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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

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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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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

Cercopithecid 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, cercopithecid 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 realtively 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, Swartkans, 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 P_3 flanges in male *Parapapio* appeared to be consistently shorter than those of male *Papio*. If the P_3 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 P_3 flange length, but also P^3 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

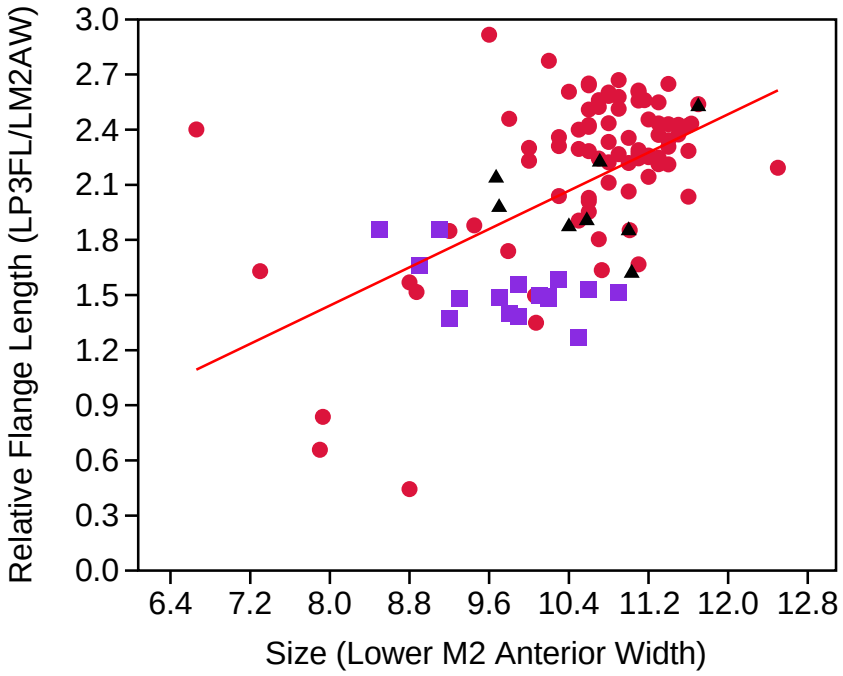
Abbreviation	Description
LM_2AW	Lower second molar anterior breadth across the mesial lophid
LP_3FL	Lower third premolar mesiodistal flange length
LP_3W	Lower third premolar buccolingual breadth
UM_2AW	Upper second molar anterior breadth across the mesial loph
UP_3FL	Upper third premolar mesiodistal flange length
UP_3W	Upper third premolar buccolingual breadth

Table 2: Key for all following figures.

Taxon	Symbol
Extant *Papio*	
Fossil *Papio*	
Parapapio	

5. Results:

Figure 1: Linear Fit Model of P_3 Flange Length vs. Size (M_2 Anterior Width).



A least square regression between size and relative P_3 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 P_3 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 P_3 flange length relative to M_2 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 P_3 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 P_3 Flange Length vs. Size (M_2 Ant. Width)

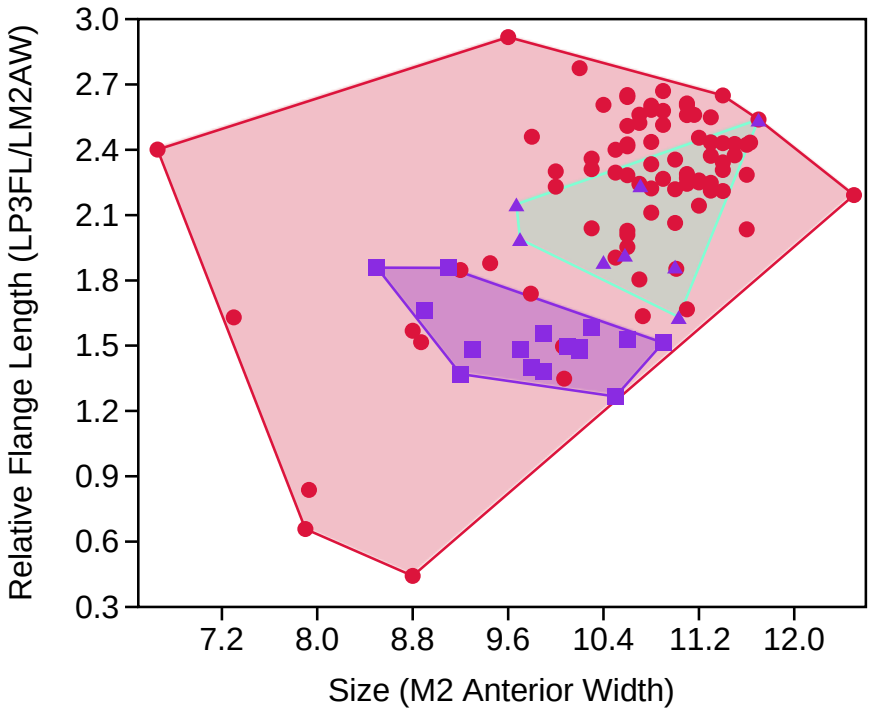
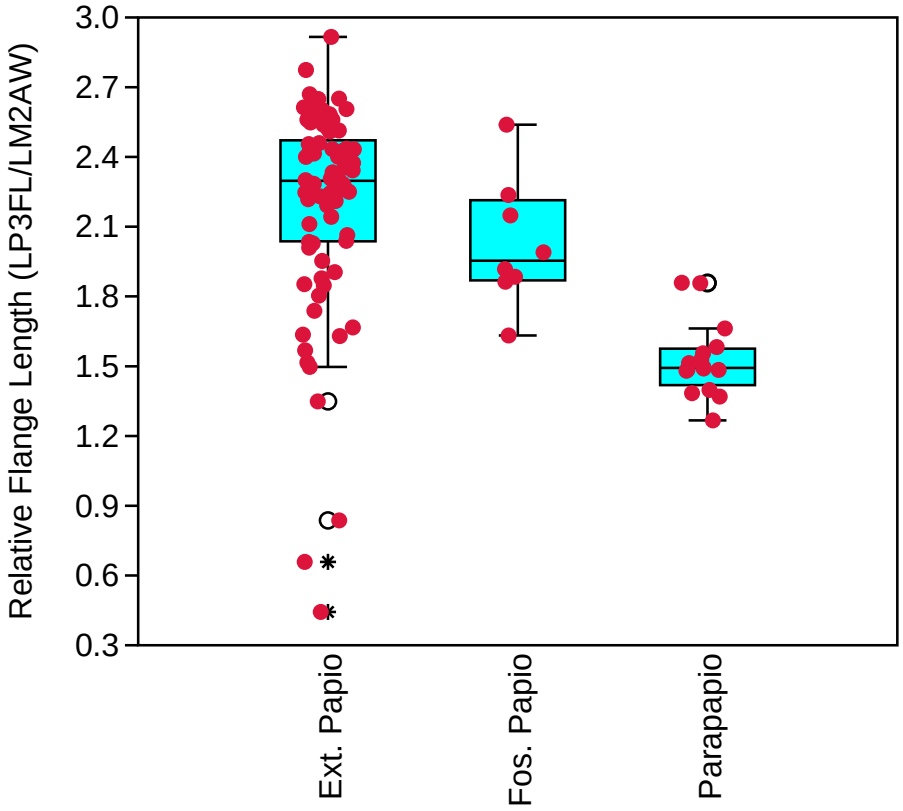
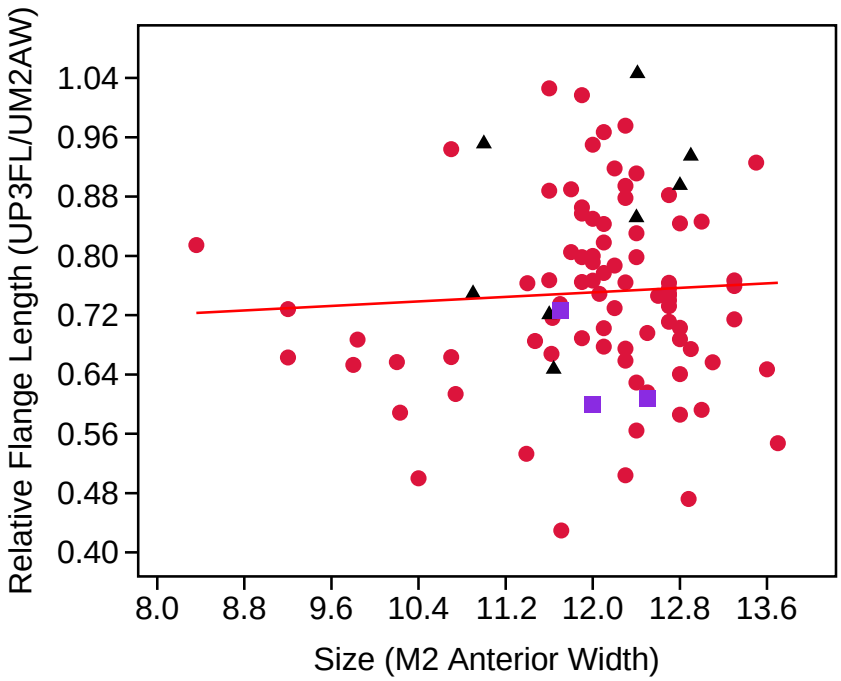


Figure 3: Relative P_3 flange length as a box and jitter plot.



Analysis of P^3 relative flange length relative to M^2 anterior width is similar. A least square regression between size and relative P^3 flange length shows no correlation with size (Fig. 4; p=0.5844 and r^2=0.0032439).

Figure 4: Linear fit model of P^3 flange length vs. size (M^2 Ant. Width)



Similar to the situation with the lower premolar flange lengths, an X-Y plot of P^3 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 P^3 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 P^3 Flange Length vs. Size (M_2 Ant. Width)

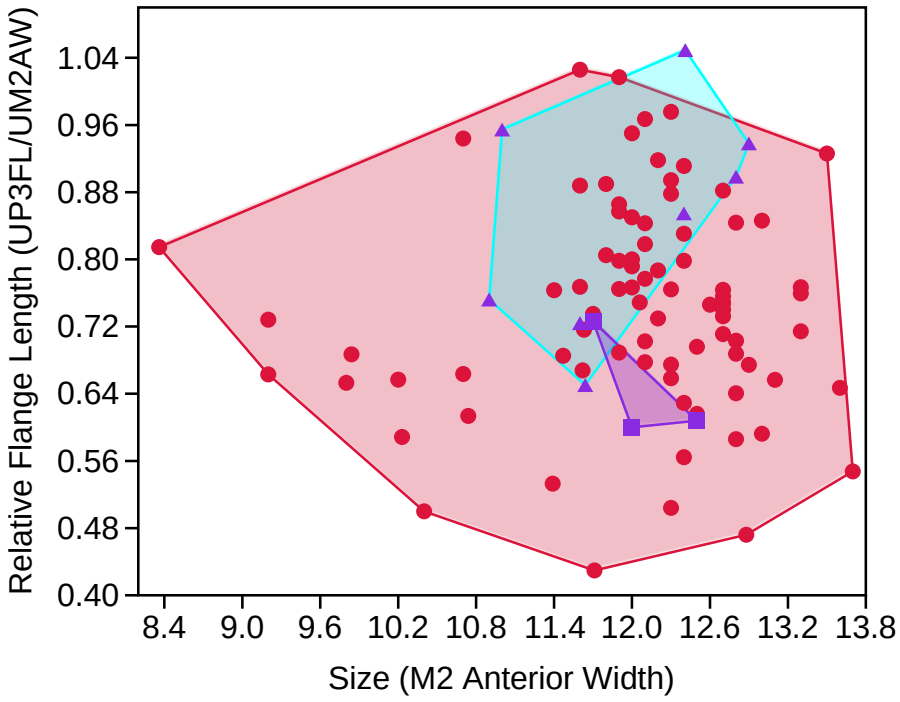
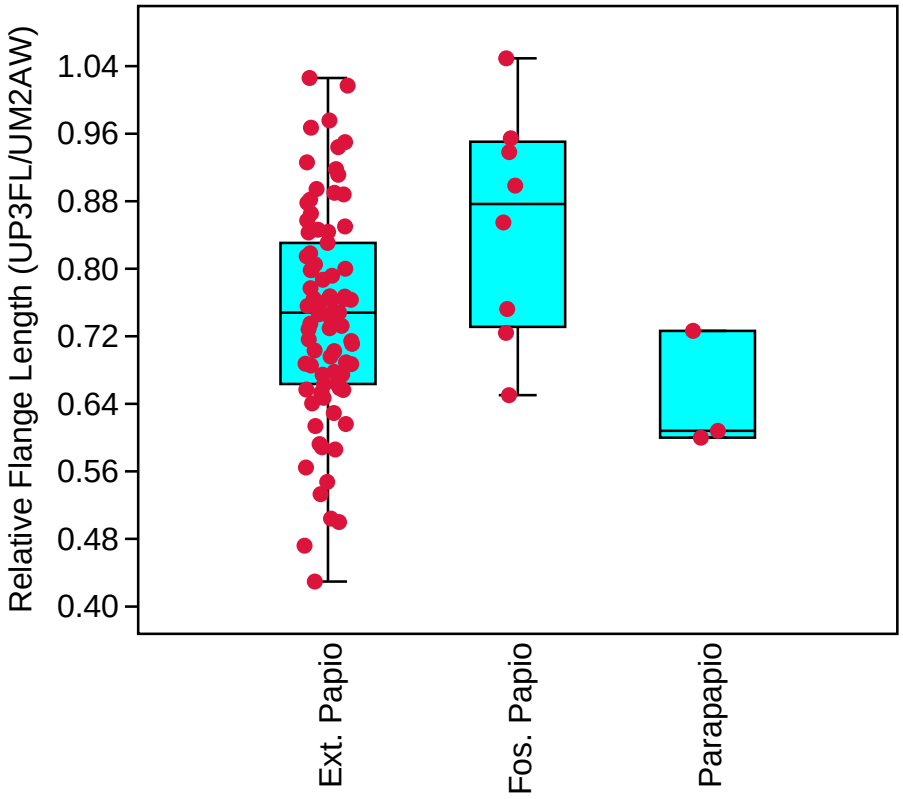
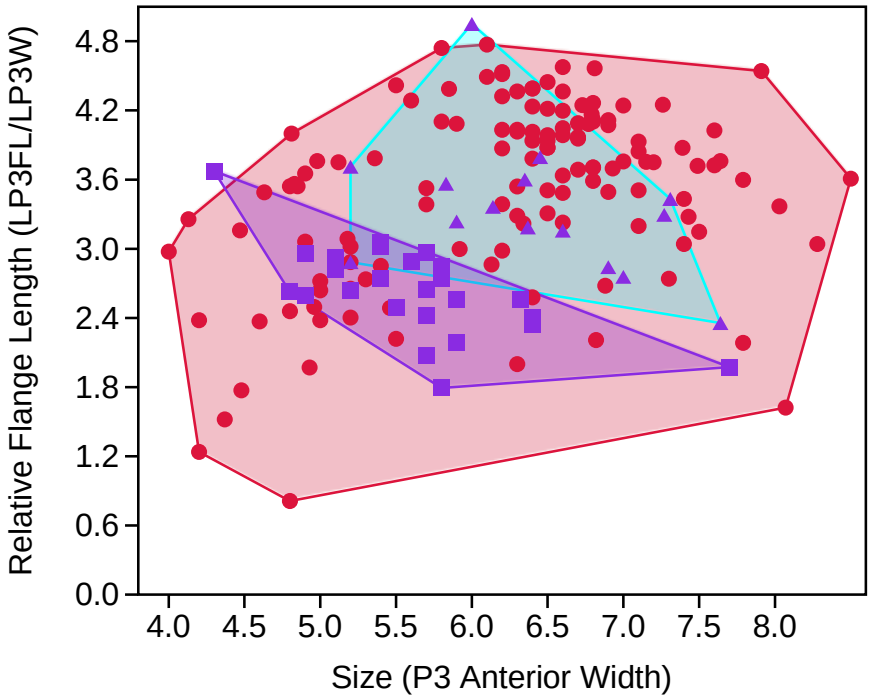


Figure 6: Relative P^3 flange length as a box and jitter plot.



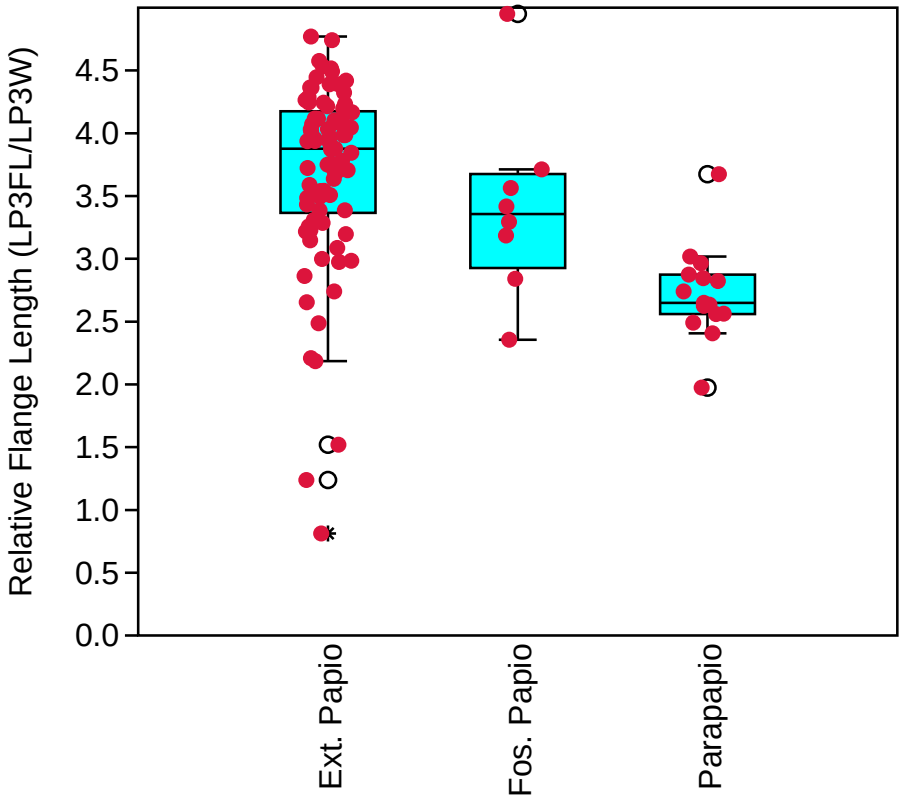
To include more specimens and keep measurements internal to the third premolar, separate analyses were also conducted for relative P_3 and P^3 flange length using P3 breadth as the denominator. The results are very similar to those using M^2 anterior width as the size correction (see Figs. 7-10). An X-Y plot of P_3 mesiodistal flange length vs. P_3 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 P_3 flange length at any given P_3 breadth (one known fossil *Papio* specimen overlaps the *Parapapio* range).

Figure 7. X-Y plot with convex hulls for relative P_3 Flange Length vs. Size (P_3 max width).



Just like with M_2 anterior breadth as the size correlate, an ANOVA between groups for the P_3 relative flange length ratio using P_3 anterior width is highly significant ($p<0.0001$), and post-hoc comparisons reveal that extant *Papio* and fossil *Papio* have significantly longer P_3 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 P_3 flange length as a box and jitter plot.



Finally, analysis of P^3 relative flange length using P^3 maximum breadth in the demominator 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 P^3 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 P^3 Flange Length vs. Size (P^3 max width).

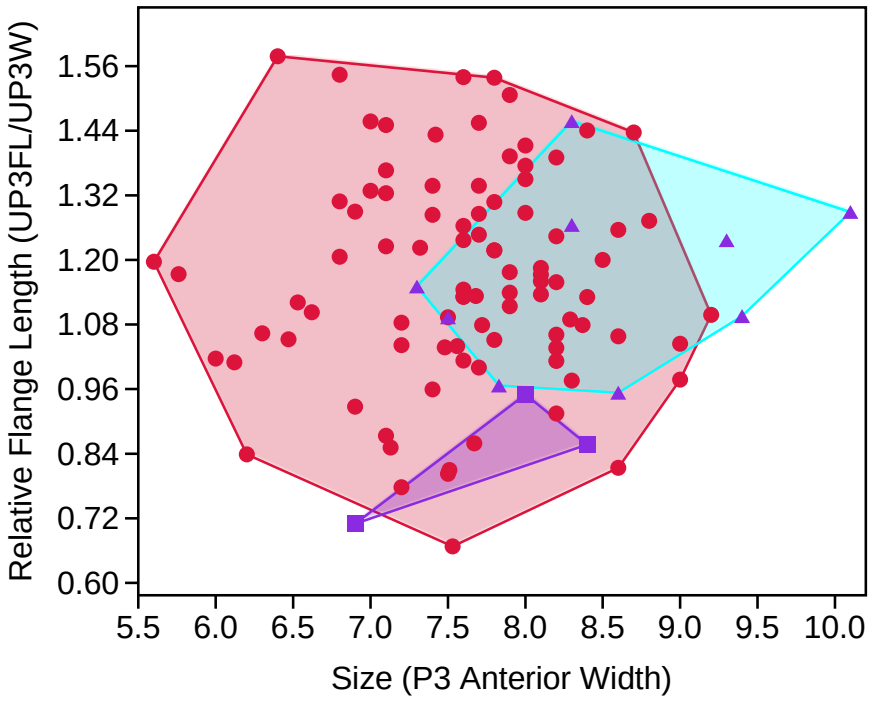
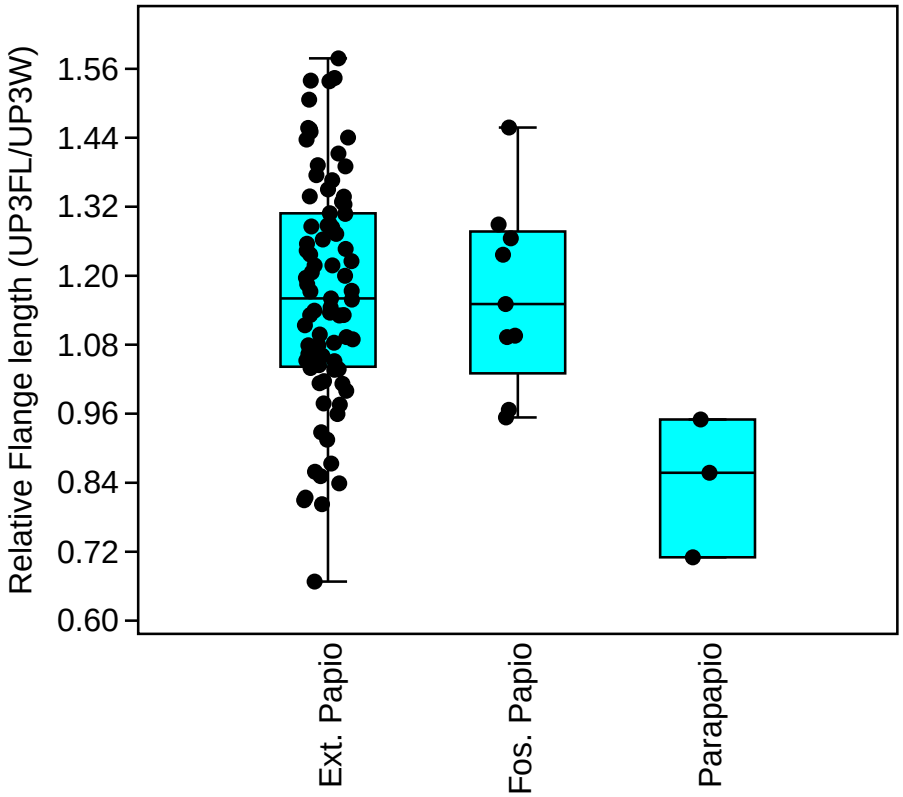


Figure 10. Relative P^3 flange length as a box and jitter plot.



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 extat *Papio* taxa; previous authors have suggestd 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)
Papio anubis	52677	Extant	Extant *Papio*	11.63	2.4325	6.79	4.1664
Papio anubis	55446	Extant	Extant *Papio*	10.73	1.6356	6.13	2.863
Papio anubis	161116	Extant	Extant *Papio*	9.79	1.7385	7.79	2.1849
Papio anubis	161117	Extant	Extant *Papio*	10.06	1.497	6.82	2.2082
Papio cynocephalus	161734	Extant	Extant *Papio*	9.45	1.8783	5.92	2.9983
Papio hamadryas	90419	Extant	Extant *Papio*	10.5	1.9048	7.3	2.7397
Papio hamadryas	200886	Extant	Extant *Papio*	10.6	2.0283	6.5	3.3077
Papio kindae	80796	Extant	Extant *Papio*	7.93	0.8373	4.37	1.5195
Papio kindae	ZD.1961.753	Extant	Extant *Papio*	8.8	1.5682	5.2	2.6538
Papio kindae	ZD.1961.766	Extant	Extant *Papio*	8.8	0.4432	4.8	0.8125
Papio kindae	ZD.1961.769	Extant	Extant *Papio*	7.9	0.6582	4.2	1.2381
Papio kindae	ZD.1961.770	Extant	Extant *Papio*	8.87	1.5163	4.13	3.2567
Papio kindae	ZD.1961.775	Extant	Extant *Papio*	7.3	1.6301	4	2.975

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

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

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

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

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

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

Parapapio broomi	MP 11 (=M 211)	Makapansgat	*Parapapio*			5.4	3.0556
Parapapio broomi	MP 15 (=M 215)	Makapansgat	*Parapapio*			5.7	2.0702
Parapapio broomi	MP 92 (=M 2978)	Makapansgat	*Parapapio*	10.1	1.495	5.9	2.5593
Parapapio cf. jonesi	AL 363-1	Hadar	*Parapapio*	9.2	1.3696	4.8	2.625
Parapapio jonesi	STS 125B	Sterkfontein Type Site	*Parapapio*			4.9	2.9592
Parapapio jonesi	STS 348	Sterkfontein Type Site	*Parapapio*			4.9	2.5918
Parapapio jonesi	SWP 15/245	Sterkfontein Member 4	*Parapapio*	8.5	1.8588	4.3	3.6744
Parapapio jonesi	SWP 3	Sterkfontein Member 4	*Parapapio*	8.9	1.6629	5.4	2.7407
Parapapio whitei	M 3062	Makapansgat	*Parapapio*	10.6	1.5283	6.32	2.5633
Parapapio whitei	M 3085	Makapansgat	*Parapapio*	10.2	1.4902	7.7	1.974
Parapapio whitei	STS 389	Sterkfontein Type Site	*Parapapio*			5.6	2.8929
Parapapio whitei	STS 414A	Sterkfontein Type Site	*Parapapio*	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)
Papio anubis	52677	Extant	Extant *Papio*	12.7	0.711	8.29	1.0893
Papio anubis	55446	Extant	Extant *Papio*	12.88	0.472	7.51	0.8096
Papio anubis	161116	Extant	Extant *Papio*	10.74	0.6136	7.67	0.8592
Papio anubis	161117	Extant	Extant *Papio*	11.47	0.6853	7.56	1.0397
Papio cynocephalus	161734	Extant	Extant *Papio*	10.23	0.5885	7.5	0.8027
Papio hamadryas	90419	Extant	Extant *Papio*	12.1	0.7025	8.2	1.0366
Papio hamadryas	200886	Extant	Extant *Papio*	11.9	0.7647	8.6	1.0581
Papio hamadryas	1	Extant	Extant *Papio*	11.62	0.6678	7.48	1.0374
Papio kindae	80796	Extant	Extant *Papio*	8.36	0.8146	6.47	1.0526
Papio kindae	ZD.1961.753	Extant	Extant *Papio*	9.8	0.6531	6.9	0.9275
Papio kindae	ZD.1961.766	Extant	Extant *Papio*	10.2	0.6569	5.6	1.1964
Papio kindae	ZD.1961.769	Extant	Extant *Papio*	9.2	0.7283	6.3	1.0635
Papio kindae	ZD.1961.770	Extant	Extant *Papio*	10.4	0.5	6.2	0.8387

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

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

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

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

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

whitei							
Parapapio whitei	MP 223	Makapansgat	*Parapapio*	12	0.6	8.4	0.8571