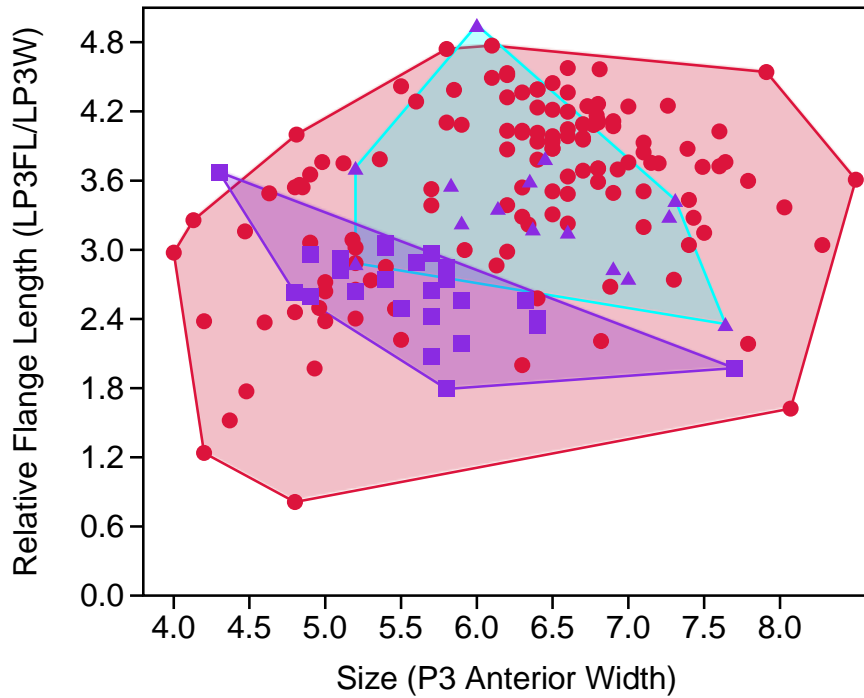


Figure 6: Relative P³ flange length as a box and jitter plot.



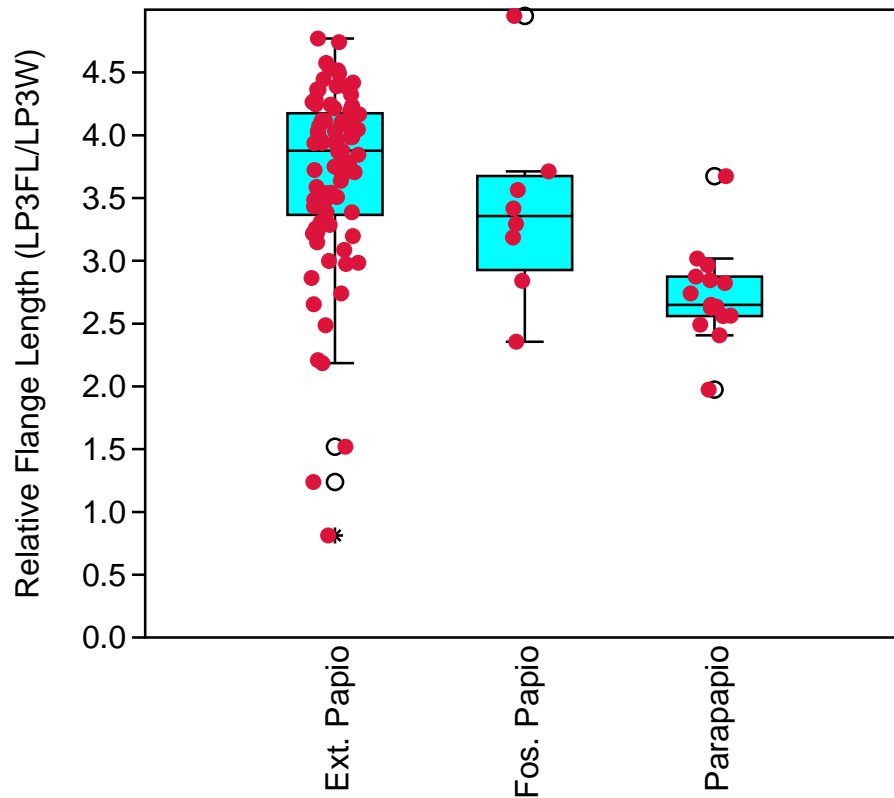
To include more specimens and keep measurements internal to the third premolar, separate analyses were also conducted for relative P₃ and P³ flange length using P₃ breadth as the denominator. The results are very similar to those using M² anterior width as the size correction (see Figs. 7-10). An X-Y plot of P₃ mesiodistal flange length vs. P₃ maximum breadth again shows that both fossil *Papio* (aquablue triangles) and *Parapapio* (blueviolet squares) are largely contained within the range for extant *Papio* (crimson dots) (Fig. 7). However, note that among fossil taxa, *Parapapio* and fossil *Parapapio* still display very little overlap in P₃ flange length at any given P₃ breadth (one known fossil *Papio* specimen overlaps the *Parapapio* range).

Figure 7. X-Y plot with convex hulls for relative P₃ Flange Length vs. Size (P₃ max width).



Just like with M₂ anterior breadth as the size correlate, an ANOVA between groups for the P₃ relative flange length ratio using P₃ anterior width is highly significant ($p < 0.0001$), and post-hoc comparisons reveal that extant *Papio* and fossil *Papio* have significantly longer P₃ flanges compared to known specimens of *Parapapio* (*Papio* vs. *Parapapio* $p < 0.001$; fossil *Papio* vs. *Parapapio* $p < 0.01$) (see also boxplots; Fig. 8).

Figure 8. Relative P₃ flange length as a box and jitter plot.



Finally, analysis of P³ relative flange length using P³ maximum breadth in the denominator show the same pattern as the lower flange length analyses: both fossil groups are with the extant *Papio* distribution, but the ANOVA is significant ($p < 0.05$) and both extant *Papio* and fossil *Papio* have significantly longer P³ flanges compared to *Parapapio* (see Figs. 9-10; Tukey's pairwise $p < 0.01$ in both cases).

Figure 9. X-Y plot with convex hulls for relative P³ Flange Length vs. Size (P³ max width).

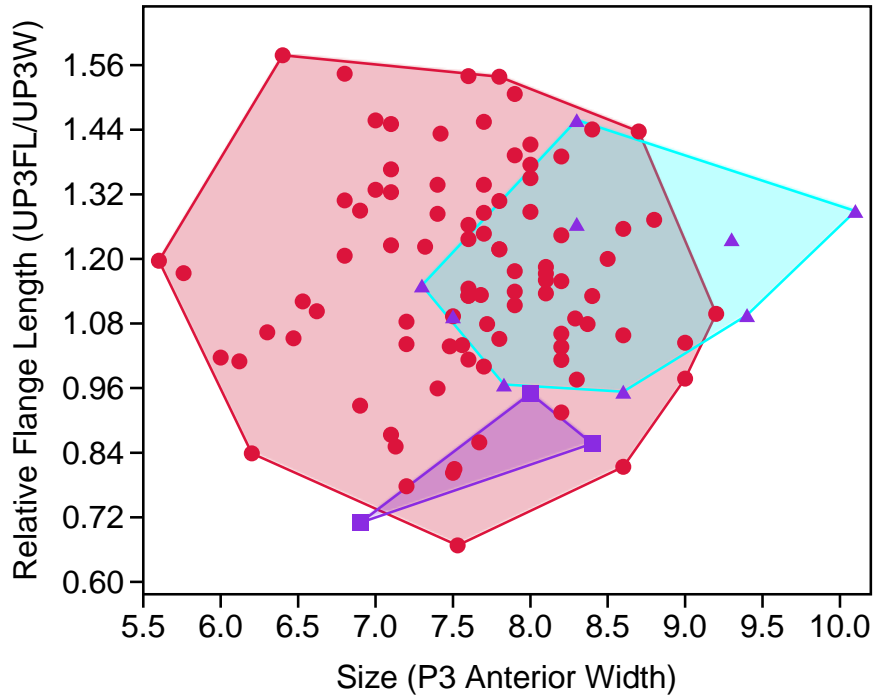
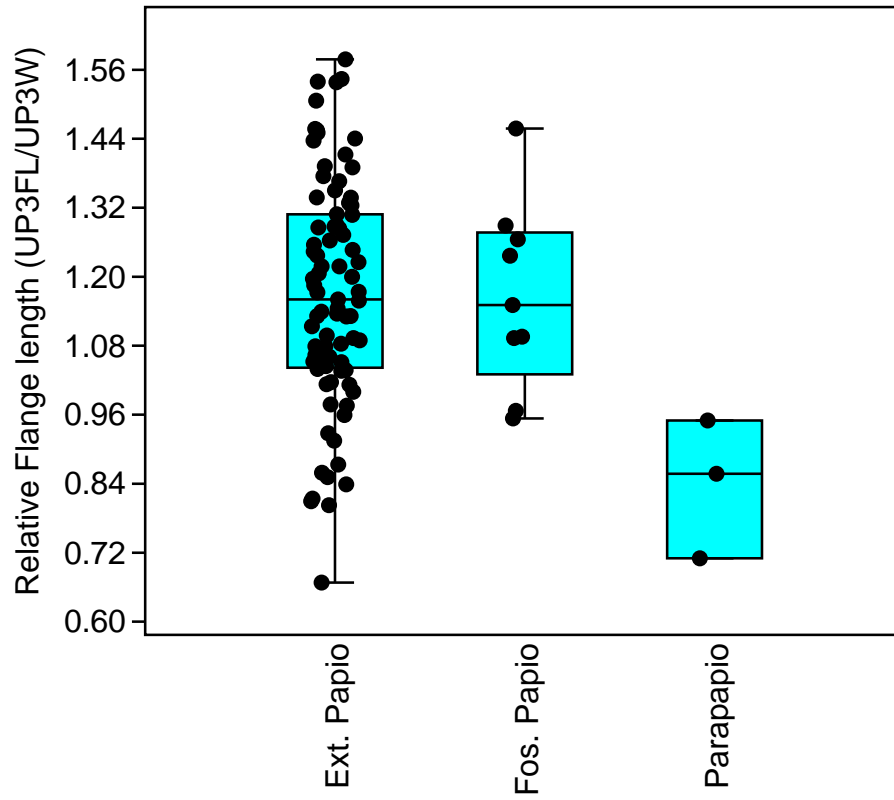


Figure 10. Relative P³ flange length as a box and jitter plot.



Discussion:

This study set out to investigate a dental feature that potentially separates *Parapapio* from *Papio*, namely relative male P3 flange length in the upper and lower dentitions. Relative male flange length was measured in two different ways: 1) relative to upper and lower anterior width, a close correlate of body mass (Delson et al., 2000), and 2) relative to P3 maximum width, making the shape index reliant on only the preservation of the P3 for its calculation. In all comparisons, X-Y plots of relative flange length versus size demonstrate that both *Parapapio* and fossil *Papio* are largely if not completely contained within the range of variation exhibited by extant *Papio*. However, confirmed fossil *Papio* and *Parapapio* specimens rarely overlap in their distributions of relative flange length at any given M2 or P3 breadth, and statistical comparisons demonstrate that both extant and fossil *Papio* specimens have significantly longer P3 flanges compared to *Parapapio*. Thus, there is a real and statistically significant difference between an average *Parapapio* specimen and an average *Papio* specimen when it comes to relative P3 flange length, and this represents one of the only potential dental characters that separate the two genera.

While *Parapapio* and *Papio* show a distinguishable difference, there is still overlap between two taxa (see Figures 1-10). Therefore, caution still seems warranted, and an increased sample size might help to determine just how distinct the differences between *Parapapio* and *Papio* P3s truly are. Ideally, P3 flange length should not be the only feature that is examined. However, when examining isolated craniodental specimens, the analyses presented here suggest that relative P3 flange length can be a useful tool in helping to narrow down the potential taxon the specimen belongs to. This

feature might be particularly useful for assigning fragmentary specimens at sites where confirmed specimens of both *Parapapio* and *Papio* are known to occur, such as Sterkfontein Member 4 and Bolt's Farm Pit 23. In addition, it might be an interesting feature to examine at Taung, where *?Papio izodi* occurs and has been argued to be more primitive than all other *Papio* species. If all Taung specimens fall within the more primitive *Parapapio* range, it might be further evidence that *?P. izodi* represents a distinct genus. If some Taung specimens fall more clearly in the fossil *Papio* or exclusive extant *Papio* range, it might be evidence of a derived feature linking *?P. izodi* with the other fossil *Papio* taxa and allowing the identification of isolated mandibular and maxillary material at Taung.

Functionally, it is unclear why *Parapapio* appears to have a significantly shorter P3 flange. It is possible that the reduced male P3 flange relates to reduced sexual dimorphism within *Parapapio* compared to similar sized extant *Papio* taxa; previous authors have suggested that *Parapapio* is less dimorphic than extant taxa (e.g., Freedman, 1957; Szalay and Delson, 1979; Jablonski, 2002), particularly in its molar dimensions (e.g., Szalay and Delson, 1979). More recently, however, Gilbert and Grine (2010) have demonstrated that *Parapapio* is no less dimorphic in terms of molar dimensions than most other extant and fossil papionin taxa, although it is slightly less dimorphic than extant *Papio*. Since this study focused on male P3 flanges, it is also unclear whether P3 flanges are significantly shorter in female *Parapapio* specimens compared to *Papio*. Future studies should examine female P3 flange length in these taxa and possibly look at the levels of sexual dimorphism expressed in this feature between *Papio* and *Parapapio* as well. Ultimately, cranial size dimorphism would probably be a more accurate

assessment of overall dimorphism in *Parapapio* compared to *Papio*, but it would be interesting to know if different aspects of the dentition have indeed become more dimorphic through increased sexual selection in *Papio* compared to earlier and more primitive taxa such as *Parapapio*. This situation might suggest an increased level of sexual selection during the course of *Papio* and, perhaps, papionin evolution more broadly, perhaps in a runaway selection type of fashion. It also might suggest mosaic sexual selection by which body size, cranial size, and dental size dimorphism evolved in a mosaic fashion rather than all at once in a single package. Resolution of these issues awaits future analyses of papionin morphological data.

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Appendix 1. Lower premolar and molar measurements used in this study by specimen.

Taxon Name	Specimen ID	Site	Fossil or Extant	Lower Molar Anterior Width (LM2AW)	Relative Flange Length (LP3FL/LM2AW)	Lower Third Premolar Width (LP3W)	Relative Flange Length (LP3FL/LP3W)
<i>Papio anubis</i>	52677	Extant	Extant <i>Papio</i>	11.63	2.4325	6.79	4.1664
<i>Papio anubis</i>	55446	Extant	Extant <i>Papio</i>	10.73	1.6356	6.13	2.863
<i>Papio anubis</i>	161116	Extant	Extant <i>Papio</i>	9.79	1.7385	7.79	2.1849
<i>Papio anubis</i>	161117	Extant	Extant <i>Papio</i>	10.06	1.497	6.82	2.2082
<i>Papio cynocephalus</i>	161734	Extant	Extant <i>Papio</i>	9.45	1.8783	5.92	2.9983
<i>Papio hamadryas</i>	90419	Extant	Extant <i>Papio</i>	10.5	1.9048	7.3	2.7397
<i>Papio hamadryas</i>	200886	Extant	Extant <i>Papio</i>	10.6	2.0283	6.5	3.3077
<i>Papio kindae</i>	80796	Extant	Extant <i>Papio</i>	7.93	0.8373	4.37	1.5195
<i>Papio kindae</i>	ZD.1961.753	Extant	Extant <i>Papio</i>	8.8	1.5682	5.2	2.6538
<i>Papio kindae</i>	ZD.1961.766	Extant	Extant <i>Papio</i>	8.8	0.4432	4.8	0.8125
<i>Papio kindae</i>	ZD.1961.769	Extant	Extant <i>Papio</i>	7.9	0.6582	4.2	1.2381
<i>Papio kindae</i>	ZD.1961.770	Extant	Extant <i>Papio</i>	8.87	1.5163	4.13	3.2567
<i>Papio kindae</i>	ZD.1961.775	Extant	Extant <i>Papio</i>	7.3	1.6301	4	2.975

<i>Papio kindae</i>	ZD.1969.555	Extant	Extant <i>Papio</i>	9.2	1.8478	4.8	3.5417
<i>Papio kindae</i>	ZD.1969.556	Extant	Extant <i>Papio</i>	6.66	2.4009	5.18	3.0869
<i>Papio papio</i>	ZD.1919.7.7.3696	Extant	Extant <i>Papio</i>	11.1	1.6667	6.2	2.9839
<i>Papio ursinus</i>	80774	Extant	Extant <i>Papio</i>	11.01	1.8529	6.34	3.2177
<i>Papio ursinus</i>	81811	Extant	Extant <i>Papio</i>	11.16	2.56	6.73	4.2452
<i>Papio ursinus</i>	169432	Extant	Extant <i>Papio</i>	10.07	1.3486	5.46	2.4872
<i>Papio ursinus</i>	721	Extant	Extant <i>Papio</i>	10	2.23	6.3	3.5397
<i>Papio ursinus</i>	722	Extant	Extant <i>Papio</i>	10.6	2.6415	6.8	4.1176
<i>Papio ursinus</i>	755	Extant	Extant <i>Papio</i>	10.7	2.5607	6.1	4.4918
<i>Papio ursinus</i>	756	Extant	Extant <i>Papio</i>	11.2	2.25	6.8	3.7059
<i>Papio ursinus</i>	757	Extant	Extant <i>Papio</i>	10.3	2.0388	6.2	3.3871
<i>Papio ursinus</i>	774	Extant	Extant <i>Papio</i>	11.5	2.3739	7.1	3.8451
<i>Papio ursinus</i>	780	Extant	Extant <i>Papio</i>	10.8	2.5833	7.1	3.9296
<i>Papio ursinus</i>	781	Extant	Extant <i>Papio</i>	10.6	2.4245	6.4	4.0156
<i>Papio ursinus</i>	783	Extant	Extant <i>Papio</i>	11.3	2.5487	6.6	4.3636
<i>Papio ursinus</i>	785	Extant	Extant <i>Papio</i>	11.4	2.307	7	3.7571
<i>Papio</i>	786	Extant	Extant	11.6	2.2845	6.7	3.9552

<i>ursinus</i>			<i>Papio</i>				
<i>Papio ursinus</i>	788	Extant	Extant <i>Papio</i>	10.9	2.2661	6.7	3.6866
<i>Papio ursinus</i>	789	Extant	Extant <i>Papio</i>	11.6	2.4224	6.9	4.0725
<i>Papio ursinus</i>	791	Extant	Extant <i>Papio</i>	11.3	2.3717	6.2	4.3226
<i>Papio ursinus</i>	792	Extant	Extant <i>Papio</i>	11.1	2.2883	6.3	4.0317
<i>Papio ursinus</i>	793	Extant	Extant <i>Papio</i>	11.3	2.4336	5.8	4.7414
<i>Papio ursinus</i>	795	Extant	Extant <i>Papio</i>	11.1	2.6126	6.8	4.2647
<i>Papio ursinus</i>	796	Extant	Extant <i>Papio</i>	11	2.3545	6.5	3.9846
<i>Papio ursinus</i>	797	Extant	Extant <i>Papio</i>	11.2	2.4554	6.3	4.3651
<i>Papio ursinus</i>	799	Extant	Extant <i>Papio</i>	10.7	2.243	5.6	4.2857
<i>Papio ursinus</i>	800	Extant	Extant <i>Papio</i>	10.6	1.9528	6.3	3.2857
<i>Papio ursinus</i>	801	Extant	Extant <i>Papio</i>	10.3	2.3592	5.5	4.4182
<i>Papio ursinus</i>	803	Extant	Extant <i>Papio</i>	10.8	2.3333	6.5	3.8769
<i>Papio ursinus</i>	804	Extant	Extant <i>Papio</i>	10.9	2.6697	6.1	4.7705
<i>Papio ursinus</i>	805	Extant	Extant <i>Papio</i>	11.1	2.6036	6.5	4.4462
<i>Papio ursinus</i>	806	Extant	Extant <i>Papio</i>	10.7	2.5234	7.2	3.75
<i>Papio ursinus</i>	808	Extant	Extant <i>Papio</i>	10.8	2.6019	6.2	4.5323

<i>Papio ursinus</i>	809	Extant	Extant <i>Papio</i>	10.3	2.3107	5.8	4.1034
<i>Papio ursinus</i>	811	Extant	Extant <i>Papio</i>	10.9	2.578	6.4	4.3906
<i>Papio ursinus</i>	911	Extant	Extant <i>Papio</i>	11.4	2.2105	6.5	3.8769
<i>Papio ursinus</i>	919	Extant	Extant <i>Papio</i>	11.7	2.5385	7	4.2429
<i>Papio ursinus</i>	931	Extant	Extant <i>Papio</i>	10.6	2.6509	6.4	4.3906
<i>Papio ursinus</i>	1895	Extant	Extant <i>Papio</i>	10.8	2.4352	6.6	3.9848
<i>Papio ursinus</i>	3194	Extant	Extant <i>Papio</i>	10.4	2.6058	6.4	4.2344
<i>Papio ursinus</i>	3929	Extant	Extant <i>Papio</i>	11.4	2.4298	6.6	4.197
<i>Papio ursinus</i>	4443	Extant	Extant <i>Papio</i>	10.2	2.7745	7.6	3.7237
<i>Papio ursinus</i>	6614	Extant	Extant <i>Papio</i>	11.1	2.2432	7.1	3.507
<i>Papio ursinus</i>	6615	Extant	Extant <i>Papio</i>	12.5	2.192	6.5	4.2154
<i>Papio ursinus</i>	7051	Extant	Extant <i>Papio</i>	11.1	2.2703	6.8	3.7059
<i>Papio ursinus</i>	8967	Extant	Extant <i>Papio</i>	11.4	2.6491	6.6	4.5758
<i>Papio ursinus</i>	9946	Extant	Extant <i>Papio</i>	10.5	2.2952	5.9	4.0847
<i>Papio ursinus</i>	11505	Extant	Extant <i>Papio</i>	10	2.3	6.6	3.4848
<i>Papio ursinus</i>	11705	Extant	Extant <i>Papio</i>	10.6	2.0094	6.6	3.2273
<i>Papio</i>	11707	Extant	Extant	10.9	2.5138	6.7	4.0896

<i>ursinus</i>			<i>Papio</i>				
<i>Papio ursinus</i>	11709	Extant	Extant <i>Papio</i>	11.2	2.2589	6.3	4.0159
<i>Papio ursinus</i>	11710	Extant	Extant <i>Papio</i>	9.6	2.9167	6.2	4.5161
<i>Papio ursinus</i>	11711	Extant	Extant <i>Papio</i>	11	2.2182	6.8	3.5882
<i>Papio ursinus</i>	11712	Extant	Extant <i>Papio</i>	10.5	2.4	6.4	3.9375
<i>Papio ursinus</i>	11940	Extant	Extant <i>Papio</i>	10.6	2.4151	6.5	3.9385
<i>Papio ursinus</i>	11941	Extant	Extant <i>Papio</i>	11.5	2.4261	6.8	4.1029
<i>Papio ursinus</i>	11942	Extant	Extant <i>Papio</i>	11.3	2.2478	7.4	3.4324
<i>Papio ursinus</i>	11967	Extant	Extant <i>Papio</i>	11.3	2.2124	6.2	4.0323
<i>Papio ursinus</i>	12351	Extant	Extant <i>Papio</i>	10.7	1.8037	5.7	3.386
<i>Papio ursinus</i>	(IA)4	Extant	Extant <i>Papio</i>	11.2	2.1429	6.2	3.871
<i>Papio ursinus</i>	1025A	Extant	Extant <i>Papio</i>	10.6	2.283	6.4	3.7813
<i>Papio ursinus</i>	1025B	Extant	Extant <i>Papio</i>	10.8	2.1111	6.5	3.5077
<i>Papio ursinus</i>	784B	Extant	Extant <i>Papio</i>	11.4	2.3421	6.6	4.0455
<i>Papio ursinus</i>	807B	Extant	Extant <i>Papio</i>	11.1	2.5586	6.9	4.1159
<i>Papio ursinus</i>	NO#A	Extant	Extant <i>Papio</i>	11.6	2.0345	7.5	3.1467
<i>Papio ursinus</i>	7779	Extant	Extant <i>Papio</i>	9.8	2.4592	6.9	3.4928

<i>Papio ursinus</i>	ZA 233	Extant	Extant <i>Papio</i>	10.6	2.5094	6.7	3.9701
<i>Papio ursinus</i>	ZA 663	Extant	Extant <i>Papio</i>	11	2.0636	7.1	3.1972
<i>Papio ursinus</i>	ZA 696	Extant	Extant <i>Papio</i>	10.8	2.2222	6.6	3.6364
<i>Papio angusticeps</i>	CO 103+115	Cooper's A	Fossil <i>Papio</i>	9.7	1.9897	5.2	3.7115
<i>Papio angusticeps</i>	CO 134B/D	Cooper's A	Fossil <i>Papio</i>	11.7	2.5385	6	4.95
<i>Papio angusticeps</i>	COB 1	Cooper's A	Fossil <i>Papio</i>			5.2	2.8846
<i>Papio angusticeps</i>	KA 166A	Kromdraai A	Fossil <i>Papio</i>			5.9	3.2373
<i>Papio angusticeps</i>	56766	Bolt's Farm Pit 6	Fossil <i>Papio</i>	9.67	2.1489	5.83	3.5643
<i>Papio angusticeps</i>	56768	Bolt's Farm Pit 6	Fossil <i>Papio</i>	11.03	1.6319	7.64	2.356
<i>Papio angusticeps</i>	56773	Bolt's Farm Pit 6	Fossil <i>Papio</i>	10.58	1.9178	6.37	3.1852
<i>Papio cf. robinsoni</i>	KB 288	Kromdraai B	Fossil <i>Papio</i>			5.5	3.9455
<i>Papio cf. robinsoni</i>	KB 3416	Kromdraai B	Fossil <i>Papio</i>			5.4	2.2222
<i>Papio robinsoni</i>	SK 406	Swartkrans	Fossil <i>Papio</i>			7.31	3.4323
<i>Papio robinsoni</i>	SK 408	Swartkrans	Fossil <i>Papio</i>	10.71	2.2362	7.27	3.2944
<i>Papio robinsoni</i>	SK 434	Swartkrans	Fossil <i>Papio</i>			7	2.7571
<i>Papio robinsoni</i>	Skx 4810	Swartkrans	Fossil <i>Papio</i>			6.14	3.3632
<i>Papio</i>	Skx 6771	Swartkrans	Fossil			6.35	3.6

<i>robinsoni</i>			<i>Papio</i>				
<i>Papio robinsoni</i>	Skx 8394	Swartkrans	Fossil <i>Papio</i>			6.45	3.7953
<i>Papio robinsoni</i>	Skx 8635	Swartkrans	Fossil <i>Papio</i>			6.6	3.1576
<i>Papio robinsoni</i>	STS 358	Swartkrans	Fossil <i>Papio</i>	10.4	1.8846	6.9	2.8406
<i>Parapapio ado</i>	LAET 78-5288	Laetoli	<i>Parapapio</i>			5.8	1.7931
<i>Parapapio broomi</i>	M 3067	Makapansgat	<i>Parapapio</i>	9.7	1.4845	5.1	2.8235
<i>Parapapio broomi</i>	STS 258	Sterkfontein Type Site	<i>Parapapio</i>	9.9	1.3838	5.5	2.4909
<i>Parapapio broomi</i>	STS 270	Sterkfontein Type Site	<i>Parapapio</i>	9.1	1.8571	5.7	2.9649
<i>Parapapio broomi</i>	STS 283	Sterkfontein Type Site	<i>Parapapio</i>			5.1	2.9216
<i>Parapapio broomi</i>	STS 296	Sterkfontein Type Site	<i>Parapapio</i>			5.7	2.4211
<i>Parapapio broomi</i>	STS 323	Sterkfontein Type Site	<i>Parapapio</i>			5.8	2.7414
<i>Parapapio broomi</i>	STS 337	Sterkfontein Type Site	<i>Parapapio</i>	9.8	1.398	5.2	2.6346
<i>Parapapio broomi</i>	STS 360	Sterkfontein Type Site	<i>Parapapio</i>	10.5	1.2667		
<i>Parapapio broomi</i>	STS 379	Sterkfontein Type Site	<i>Parapapio</i>	9.9	1.5556	6.4	2.4063
<i>Parapapio broomi</i>	STS 440	Sterkfontein Type Site	<i>Parapapio</i>			5.9	2.1864
<i>Parapapio broomi</i>	STS 533	Sterkfontein Type Site	<i>Parapapio</i>	10.9	1.5138	5.8	2.8448
<i>Parapapio broomi</i>	MP 10 (=M 210)	Makapansgat	<i>Parapapio</i>	10.3	1.5825	5.4	3.0185

<i>Parapapio broomi</i>	MP 11 (=M 211)	Makapansgat	<i>Parapapio</i>			5.4	3.0556
<i>Parapapio broomi</i>	MP 15 (=M 215)	Makapansgat	<i>Parapapio</i>			5.7	2.0702
<i>Parapapio broomi</i>	MP 92 (=M 2978)	Makapansgat	<i>Parapapio</i>	10.1	1.495	5.9	2.5593
<i>Parapapio cf. jonesi</i>	AL 363-1	Hadar	<i>Parapapio</i>	9.2	1.3696	4.8	2.625
<i>Parapapio jonesi</i>	STS 125B	Sterkfontein Type Site	<i>Parapapio</i>			4.9	2.9592
<i>Parapapio jonesi</i>	STS 348	Sterkfontein Type Site	<i>Parapapio</i>			4.9	2.5918
<i>Parapapio jonesi</i>	SWP 15/245	Sterkfontein Member 4	<i>Parapapio</i>	8.5	1.8588	4.3	3.6744
<i>Parapapio jonesi</i>	SWP 3	Sterkfontein Member 4	<i>Parapapio</i>	8.9	1.6629	5.4	2.7407
<i>Parapapio whitei</i>	M 3062	Makapansgat	<i>Parapapio</i>	10.6	1.5283	6.32	2.5633
<i>Parapapio whitei</i>	M 3085	Makapansgat	<i>Parapapio</i>	10.2	1.4902	7.7	1.974
<i>Parapapio whitei</i>	STS 389	Sterkfontein Type Site	<i>Parapapio</i>			5.6	2.8929
<i>Parapapio whitei</i>	STS 414A	Sterkfontein Type Site	<i>Parapapio</i>	10.2	1.4804	5.7	2.6491

Appendix 2. Upper premolar and molar measurements used in this study by specimen.

Taxon Name	Specimen ID	Site	Fossil or Extant	Upper Molar Anterior Width (UM2AW)	Relative Flange Length (UP3FL/UM2AW)	Upper Third Premolar Width (UP3W)	Relative Flange Length (UP3FL/UP3W)
<i>Papio anubis</i>	52677	Extant	Extant <i>Papio</i>	12.7	0.711	8.29	1.0893
<i>Papio anubis</i>	55446	Extant	Extant <i>Papio</i>	12.88	0.472	7.51	0.8096
<i>Papio anubis</i>	161116	Extant	Extant <i>Papio</i>	10.74	0.6136	7.67	0.8592
<i>Papio anubis</i>	161117	Extant	Extant <i>Papio</i>	11.47	0.6853	7.56	1.0397
<i>Papio cynocephalus</i>	161734	Extant	Extant <i>Papio</i>	10.23	0.5885	7.5	0.8027
<i>Papio hamadryas</i>	90419	Extant	Extant <i>Papio</i>	12.1	0.7025	8.2	1.0366
<i>Papio hamadryas</i>	200886	Extant	Extant <i>Papio</i>	11.9	0.7647	8.6	1.0581
<i>Papio hamadryas</i>	1	Extant	Extant <i>Papio</i>	11.62	0.6678	7.48	1.0374
<i>Papio kindae</i>	80796	Extant	Extant <i>Papio</i>	8.36	0.8146	6.47	1.0526
<i>Papio kindae</i>	ZD.1961.753	Extant	Extant <i>Papio</i>	9.8	0.6531	6.9	0.9275
<i>Papio kindae</i>	ZD.1961.766	Extant	Extant <i>Papio</i>	10.2	0.6569	5.6	1.1964
<i>Papio kindae</i>	ZD.1961.769	Extant	Extant <i>Papio</i>	9.2	0.7283	6.3	1.0635
<i>Papio kindae</i>	ZD.1961.770	Extant	Extant <i>Papio</i>	10.4	0.5	6.2	0.8387

<i>Papio kindae</i>	ZD.1961.775	Extant	Extant <i>Papio</i>	9.2	0.663	6	1.0167
<i>Papio kindae</i>	ZD.1969.555	Extant	Extant <i>Papio</i>	10.7	0.6636	7.4	0.9595
<i>Papio kindae</i>	ZD.1969.556	Extant	Extant <i>Papio</i>	9.84	0.687	5.76	1.1736
<i>Papio papio</i>	ZD.1919.7.7.3696	Extant	Extant <i>Papio</i>	12.4	0.5645	8.6	0.814
<i>Papio ursinus</i>	80774	Extant	Extant <i>Papio</i>	11.63	0.7163	7.72	1.079
<i>Papio ursinus</i>	81811	Extant	Extant <i>Papio</i>	12.06	0.7488	8.37	1.0789
<i>Papio ursinus</i>	169432	Extant	Extant <i>Papio</i>	11.39	0.5329	7.13	0.8513
<i>Papio ursinus</i>	216249	Extant	Extant <i>Papio</i>	11.71	0.4295	7.53	0.668
<i>Papio ursinus</i>	721	Extant	Extant <i>Papio</i>	12	0.7917	7.4	1.2838
<i>Papio ursinus</i>	722	Extant	Extant <i>Papio</i>	11.9	1.0168	8.4	1.4405
<i>Papio ursinus</i>	755	Extant	Extant <i>Papio</i>	12	0.85	7.8	1.3077
<i>Papio ursinus</i>	756	Extant	Extant <i>Papio</i>	13.3	0.7143	8.2	1.1585
<i>Papio ursinus</i>	774	Extant	Extant <i>Papio</i>	12.3	0.9756	7.8	1.5385
<i>Papio ursinus</i>	780	Extant	Extant <i>Papio</i>	12.1	0.9669	7.6	1.5395
<i>Papio ursinus</i>	783	Extant	Extant <i>Papio</i>	12.4	0.7984	7.7	1.2857
<i>Papio ursinus</i>	785	Extant	Extant <i>Papio</i>	12.5	0.696	7.6	1.1447
<i>Papio</i>	786	Extant	Extant	12.8	0.7031	7.9	1.1392

<i>ursinus</i>			<i>Papio</i>				
<i>Papio ursinus</i>	788	Extant	Extant <i>Papio</i>	12.2	0.918	8.8	1.2727
<i>Papio ursinus</i>	789	Extant	Extant <i>Papio</i>	12.8	0.6406	6.8	1.2059
<i>Papio ursinus</i>	791	Extant	Extant <i>Papio</i>	12.3	0.7642	7.1	1.3239
<i>Papio ursinus</i>	792	Extant	Extant <i>Papio</i>	11.9	0.7983	8.1	1.1728
<i>Papio ursinus</i>	793	Extant	Extant <i>Papio</i>	12.7	0.7638	7.1	1.3662
<i>Papio ursinus</i>	795	Extant	Extant <i>Papio</i>	12.8	0.6875	7.9	1.1139
<i>Papio ursinus</i>	796	Extant	Extant <i>Papio</i>	11.6	0.8879	7.7	1.3377
<i>Papio ursinus</i>	797	Extant	Extant <i>Papio</i>	12.1	0.8182	7.4	1.3378
<i>Papio ursinus</i>	799	Extant	Extant <i>Papio</i>	12.1	0.843	7	1.4571
<i>Papio ursinus</i>	800	Extant	Extant <i>Papio</i>	12.9	0.6744	8.2	1.061
<i>Papio ursinus</i>	801	Extant	Extant <i>Papio</i>	11.9	0.6891	7.5	1.0933
<i>Papio ursinus</i>	803	Extant	Extant <i>Papio</i>	12.7	0.748	7.8	1.2179
<i>Papio ursinus</i>	804	Extant	Extant <i>Papio</i>	11.9	0.8655	7.1	1.4507
<i>Papio ursinus</i>	805	Extant	Extant <i>Papio</i>	12.3	0.8943	8	1.375
<i>Papio ursinus</i>	806	Extant	Extant <i>Papio</i>	12.4	0.8306	8	1.2875
<i>Papio ursinus</i>	808	Extant	Extant <i>Papio</i>	12.2	0.7869	7.6	1.2632

<i>Papio ursinus</i>	809	Extant	Extant <i>Papio</i>	11.8	0.8898	6.8	1.5441
<i>Papio ursinus</i>	811	Extant	Extant <i>Papio</i>	12.2	0.7295	6.9	1.2899
<i>Papio ursinus</i>	911	Extant	Extant <i>Papio</i>	12.8	0.5859	7.2	1.0417
<i>Papio ursinus</i>	919	Extant	Extant <i>Papio</i>	13.6	0.6471	9	0.9778
<i>Papio ursinus</i>	931	Extant	Extant <i>Papio</i>	12.4	0.9113	8	1.4125
<i>Papio ursinus</i>	1895	Extant	Extant <i>Papio</i>	12	0.8	7.7	1.2468
<i>Papio ursinus</i>	3194	Extant	Extant <i>Papio</i>	12	0.95	8.2	1.3902
<i>Papio ursinus</i>	3929	Extant	Extant <i>Papio</i>	13.1	0.6565	7.6	1.1316
<i>Papio ursinus</i>	4443	Extant	Extant <i>Papio</i>	12.7	0.7559	8.1	1.1852
<i>Papio ursinus</i>	6614	Extant	Extant <i>Papio</i>	12	0.7667	8.1	1.1358
<i>Papio ursinus</i>	6615	Extant	Extant <i>Papio</i>	13.7	0.5474	8.2	0.9146
<i>Papio ursinus</i>	6617	Extant	Extant <i>Papio</i>	12.1	0.6777	7.8	1.0513
<i>Papio ursinus</i>	7051	Extant	Extant <i>Papio</i>	12.6	0.746	9	1.0444
<i>Papio ursinus</i>	8967	Extant	Extant <i>Papio</i>	12.7	0.748	8.4	1.131
<i>Papio ursinus</i>	11505	Extant	Extant <i>Papio</i>	11.9	0.8571	8.2	1.2439
<i>Papio ursinus</i>	11705	Extant	Extant <i>Papio</i>	11.7	0.735	7.6	1.1316
<i>Papio</i>	11706	Extant	Extant	10.7	0.9439	6.4	1.5781

<i>ursinus</i>			<i>Papio</i>				
<i>Papio ursinus</i>	11707	Extant	Extant <i>Papio</i>	13.3	0.7669	8.5	1.2
<i>Papio ursinus</i>	11709	Extant	Extant <i>Papio</i>	12.7	0.7402	8.1	1.1605
<i>Papio ursinus</i>	11710	Extant	Extant <i>Papio</i>	11.6	1.0259	7.9	1.5063
<i>Papio ursinus</i>	11711	Extant	Extant <i>Papio</i>	12.3	0.878	8.6	1.2558
<i>Papio ursinus</i>	11712	Extant	Extant <i>Papio</i>	11.8	0.8051	7.8	1.2179
<i>Papio ursinus</i>	11940	Extant	Extant <i>Papio</i>	12.7	0.7323	7	1.3286
<i>Papio ursinus</i>	11941	Extant	Extant <i>Papio</i>	13.5	0.9259	8.7	1.4368
<i>Papio ursinus</i>	11942	Extant	Extant <i>Papio</i>	12.8	0.8438	8	1.35
<i>Papio ursinus</i>	11967	Extant	Extant <i>Papio</i>	13	0.5923	7.6	1.0132
<i>Papio ursinus</i>	12351	Extant	Extant <i>Papio</i>	12.3	0.5041	7.1	0.8732
<i>Papio ursinus</i>	19837	Extant	Extant <i>Papio</i>	12.3	0.6748	8.2	1.0122
<i>Papio ursinus</i>	1025A	Extant	Extant <i>Papio</i>	12.1	0.7769	7.6	1.2368
<i>Papio ursinus</i>	1025B	Extant	Extant <i>Papio</i>	11.4	0.7632	7.1	1.2254
<i>Papio ursinus</i>	784B	Extant	Extant <i>Papio</i>	13	0.8462	7.9	1.3924
<i>Papio ursinus</i>	807B	Extant	Extant <i>Papio</i>	12.7	0.8819	7.7	1.4545
<i>Papio ursinus</i>	NO#A	Extant	Extant <i>Papio</i>	13.3	0.7594	9.2	1.0978

<i>Papio ursinus</i>	7779	Extant	Extant <i>Papio</i>	11.6	0.7672	6.8	1.3088
<i>Papio ursinus</i>	ZA 233	Extant	Extant <i>Papio</i>	12.5	0.616	7.7	1
<i>Papio ursinus</i>	ZA 663	Extant	Extant <i>Papio</i>	12.4	0.629	7.2	1.0833
<i>Papio ursinus</i>	ZA 696	Extant	Extant <i>Papio</i>	12.3	0.6585	8.3	0.9759
<i>Papio angusticeps</i>	CO 100	Cooper's A	Fossil <i>Papio</i>	10.9	0.7523	7.5	1.0933
<i>Papio angusticeps</i>	CO 117	Cooper's A	Fossil <i>Papio</i>	11	0.9545	8.3	1.2651
<i>Papio angusticeps</i>	CO 134B/D	Cooper's A	Fossil <i>Papio</i>	12.9	0.938	8.3	1.4578
<i>Papio angusticeps</i>	KA 156	Kromdraai A	Fossil <i>Papio</i>	11.6	0.7241	7.3	1.1507
<i>Papio angusticeps</i>	56766	Bolt's Farm Pit 6	Fossil <i>Papio</i>	11.64	0.6503	7.83	0.9668
<i>Papio robinsoni</i>	SK 449	Swartkrans	Fossil <i>Papio</i>			9.4	1.0957
<i>Papio robinsoni</i>	SK 466	Swartkrans	Fossil <i>Papio</i>			8.6	0.9535
<i>Papio robinsoni</i>	SK 547	Swartkrans	Fossil <i>Papio</i>	12.4	0.9274		
<i>Papio robinsoni</i>	SK 555	Swartkrans	Fossil <i>Papio</i>	12.8	0.8984	9.3	1.2366
<i>Papio robinsoni</i>	SK 602	Swartkrans	Fossil <i>Papio</i>	12.41	1.0492	10.1	1.2891
<i>Papio robinsoni</i>	BF 38	Bolt's Farm Pit 23	Fossil <i>Papio</i>	12.4	0.8548		
<i>Parapapio whitei</i>	M 3072	Makapansgat	<i>Parapapio</i>	12.5	0.608	8	0.95
<i>Parapapio</i>	MP 221	Makapansgat	<i>Parapapio</i>	11.7	0.7265		

<i>whitei</i>							
<i>Parapapio whitei</i>	MP 223	Makapansgat	<i>Parapapio</i>	12	0.6	8.4	0.8571