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An Evaluation of Niche Separation in the Terrestrial Primate Fauna of Plio-Pleistocene South Africa Using Biogeochemical Data

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Human evolution in the Plio-Pleistocene occurred in the context of a community of large-bodied terrestrial primates which may have shaped aspects of australopithecine ecology. Ecological theory would predict a degree of niche separation between these closely related sympatric species. Here, data from published biogeochemical paleodiet studies are used to test this hypothesis. The use of biogeochemistry in approximating niche width has been suggested on the basis of its reflection of an average of the total diet of an organism and its linear comparability between observations (Bearhop et al. 2004). Data on two measures, δ13C, which indicates the photosynthetic pathway of the dominant plants in the trophic chain of an organism, and Sr:Ba ratios, which can indicate trophic level, were analyzed using ANOVA and Tukey's test for significant difference in 8 Plio-Pleistocene primate species and groups of C3 browsers and C4 grazers. In δ13C, three groups were distinguished: grazers and Theropithecus; Australopithecus, Parapapio, Papio, *and* Cercopithecoides; *and* Papio, Cercopithecoides, *and the browsers. In Ba:Sr, two groups were distinguished:* A. africanus, A. robustus, *and* Papio; *and* A. robustus, Papio, *and* Parapapio. *Due to the significant degree of overlap between genera in both metrics, with the exception of* Theropithecus, *there is a lack of support for a strong degree of niche separation in this sample. It is possible that these taxa were able to coexist by adopting seasonally or spatially variable feeding behaviors, or their diets were less similar than appears from these biogeochemical indicators alone.*

Introduction

A large number of terrestrial, large bodied primates inhabited the Makapans and Sterkfontein Valleys in South Africa during the Plio-Pleistocene. This included members of the genera *Papio*, *Parapapio*, *Theropithecus*, *Cecopithecoides*, and human beings' own ancestors *Australopithecus* (Fleagle 1998). The ecological principle of competitive exclusion would

predict some degree of niche differentiation between these sympatric species. This concept has been demonstrated among primates, notable in the guenons (*Cercopithecus*) of Central Africa. Morphologically and dietarily similar guenons live sympatrically by vertically partitioning forest resources (Fleagle 1998). As pointed out by Fourie et al. (2008), this spatial partitioning by canopy level is impossible in terrestrial systems, so utilization of similar food resources may be less feasible. Modern savanna primates are sympatric only rarely, so Fourie et al. compared stable isotope and trace element ratios in the diets of terrestrial cercopithecoids from the Pleistocene when the fauna was more complex (2008). They found evidence of dietary differences both between and within the genera studied. However, they did not include hominins in their study, despite their presence on the Plio-Pleistocene savanna and the biogeochemical data available in the published literature on their dietary behavior.

Biogeochemical data from bioapatite in fossil enamel have proven informative in reconstructing dietary behavior in fossil species, yielding quantitative and linearly comparable data as well as information about niche width (Bearhop et al. 2004). The ratio of the stable carbon (C) isotope C^{13} to C^{12}, expressed as $\delta 13C$, is used to indicate the relative contribution of C3 and C4 photosynthetic pathway plants to the diet of a primary consumer and to the diets of the prey of secondary consumers (Lee-Thorp and Sponheimer 2006). Trace element ratios, particularly strontium to calcium (Sr:Ca) and barium to calcium (Ba:Ca), give complementary indication of both food source and dietary trophic level, although the uneven distribution of these elements within different parts of plants complicates this interpretation (Sponheimer and Lee-Thorp 2006). The fossils of higher trophic consumers should be relatively enriched in Sr and Ba as compared to Ca. However, heavier Sr and Ba molecules move up plant xylem more slowly than Ca so structures like roots may be relatively enriched in these ratios while fruits and flowers may be relatively deficient (Lee-Thorp and Sponheimer 2006). These two ratios may be combined into one Sr:Ba ratio which contains information about both in one measure.

If the terrestrial primate communities of South Africa in the Plio-Pleistocene were characterized by a high degree of niche separation, there should be significant differences between the means of these biochemical ratios in the primate fossils sampled. Evidence of niche displacement might indicate that the pattern of hominin adaptation was strongly influenced by the changing composition of primate communities in the Plio-Pleistocene. This synecological approach to human evolution may yield insights beyond those available by studying hominin trophic behavior in isolation. The survival of certain hominin groups (e.g. *Homo*) and the decline of others (e.g., the robust australopithecines) may have been linked to their ability to compete with their terrestrial primate contemporaries.

Methods

Data from published sources on $\delta 13C$ were combined and analyzed with One-Way ANOVA and Tukey's Test for significant difference between the means of eight primate species (*Australopithecus africanus*, *A. robustus*, *Papio robinsoni*, *P.* (*Dinopithecus*) *ingens*, *Parapapio broomi*, *Pp. jonesi*, *Pp. whitei*, and *Cercopithecoides williamsi*) and a sample of archetypal C3 browsers and C4 grazers (N=111). Data on primate specimens identified only to genus were not included in the means for analysis. Sources and sample sizes are described in Table 1 in the Appendix. Data on Sr:Ba trace element ratios in enamel in fossil grazers, browsers, carnivores, papionins, *A. africanus* and *A. robustus* from Sterkfontein and Swartkrans presented in Sponheimer and Lee- Thorp (2006), and also analyzed in

Sponheimer et al. (2005) and Lee-Thorp and Sponheimer (2006), were combined with data on the genera *Cercopithecoides*, *Parapapio*, and *Theropithecus* from Makapansgat presented in Fourie et al. (2008) and analyzed for significant difference. Earlier studies on trace element ratios drawn from bone (Sillen 1992, Sillen et al. 1995) were excluded on the basis of the severe diagenetic issues with this method (Lee-Thorp and Sponheimer 2006).

Results

The C4 grazers and *Theropithecus* were significantly different from all other taxa in $\delta13C$ values. *Australopithecus*, *Parapapio*, *Papio*, and *Cercopithecoides* formed a group of no significant difference among themselves, as did *Papio*, *Cercopithecoides*, and the C3 browsers (P<0001). Means and standard deviations are summarized in Table 2 (Appendix) and Figure 1. Means of Sr:Ba ratios were significantly different at an α value of .05 (P=.017). *A. africanus* had the highest mean Sr:Ba ratio at 7.52 ± 2.71, followed by *A. robustus* at 4.31 ± 1.73, and then *Parapapio* (3.86 ± 2.04) and *Papio* (3.20 ± 2.95). *Theropithecus* was represented by a single specimen with a Sr:Ba ratio of 1.97. However, excluding *Theropithecus*, the means of *A. africanus*, *A. robustus*, and *Papio* showed no significant difference, while the means of *A. robustus*, *Papio*, and *Parapapio* also showed no significant difference.

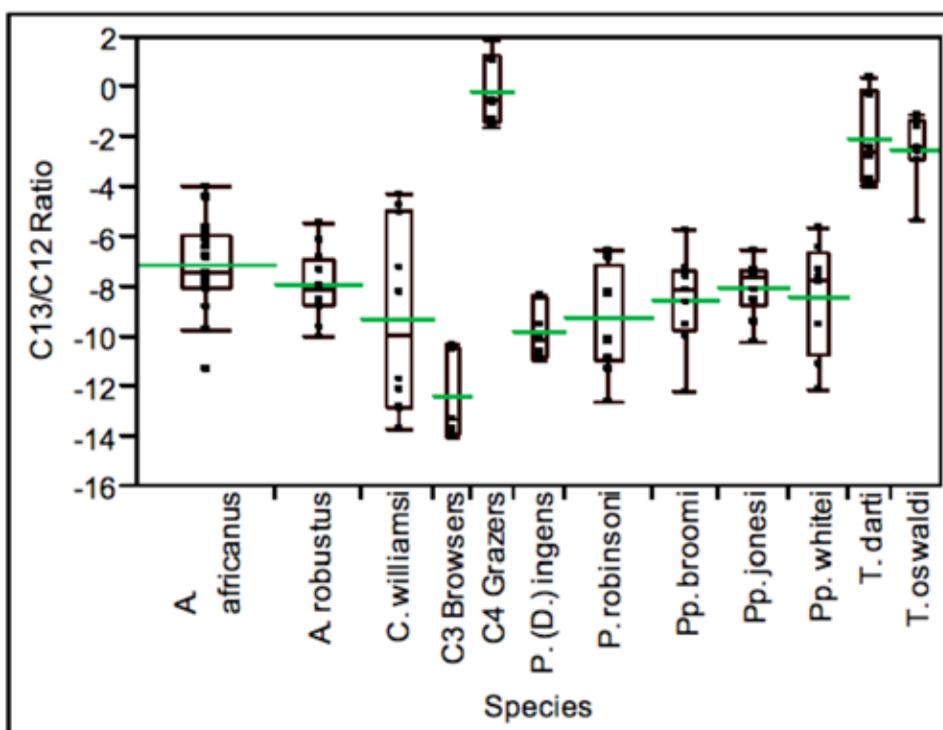**Figure 1: δ13C by species for the fossil primate sample as well as a sample of C3 browsing and C4 grazing species. Boxes represent the 25th–75th percentiles with medians represented as a central line and means by a green line. Whiskers represent non-outlier range. Each square represents a data point.**
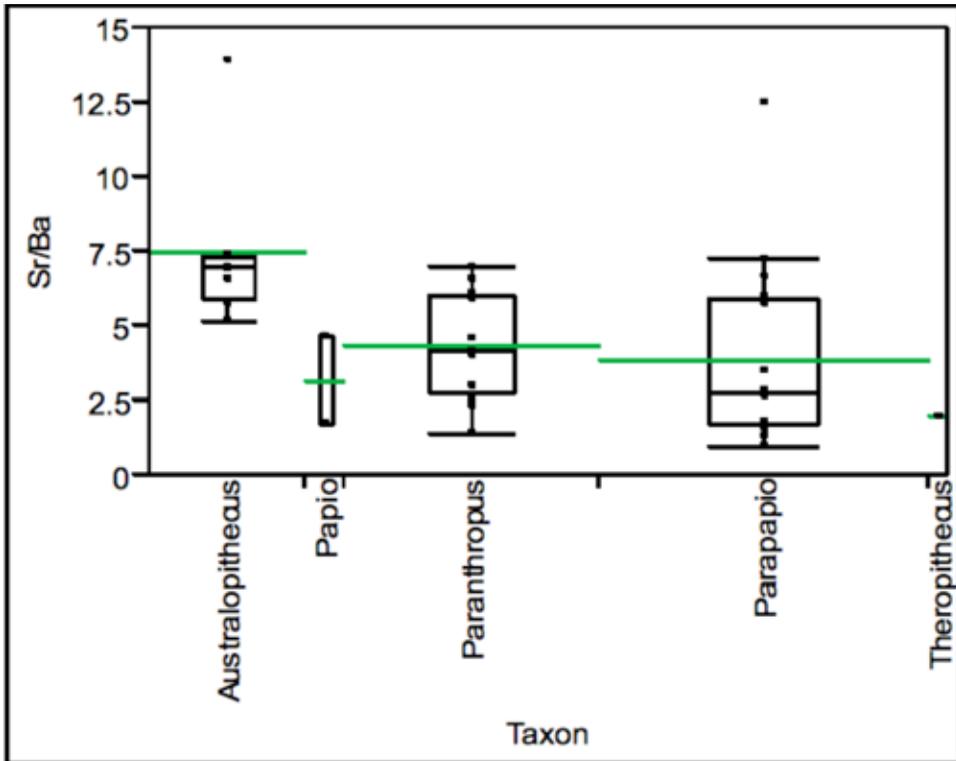
Figure 2: Sr:Ba ratios for the fossil primate sample. Boxes represent the 25th–75th percentiles with medians represented as a central line and means by a green line. Whiskers represent nonoutlier range. Each square represents a datapoint.

Discussion

δ13C data would appear to indicate a high degree of dietary overlap among all of the primate taxa but *Theropithecus*. The modern *Theropithecus gelada* is an intensive herbivore and granivore, and the fossil species of the genus appeared to have shared this adaptation (Fleagle 1998). Ratios for the other taxa were intermediate between browsers and grazers. They appear to indicate some mix between C3 and C4 plant resource utilization (e.g. Sponheimer and Lee-Thorp 2006). What δ13C cannot distinguish is the source of C4 or C3 plants in the trophic sequence of the diets of the species studied. Possibilities for C4 inputs into diet range from grass to sedge to insect or grazing herbivore consumption (Sponheimer and Lee-Thorp 2006).

Trace element analyses hold the promise of distinguishing among some of these possibilities. The Sr:Ba ratios appear to separate the primate taxa into largely overlapping groups. The genus level ratio results calculated here are only able to distinguish between *A. africanus* and *Parapapio* with significance. The high Sr:Ba ratios reported for *A. africanus* in Sponheimer and Lee-Thorp (2005) and found here were tentatively suggested to represent root and rhizome consumption based on a mole rat model. Lee-Thorp and Sponheimer (2006) found that Sr:Ca ratios in *A. africanus* were also significantly higher than in *A. robustus* and the combined papionin sample (*Parapapio* and *Papio*) from Sterkfontein, perhaps suggesting the hominins were consuming prey at a higher trophic level. The data presented in Fourie et al. (2008) on *Parapapio* may also indicate some niche differentiation

on the basis of Sr:Ba, with *Pp. broomi* appearing to consume resources with a high Sr:Ca but low Sr:Ba ratio, similar to *A. africanus*. If significant differences did in fact exist between the dietary ecologies of papionins and hominins, then a more extensive battery of trace element analyses, such as those employed by Fourie et al. (2008) on their cercopithecoid sample, may be necessary to find them.

The lack of clear niche separation may indicate that subtle and highly variable dietary differences produced sufficient niche differentiation for these taxa to co-exist. Corroborating evidence for the variability of hominin diets was provided by Sponheimer et al. (2006) who found seasonal variability in the δ13C values of A. robustus, based on perikymata counts. This may suggest that competitive interactions with other primates were less important in hominin evolution than other factors, except perhaps in selecting for greater dietary breadth, already likely a hallmark of baboon and hominin trophic behavior in the Pliocene. More information on regional, seasonal, and opportunistic variability in the diets of Plio-Pleistocene terrestrial primates may help clarify the contours of trophic niche overlap among these taxa. Alternatively, these biogeochemical metrics may be poor indicators of true paleodiet, at least at the resolution required to distinguish between niches.

Appendix

Table 1: Specimens and Sources

Species	Site	N	Source
Australopithecus africanus	Sterkfontein M4	15	(Sponheimer et al. 2005), (van der Merwe et al. 2003)
A. africanus	Makapansgat M3	4	(Sponheimer and Lee-Thorp 1999)
A. robustus	Swartkrans M1, M2, M3	12	(Lee-Thorp et al. 1994), (Sponheimer et al. 2006)
Theropithecus darti	Swartkrans M1	5	(Lee-Thorp et al. 1989)
T. darti	Makapansgat M3	1	(Fourie et al. 2008)
T. oswaldi	Sterkfontein M4	1	(van der Merwe et al. 2003)
T. oswaldi	Swartkrans M1, M2	6	(Codron et al. 2005)
Papio robinsoni	Swartkrans M1	5	(Lee-Thorp et al. 1989)
P. robinsoni	Swartkrans M1, M2	7	(Codron et al. 2005)
P. (Dinopithecus) ingens	Swartkrans M1	3	(Lee-Thorp et al. 1994)
P. (D.) ingens	Swartkrans M1, M2	4	(Codron et al. 2005)
Parapapio broomi	Sterkfontein M4	6	(van der Merwe et al. 2003), (Codron et al. 2005)
Pp. broomi	Makapansgat M3	3	(Fourie et al. 2008)
Pp. jonesi	Sterkfontein M4	4	(van der Merwe et al. 2003), (Codron et al. 2005)
Pp. jonesi	Makapansgat M3	2	(Fourie et al. 2008)
Pp. jonesi	Swartkrans M1, M2	2	(Codron et al. 2005)
Pp. whitei	Sterkfontein M4	3	(Codron et al. 2005)
Pp. whitei	Makapansgat M3	5	(Fourie et al. 2008)
Cercopithecoides williamsi	Swartkrans M1, M2	3	(Codron et al. 2005)
C. williamsi	Sterkfontein M4	5	(Codron et al. 2005)
C. williamsi	Makapansgat M3	2	(Fourie et al. 2008)
C3 Browsers	Sterkfontein M4	5	(Codron et al. 2005)
C4 Grazers	Sterkfontein M4	6	(Codron et al. 2005)

Table 2: Specimens and Mean δ13C

Species	N	Mean δ13C	SD
A. africanus	19	-7.1421053	1.7407903
A. robustus	12	-7.9333333	1.3513181
C. williamsi	10	-9.254	3.78290672
C3 Browsers	5	-12.36	1.90776105
C4 Grazers	6	-0.16666667	1.37937184
P. (D.) ingens	7	-9.8	1.0984838
P. robinsoni	12	-9.2083333	2.041594
Pp. broomi	9	-8.4811111	1.8817176
Pp. jonesi	10	-7.982	1.1006306
Pp. whitei	8	-8.425	2.27406496
T. darti	6	-2.1333333	1.8018509
T. oswaldi	7	-2.571429	1.42695146

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About the Author

Ethan Fulwood is a senior in anthropology and ecology and evolutionary biology at the University of Tennessee. He is interested in primate paleontology and paleoanthropology and hopes to pursue graduate studies in biological anthropology. His undergraduate thesis compared intraspecific variability in the crania and postcrania of prosimians. He is currently involved in a bird taphonomy research project. He is also an involved member of UT's Undergraduate Anthropology Association, Naturalist Club, and Secular Student Alliance.

About the Advisor

Dr. Andrew Kramer received his B.A. in Anthropology in 1980 from the University of California, Berkeley. He received both his M.A. in Anthropology in 1982 and his Ph.D. in Anthropology in 1989 from the University of Michigan, Ann Arbor. He is an Associate Professor and Head of the Department of Anthropology at the University of Tennessee, where he has taught since 1990. His research interests include biological anthropology, paleoanthropology, and the teaching of evolution.