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Cover Page Footnote

The specimens studied were cast from original specimens and the authors thank the curators who generously provided access to the fossils at the Witwatersrand University Medical School, the South African Museum, the Transvaal Museum, and the Museum of Comparative Zoology. This research was also greatly helped by the addition of two new microscopes, fiber optic light sources, and tri-nocular camera attachments & software to the laboratory, made possible by a Tech Fee grant from the Vice President for Research at Georgia State University. William G. Anderson wishes to thank to Dr. Frank L'Engle Williams for co-authoring this research, and providing mentorship and support throughout the years. Brian Carter kindly provided a photograph of *C. williamsi* specimen STS 344 (Figure 1).

Reconstructing the Dietary Signal of the Primate Taxon *Cercopithecoides williamsi* from the Plio-Pleistocene Caves of South Africa

The extinct taxon known as *Cercopithecoides williamsi*, an Old World monkey, has been reconstructed as a terrestrial primate folivore (primary leaf-eater) from its dental morphology and heavy dental microwear. Dental microwear, which results from the repeated use of the teeth during the mastication of foods, is expressed as a variety of pits and scratches on the enamel surface and can indicate dietary proclivities as well as paleoecological conditions. *Cercopithecoides williamsi* is preserved at a number of Plio-Pleistocene (2.5-1.5 mya) caves in South Africa, including Makapansgat, Sterkfontein Member 4, Sterkfontein West Pit and Bolt's Farm. In South Africa, the Plio-Pleistocene time period witnessed the emergence of stone tools, the appearance of the genus *Homo*, *Australopethicus robustus*, and terrestrial primate folivores such as *C. williamsi*. The significance of the study is that the evolution of diet in *C. williamsi* indicates a change from a warmer and wetter to a cooler and drier paleoecology. These changes also affected the evolution of technology, the genus *Homo*, and the robust australopiths in southern Africa during this transitional time frame.

Cercopithecoides williamsi has been described as a folivore primarily from its tall shearing crests (Figure 1) which are often found in leaf monkeys from Africa and Asia, as well as in howler monkeys from the Neotropics. Furthermore, it exhibits a broad intraorbital pillar, which is a known characteristic of paleotropical folivorous monkeys of the Colobinae family. *Cercopithecoides williamsi* has been characterized as a primarily terrestrial animal from postcranial fragments from East Africa and its heavy dental wear, which suggests the ingestion of grit in its diet, suggestive of terrestriality (Williams and Geissler, 2014). For the purposes of corroborating or contradicting previous dietary reconstructions, six dental casts of *Cercopithecoides williamsi* were examined and compared with specimens from nonhuman extant primate species with known diets.



Figure 1: *C. williamsi* Specimen STS 344 showing molars with high cusps

Materials and Methods

The *Cercopithecoides williamsi* material included BF 42A and BF 42B from Bolt's Farm, MP 3 from Makapansgat, SWP 495 from Sterkfontein West Pit, and STS 270 and STS 282 from Sterkfontein Member 4. The comparative sample included *Papio ursinus* (Cape Baboon) (n = 5), *Papio cynocephalus* (Yellow Baboon) (n = 5) and *Colobus polykomos* (King Colobus) (n = 5). Low-magnification stereomicroscopy was employed to observe the dental microwear, defined as any scars on tooth enamel that directly result from pabulum mastication. Simply put, dental microwear is microscopic damage to teeth that results from chewing food. Diet was inferred by counting dental microwear features, including small, large, and puncture pits, and fine, coarse, and hypercoarse scratches (Figure 2). Small pits are shallow and therefore refractive indentations on the enamel surface, whereas large pits are twice the size of small pits and thus less refractive. Puncture pits are crater-like perforations with round edges, and un-refractive. Fine scratches are shallow and refractive

striations in the enamel, whereas coarse scratches are deeper striations and thus less refractive.

Hypercoarse scratches are deep trench-like structures that are non-refractive and require a great deal of applied force to create. Observations of these dental microwear features were taken twice within an ocular reticle (0.04 mm x 0.04 mm) and averaged as a standard sampling strategy (Godfrey et al., 2004; Semprebon et al., 2004; Williams & Patterson, 2010; Williams & Holmes, 2011; Williams and Geissler, 2014). These raw averages of feature occurrence were compiled into a dataset for each specimen and analyzed statistically using least Squares Means, Analyses of Variance, and Tukey's post-hoc tests of significance to detect significant signals in the dataset.

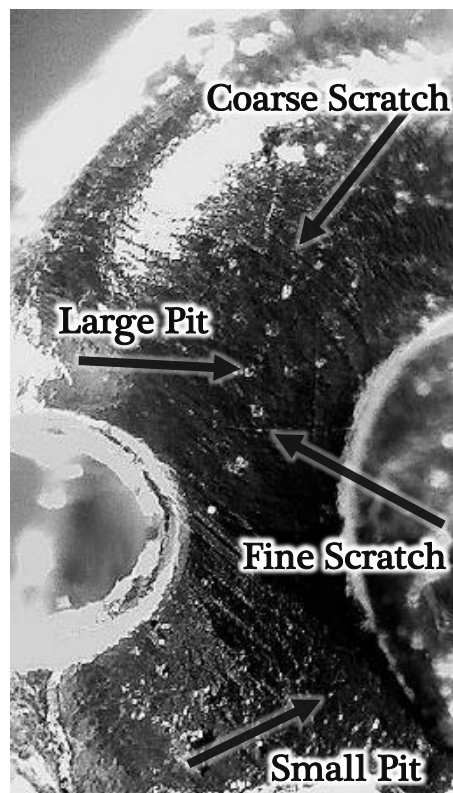


Figure 2: A cusp view of STS 270, *Cercopithecoides williamsi*, illustrating a variety of pits and scratches.

Results

The ANOVA results intimate that all of the microwear features are significant, with p values <0.001. The F values reinforce the presence of between-group differences, and range between 114.819 for fine scratches to 17.107 for coarse scratches. Puncture pits and hypercoarse scratches

were only observed sporadically and were not considered further. Tukey's post-hoc test results, reflected in least squares means (Figures 3 and 4), suggest *P. ursinus* is significantly distinct from the other specimens in its low small pit count ($p < 0.001$) and high coarse scratch frequency ($p < 0.001$), indicative of the consumption of grass blades and underground storage organs. Furthermore, *C. williamsi* is distinct from *C. polykomos* ($p = 0.029$) in fine scratches, suggesting that the dental microwear of the fossil taxon is distinct from that of arboreal (tree-living), folivorous *C. polykomos*. *Papio ursinus* is also significantly different from the other taxa in its coarse scratch count ($p < 0.001$). *Cercopithecus williamsi* generally has a smaller number of large pits compared to *C. polykomos* although the difference is not significant. *Papio ursinus* is distinct in the lack of small pits compared to the other taxa ($p < 0.001$). Meanwhile, *C. polykomos* differs from the other taxa in its excess of large pits ($p < 0.001$), perhaps indicating folivory or some other dietary resource. *Cercopithecoides williamsi* generally falls between *C. polykomos* and both *Papio* species by exhibiting moderate amounts of pits and a relatively low number of scratches on average, which is overall more similar to *C. polykomos*, corroborating prior inferences of folivory in this taxon. The Sterkfontein West Pit specimen, SWP 495, is somewhat distinct from the other *C. williamsi* specimens in its heavier scratch count, indicating a mixed diet, perhaps from a drier habitat at the terminal Pliocene or early Pleistocene, ~2 million years ago.

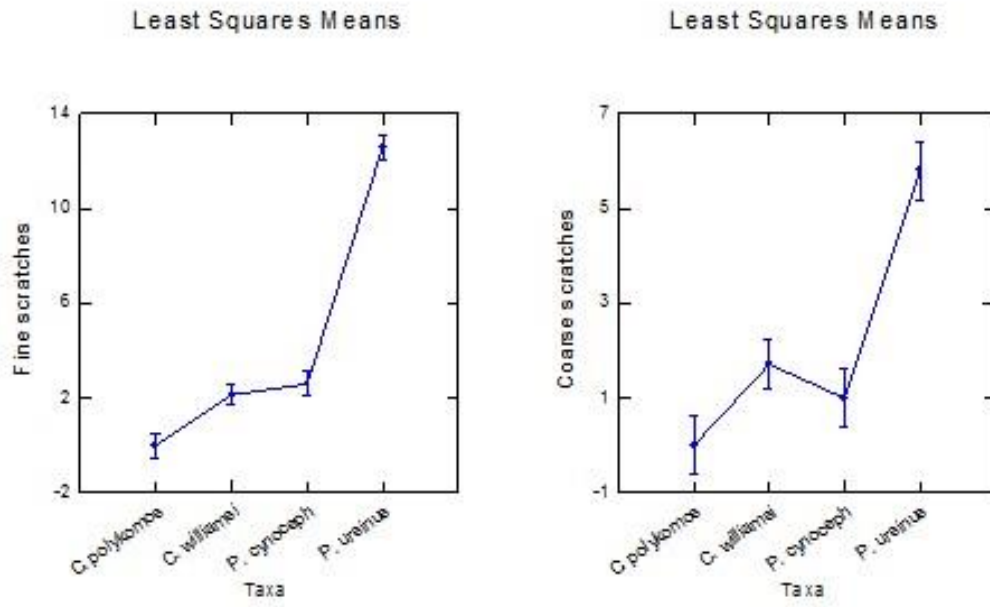


Figure 3: Least square means for fine (left) and coarse (right) scratches

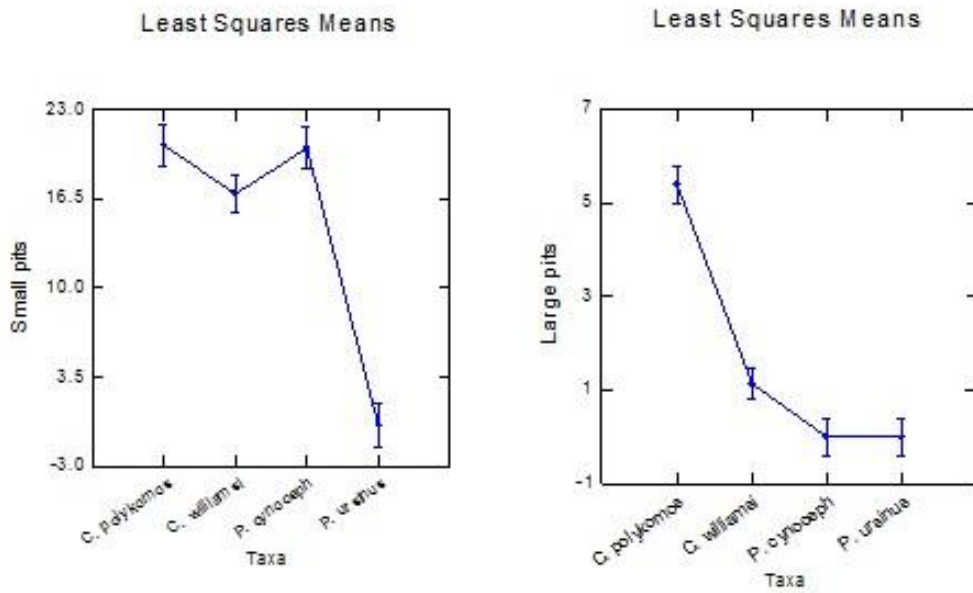


Figure 4: Least square means for small (left) and large (right) pits

Discussion and Conclusions

Cercopithecoides williamsi is distinct from extant *Papio*, and is most similar to *C. polykomos*, suggesting that folivory was an important component of its dietary repertoire. However, it is not identical to *C. polykomos*, indicating differences in diet between the two. The positioning of *C. williamsi* within the comparative data suggests that its diet comprised some gritty foods, such as grass blades and underground storage organs. Because these food items are found close to the ground, the presence of these features most likely indicate terrestriality, or perhaps semi-terrestrial activity. The Sterkfontein West Pit specimen SWP 495, however, has a much heavier scratch count compared to the other specimens from Sterkfontein Member 4, which is indicative of a drier habitat and a diet depending primarily on grasses. Sterkfontein Member 4 has been reconstructed as a woodland habitat with some permanent water sources in the region, whereas Sterkfontein West Pit likely derives from a Pleistocene context which was drier and cooler, with fewer forest resources and greater prevalence of grassland habitats (Codron et al., 2005; Lee-Thorp et al., 2007; Reed, 1997). The heavy dental microwear features of SWP 495 corroborate these habitat reconstructions and indicate that *C. williamsi* at this time must have been pressured to consume less preferred foods than their counterparts in the Pliocene sites of Sterkfontein Member 4, Bolt's Farm, and Makapansgat. *C. williamsi* was one of the only terrestrial colobines in southern Africa, and must have evolved via a reduction of forests and an expansion of open grassland environments.

These findings could therefore provide insights into the causes and implications of the emergence of stone and bone tools in contemporaneous *Australopithecus robustus* and the genus *Homo*. In other words, evidence of terrestrial and semi-terrestrial diets in *C. williamsi* provides paleoecological information that helps explain and corroborate trends in human evolution in southern Africa. These ecological trends include an expansion of open habitats

which may have selected for a greater reliance on tools, cognitive capacity, and bipedality in *Homo*, and tools and teeth in *A. robustus*.

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