

Utilization of savanna-based resources by Plio-Pleistocene baboons

Daryl Codron^{a*}, Julie Luyt^a, Julia A. Lee-Thorp^{b,c},
Matt Sponheimer^{b,d}, Darryl de Ruiter^e and
Jacqui Codron^a

We have determined the tooth enamel carbonate $\delta^{13}\text{C}$ values of five cercopithecoid taxa from the Plio-Pleistocene deposits of Swartkrans Members 1 and 2 and Sterkfontein Member 4. These data were used to determine the relative proportions of C_3 and C_4 biomass consumed by extinct baboons and contemporary non-human primates. We compared these results with data on modern *Papio hamadryas ursinus* from different savanna areas in South Africa, as well as with published isotopic data and dietary interpretations based on molar morphology of these taxa. The data reveal little evidence for use of grasses or grass-based foods by modern South African baboons. The fossil papionins *Papio hamadryas robinsoni*, *Papio (Dinopithecus) ingens*, and *Parapapio* spp., however, utilized more savanna-based C_4 resources than previously predicted (particularly in the case of *P. (D.) ingens*). *Theropithecus oswaldi* had $\delta^{13}\text{C}$ values depicting, as expected, a largely grass-based diet, and we confirm earlier conclusions that this species incorporated a wider range of food items into its diet than do modern *T. gelada*, as reported in the literature. The colobine monkey, *Cercopithecoides williamsi*, made extensive use of savanna-based C_4 foods, confirming some degree of terrestrial foraging by the species.

The feeding habits of extinct baboons and other non-human primates can provide insight into patterns of ecological niche separation that facilitated co-existence of a diversity of taxa, as well as information about the habitat conditions of early African savannas.¹⁻⁴ Indeed, while only a single baboon species, *Papio hamadryas ursinus*, occurs in modern South African savannas, at least four papionin genera or subgenera are known from South African Plio-Pleistocene deposits.^{1,5,6} Few studies have focused on the diets of Plio-Pleistocene baboons, however, and knowledge of their feeding habits is based on limited morphological and stable carbon isotopic evidence.^{1-3,7-9}

Published carbon isotopic data for papionins from Swartkrans Members 1 and 2 suggest predominantly tree, shrub, and forb (C_3 plant)-based diets for all the taxa analysed.⁷⁻⁹ These deposits have been tentatively dated at c. 1.7 and 1.5 Myr ago, respectively, and are believed to represent a fairly open savanna environment.¹⁰ No isotopic data on primates from the older deposits (~2.4–2.6 Myr) of Sterkfontein Member 4, likely representing a more closed, wooded habitat,¹⁰ are available. Evidence from molar morphology indicates that *Papio* species and *Parapapio* spp. were predominantly frugivorous.^{2,3} Previous carbon isotopic data are consistent with this interpretation, since fruits of woody

plants also have a C_3 carbon isotopic signal. However, modern savanna baboons are known to be highly opportunist feeders, using available resources to different degrees, depending on factors including climate, habitat, seasonal availability of resources, and troop or population demographics.¹¹⁻¹⁵ For example, while South African baboons seem to consume few grasses or grass-based items,^{11,14} grasses reportedly contribute significantly more to the diets of their East African counterparts, at least seasonally.^{11-13,15} Given the dietary variability displayed by modern baboons in savannas across Africa, and the limited evidence for the feeding habits of their fossil representatives, we may not assume minimal grass intake for all Plio-Pleistocene taxa. Indeed, the molar morphology of *Papio* and *Parapapio* suggests regionally different diets; East African papionins are believed to have been more frugivorous, whereas South African representatives consumed a higher proportion of leaf material.²

We determined the relative proportions of grass intake by baboons and other non-human primates from the deposits of Swartkrans Members 1 and 2, and Sterkfontein Member 4, through analysis of stable carbon isotopes. Carbon isotopic ratios ($\delta^{13}\text{C}$ values, measured in parts per mil relative to the PDB standard) of savanna animal tissues are a useful measure for reconstructing diet in terms of proportions of C_3 (trees, shrubs, forbs) and C_4 (grass) biomass intake.^{16,17} Tooth enamel carbonate has proved a reliable source of $\delta^{13}\text{C}$ data that is consistent with C_3/C_4 consumption during formation of the tooth, with isotopic fractionation resulting in values 12‰ more enriched in ^{13}C relative to the dietary value.¹⁸ Measurement of $\delta^{13}\text{C}$ values of tooth enamel carbonate followed the widely used pretreatment procedure for isolating the mineral component of tooth enamel (for example see ref. 17). Analytical precision based on repeated measurements of laboratory standards was better than 0.1 ‰.

Carbon isotopic analysis of tooth enamel carbonate in modern *P. h. ursinus* from three South African savanna habitats revealed predominantly C_3 -based diets. Mean $\delta^{13}\text{C}$ values for modern baboon specimens were $-12.2 \pm 0.7\text{‰}$ ($n = 3$) for the Mpumalanga lowveld region of Blydepoort, $-12.1 \pm 0.3\text{‰}$ ($n = 5$) for the mountainous Waterberg region in southwestern Limpopo province, and $-12.9 \pm 1.0\text{‰}$ ($n = 3$) for Mokopane in the Limpopo 'highveld' (Table 1). In the Kruger National Park, the average $\delta^{13}\text{C}$ value for C_3 plants is -26.4‰ ($n = 109$), whereas that for C_4 grasses is -12.1‰ ($n = 110$).¹⁹ Using these values as isotopic 'endpoints', and assuming that tooth enamel carbonate is 12‰ more positive than the dietary value,¹⁸ it is possible to determine a rough estimate of the percentages of grass/browse consumed. For example, a baboon with a pure C_3 diet should display an enamel $\delta^{13}\text{C}$ value around -14‰ . $\delta^{13}\text{C}$ values for modern baboons presented in Table 1 thus reflect consumption of C_4 foods between ~5% and 10%, agreeing with previous findings that grasses do not today make a large contribution to the diets of baboons in South Africa.¹⁴ In addition, stable carbon isotopic data from baboon bone collagen collected from various areas across southern Africa revealed diets that were predominantly based on dicotyledonous woody plants, with slight C_4 intake evident in samples from Limpopo province.²⁰

Published carbon isotopic data for papionins show that *Papio hamadryas robinsoni* ($-11.2 \pm 0.9\text{‰}$, $n = 5$), *Papio (Dinopithecus) ingens* ($-10.6 \pm 0.5\text{‰}$, $n = 3$) and *Parapapio jonesi* ($-11.2 \pm 2.4\text{‰}$, $n = 2$) all had mean $\delta^{13}\text{C}$ values indistinguishable from those of C_3 -browsing ungulates ($-11.4 \pm 0.8\text{‰}$, $n = 9$) from Swartkrans (Table 2). We recognize that *P. jonesi* has been identified at Swartkrans based on isolated dentognathic remains and lacking diagnostic facial morphology; hence the identification of *P. jonesi* in Swartkrans must be tentative. Nevertheless, regardless of tax-

^aQuaternary Research Centre, Department of Archaeology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa.

^bDepartment of Archaeology, University of Cape Town.

^cDepartment of Archaeological Science, Bradford University, Bradford BD7 1DP, U.K.

^dDepartment of Anthropology, University of Colorado at Boulder, Boulder, CO 80309, U.S.A.

^eDepartment of Anthropology, Texas A & M University, College Station, TX 77843-4352, U.S.A.

*Author for correspondence. E-mail: daryl@science.uct.ac.za

Table 1. $\delta^{13}\text{C}$ values of tooth enamel carbonate (per mil, relative to the PDB standard) for modern chacma baboons (*Papio hamadryas ursinus*) from various savanna environments of South Africa.

Locality	Sample ref.	$\delta^{13}\text{C}$ (‰)
Blydepoort	AZ 797	-12.8
	AZ 798	-11.5
	TM 911	-12.3
	Mean	-12.2
	s.d.	0.7
	<i>n</i>	3
Waterberg	AZ 769	-12.4
	AZ 770	-12.1
	AZ 790	-11.8
	UCT 9786	-12.4
	UCT 9787	-11.9
	Mean	-12.1
	s.d.	0.3
<i>n</i>	5	
Mokopane	BP/4 167	-14.0
	BP/4 166	-12.7
	BP/4 165	-12.1
	Mean	-12.9
	s.d.	1.0
	<i>n</i>	3

onomic concerns, previous analyses indicate that baboons that lived in the early savanna habitats of South Africa had diets similar to those of their descendants inhabiting these areas today, and paid little attention to available grasses. By contrast, *Theropithecus oswaldi* had a largely graminivorous C_4 diet (mean $\delta^{13}\text{C} = -2.1 \pm 2.0\text{‰}$, $n = 5$), similar to the specialized grass-feeding behaviour of modern *T. gelada* that today inhabits the highlands of Ethiopia.²¹

While the data presented in Tables 1 and 2 suggest comparable diets in modern and extinct South African baboons, a limited number of specimens has been available for Plio-Pleistocene taxa (total $n = 15$, representing four taxa). Thus, there is uncertainty as to whether the patterns observed in these few individuals were representative of past primate populations, particularly considering the generalist feeding behaviour of modern baboons. To remedy this, we analysed 24 previously unsampled specimens, representing five taxa, from Swartkrans Members 1 and 2. In addition, $\delta^{13}\text{C}$ tooth enamel data were obtained for primate material ($n = 15$, representing 4 taxa) from the older deposits of Sterkfontein Member 4.

New data for specimens from Swartkrans Members 1 and 2 significantly extend the range of fossil papionin diets (Table 3). Mean $\delta^{13}\text{C}$ values for *P. h. robinsoni*, *P. (D.) ingens*, and *P. jonesi*

Table 2. Previously published $\delta^{13}\text{C}$ data for primate and browsing and grazing ungulate taxa from Swartkrans Members 1 and 2.

Taxon	<i>n</i>	Mean $\delta^{13}\text{C}$ (‰)	s.d.	Ref.
C_3 feeders (browsers)				
<i>Tragelaphus cf. strepsiceros</i>	3	-10.8	0.1	7
<i>Tragelaphus cf. strepsiceros</i>	2	-11.6	1.1	8
<i>Antidorcas australis</i>	2	-11.1	0.6	8
<i>Antidorcas recki</i>	1	-12.9	-	8
<i>Oreotragus cf. oreotragus</i>	1	-11.7	-	8
	9	-11.4	0.8	
C_4 feeders (grazers)				
<i>Connochaetes sp.</i>	3	-1.2	0.4	7
<i>Equus sp.</i>	3	-1.6	1.5	8
	6	-1.4	1.0	
Primates				
<i>Papio hamadryas robinsoni</i>	5	-11.2	0.9	7
<i>Papio (Dinopithecus) ingens</i>	3	-10.6	0.5	9
<i>Parapapio jonesi</i>	2	-11.2	2.4	9
<i>Theropithecus oswaldi</i>	5	-2.1	2.0	7

Table 3. $\delta^{13}\text{C}$ values of tooth enamel carbonate (in per mil, relative to the PDB standard) for primate taxa from Swartkrans Members 1 and 2.

Taxon	Sample ref.	$\delta^{13}\text{C}$ (‰)
<i>Papio hamadryas robinsoni</i>	SKX 12443	-10.1
	SKX 1037	-8.3
	SK 457	-8.2
	SK 458	-8.2
	SKX 1036	-6.8
	SK 436	-6.6
	SK 419	-6.5
	Mean	-7.8
	s.d.	1.3
	<i>n</i>	7
<i>Papio (Dinopithecus) ingens</i>	SK 492	-10.6
	SK 455	-9.5
	SK 2170	-8.4
	SK 404	-8.3
	Mean	-9.2
	s.d.	1.1
<i>n</i>	4	
<i>Parapapio jonesi</i>	SK 472	-10.2
	SK 433	-7.6
	SK 588 B	-7.5
	SK 442	-7.3
	Mean	-8.2
	s.d.	1.4
	<i>n</i>	4
<i>Theropithecus oswaldi</i>	SK 403	-5.3
	SK 2181	-2.6
	SK 581	-2.4
	SK 491	-1.6
	SK 597	-1.3
	SKX 616	-1.1
	Mean	-2.4
	s.d.	1.6
	<i>n</i>	6
	<i>Cercopithecoides williamsi</i>	SK 412
SK 551		-12.8
SK 579		-7.2
Mean		-11.2
s.d.		3.5
<i>n</i>		3

were $-7.8 \pm 1.3\text{‰}$ ($n = 7$); $-9.2 \pm 1.1\text{‰}$ ($n = 4$); and $-8.2 \pm 1.4\text{‰}$ ($n = 4$), respectively. These values are all ^{13}C -enriched compared to the results presented in Table 2. Furthermore, whereas earlier carbon isotopic data for these taxa were indistinguishable from those of C_3 -browsing ungulates, mean $\delta^{13}\text{C}$ values for newly analysed specimens are significantly higher than those of browsers from Swartkrans Members 1 and 2 (Mann-Whitney, $P < 0.02$ for *P. h. robinsoni*, $P < 0.03$ for *P. (D.) ingens*, and $P < 0.01$ for *P. jonesi*). Hence, utilization of grass was much greater by some of the extinct baboon specimens than is the case with modern South African savanna-dwelling individuals. A similar result was obtained for *Parapapio* spp. from Sterkfontein Member 4, in that the mean $\delta^{13}\text{C}$ value for the genus was $-8.8 \pm 2.3\text{‰}$ ($n = 10$), again significantly higher than values for browsing ungulates from this site (Mann-Whitney, $P < 0.02$; Table 4). By contrast, the new and previously reported $\delta^{13}\text{C}$ values for *T. oswaldi* did not differ [mean = $-2.4 \pm 1.6\text{‰}$ ($n = 6$); and mean = $-2.1 \pm 2.0\text{‰}$ ($n = 5$), respectively]. The colobine *Cercopithecoides williamsi* displayed a wide range of $\delta^{13}\text{C}$ values across different individuals, ranging from -7.2 to -13.7‰ at Swartkrans, and -4.7 to -12.9‰ at Sterkfontein.

Combining new and previously published data for *P. h. robinsoni*, *P. (D.) ingens* and *Parapapio* spp. from both localities shows that proportions of grass utilization by these taxa varied considerably. For *P. h. robinsoni* and *Parapapio*, $\delta^{13}\text{C}$ values ranged from -12.6 to -6.5‰ , and from -12.8 to -5.7‰ , respectively (Fig. 1). Adjusting Kruger National Park C_3 and C_4 plant values to correct for a $\sim 1.5\text{‰}$ depletion in the current ^{13}C content of atmo-

spheric CO₂ — the result of the burning of fossil fuels in the twentieth century²² — these values correspond to diets comprising between ~0 and 40% C₄ grasses in both taxa. *Papio (D.) ingens* δ¹³C values varied from -11.0 to -8.3‰, denoting that between about 10% and 30% of this species' diet was C₄ material.

Molar morphology suggests that Plio-Pleistocene papionins were largely frugivorous, albeit less so in South than in East African environments.² Evidence from shear crest length suggests that both *P. h. robinsoni* from Swartkrans, and *Parapapio* spp. from Swartkrans and Sterkfontein had diets comprising between ~20% and 30% leaves and ~50–70% fruit.^{2,3} Fruits of dicotyledonous woody plants are manifest as C₃, whereas the leaf-meal could include leaves of both C₃ plants and C₄ grasses. Thus the finding that these taxa ate between ~0 and 40% grass is in accord with expectations derived from molar morphology, although δ¹³C values indicate slightly higher grass intake. Indeed, as many as half of the *P. h. robinsoni* specimens analysed had δ¹³C values consistent with a 20–40% C₄ diet (*n* = 6; Fig. 1). In the case of *Parapapio* specimens, 63% (*n* = 10) of the specimens analysed reflect a 20–40% C₄ diet, and one specimen (STS 326) ate between 40% and 60% C₄-based foods. *Papio (D.) ingens* shear crests denoted diets comprising ~15% to 20% leaves and ~60% to 80% fruits, implying that this large-bodied species was the most frugivorous of the South African Plio-Pleistocene Cercopithecoidea.² However, our data show grass intake of up to 30% for this species, which is higher than that predicted by molar morphology alone, even though carbon isotopic data do not necessarily disagree with a predominantly frugivorous diet. While the results for extinct baboon taxa reveal diets somewhat different from that of modern South African baboons, these are not necessarily different from East African specimens today.

At the other end of the isotopic scale, *T. oswaldi* values ranged between -5.3 and +0.4‰, denoting a largely C₄ diet varying from ~60% to 100% grass (Fig. 1). It was previously suggested that, although *T. oswaldi* was likely to have been predominantly graminivorous, more fruits were utilized than seen today in modern *T. gelada*,^{2,3,23} which subsist almost exclusively on seasonally available grass parts.²¹ Isotopic data for *T. oswaldi* portray a diet of at least between 20% and 40% C₃-based foods, agreeing with the interpretation of a more mixed diet in the extinct forms. Although *T. darti* was previously identified from the South African Plio-Pleistocene,¹ *T. oswaldi* and *T. darti* are now widely regarded as members of the same species.²⁴ The lack of taxonomic distinction between the two forms implies ecological similarity, and hence it appears that the extinct *Theropithecus* was indeed a more generalist feeder than its modern counterparts.

The range of δ¹³C values from *C. williamsi* was large, from -13.7 to -4.7‰. These values indicate a highly varied diet, comprising between 0 and 60% C₄ foods, a wider range of dietary preference compared to *Papio* spp., *Parapapio* spp., and *T. oswaldi* (Fig. 1). *Cercopithecoidea williamsi* has often been described as a largely

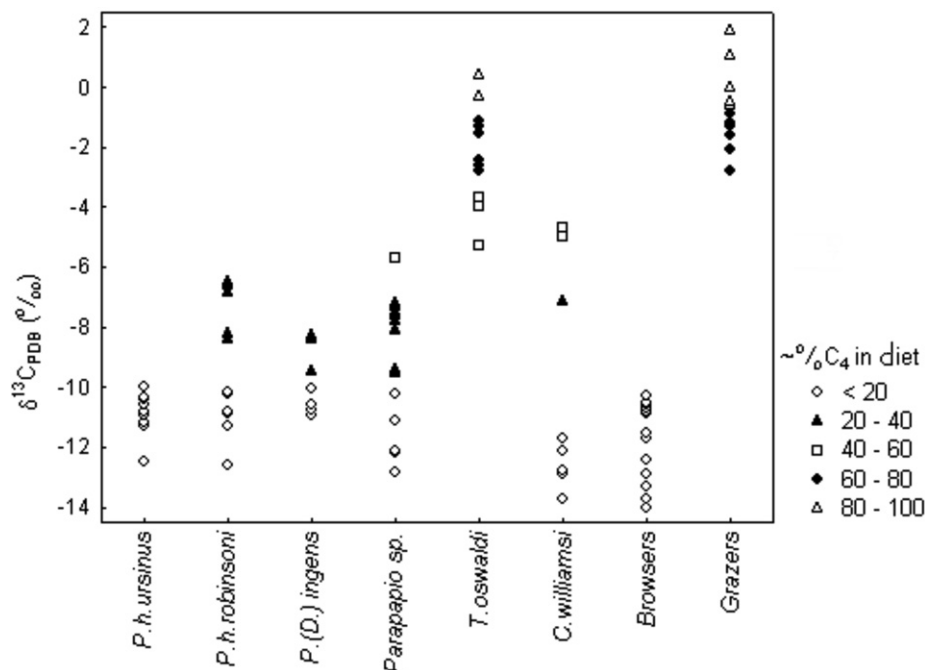


Fig. 1. δ¹³C values of tooth enamel carbonate of South African Plio-Pleistocene primates, combining published and new data for Swartkrans Members 1 and 2 and Sterkfontein Member 4. Data for C₃-feeding (browsing) and C₄-grazing ungulate taxa from these deposits are included to provide isotopic control. Data for modern *Papio hamadryas ursinus* are presented, but 1.5‰ has been added to the δ¹³C value of each specimen to correct for twentieth-century ¹³C-depletion of atmospheric CO₂ for appropriate comparison with extinct taxa.

Table 4. δ¹³C values of tooth enamel carbonate (in per mil, relative to the PDB standard) for primates and browsing and grazing ungulates from Sterkfontein Member 4.

Taxon	Sample ref.	δ ¹³ C (‰)
C₃ feeders (browsers)		
<i>Antidorcas recki</i>	STS 1944	-14.0
	STS 1435	-13.7
	STS 1325A	-13.3
	STS 2369	-10.5
	STS1573	-10.3
<i>Tragelaphus cf. strepsiceros</i>	Mean	-12.4
	s.d.	1.8
	<i>n</i>	5
C₄ feeders (grazers)		
<i>Antidorcas bondi</i>	STS 1125	-1.3
	SF 114	-1.6
<i>Connochaetes</i> sp.	SF 112	-0.5
	SF 327	-0.6
<i>Damaliscus</i> sp.	SF 328	1.1
	SF 329	1.9
	Mean	-0.2
	s.d.	1.4
	<i>n</i>	6
Primates		
<i>Parapapio broomi</i>	STS 298	-12.2
	STS 466	-8.1
	STS 337	-7.5
	STS 339	-7.2
	STS 326	-5.7
	STS 340	-9.4
<i>Parapapio jonesi</i>	STS 306	-7.3
	STS 260	-12.1
<i>Parapapio whitei</i>	STS 253	-11.1
	STS 263	-7.8
	Mean	-8.8
	s.d.	2.3
	<i>n</i>	10
<i>Cercopithecoidea williamsi</i>	STS 279	-12.9
	STS 260	-12.1
	STS 300	-11.7
	STS 394B	-5.0
	STS 282	-4.7
	Mean	-9.3
	s.d.	4.1
	<i>n</i>	5

terrestrial colobine monkey,¹⁻³ and Benefit^{2,3} suggested that *Cercopithecoides* was the only open-savanna colobine. The relatively high proportions of grass intake by *C. williamsi* confirms terrestrial foraging by the taxon, with some specimens having enamel $\delta^{13}\text{C}$ values (SK 579, -4.7‰ ; STS 394B, -5.0‰) reflecting diets of ~40 to 60% C_4 foods. Other individuals showed the lowest $\delta^{13}\text{C}$ value of all fossil primates examined (SK 412, -13.7‰ ; STS 279, -12.9‰). This bimodal split in *C. williamsi* tempts enquiry into the possibility that there are in fact two species represented in these deposits. Grass-feeding by *C. williamsi* also highlights the need for direct dietary investigations when reconstructing palaeo-ecologies, as opposed to reliance on assumptions of taxonomic uniformitarianism. Modern colobines are forest-dwellers, and are believed to be entirely C_3 consumers, hence colobines in fossil assemblages have been used as indicators of closed wooded environments.⁴ Carbon isotopic data for three colobines from the Ituri Forest, Democratic Republic of Congo, are consistent with exclusively C_3 diets.²⁵ Clearly, ecological clustering in the Colobinae today does not necessarily represent past variability within the group.

The variability observed in enamel $\delta^{13}\text{C}$ values of all fossil primates elucidates their generalist feeding behaviour as opposed to the more monotonous C_3 or C_4 diets of browsing and grazing ungulates. This variation may have resulted from socio-demographic differences in diet, but it is more likely that these patterns reflect adaptive feeding responses to changing environmental conditions through time. It may be that the Plio-Pleistocene primates adapted their diets to exploit grassland resources as the wooded landscapes gave way to more open savanna habitats.

Analysis of the carbon isotopic composition of tooth enamel carbonate in baboons and contemporary non-human primate taxa from the Plio-Pleistocene deposits of Swartkrans Members 1 and 2, and Sterkfontein Member 4, reveals that the diets of all taxa include varying amounts of C_4 grasses, or grass-based foods. The fossil papionins relied mainly on C_3 resources, but utilized significant proportions of C_4 items (up to ~40% of bulk intake), whereas modern *P. h. ursinus* from various savanna areas of South Africa appear to consume very little grass. *Cercopithecoides williamsi*, the only colobine represented in these deposits, clustered into two distinct groups; several individuals were C_3 feeders, while others had diets comprising up to 60% C_4 foods, suggesting that they did indeed spend time as terrestrial foragers. *Theropithecus oswaldi* was mainly graminivorous, albeit these baboons ate more C_3 foods than their living relatives, *T. gelada*. Extensive utilization of C_4 foods by all Cercopithecoidea that lived in South Africa during the Plio-Pleistocene exceeds expectations derived from earlier carbon isotopic analysis and molar morphology, and from analysis of modern *P. h. ursinus* in similar areas. At the very least, the emerging trend is that reconstructions of palaeodiet and palaeohabitats based on assumptions of taxonomic uniformitarianism oversimplify the true extent of naturally occurring ecological variability.

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