Stable Isotope Analysis of Cercopithecids from the Shungura Formation: Dietary Niche Partitioning of *Theropithecus* and Sympatric Monkeys

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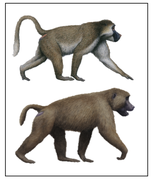
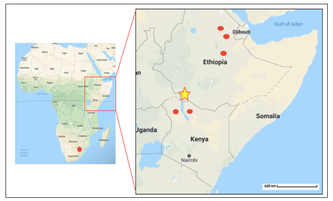
INTRODUCTION

Theropithecus (Fig. 1), a genus of Old World monkey, has been the focus of many studies investigating the terrestrial ecology of Africa in the Plio-Pleistocene. This genus is notable for its C_4-dominated diet, which can be analyzed through carbon and oxygen isotopes in its tooth enamel.



▲Fig. 1. Reconstructions of *T. brumpti* (top, Jablonski *et al.*, 2002) and *T. oswaldi* (bottom, Jablonski *et al.*, 2008)



▲ Fig. 2. Locations of isotopic analysis of *Theropithecus* samples. The study analyzed data from the Shungura Formation (yellow star).

Objective: This study considers species of *Theropithecus* and other sympatric monkeys (the terrestrial genus *Papio,* the arboreal colobine *Rhinocolobus turkanaensis,* and the terrestrial colobine *Paracolobus mutiwa*) to learn about dietary niche partitioning of primates in the Shungura Formation from 3.6 to ~1 Ma. These samples of *Theropithecus* are compared to data from past studies in other locations to clarify the evolution of the genus's C_4-dominated diet over time and space.

METHODS

We measured carbon and oxygen isotopes in enamel carbonate samples of 23 *Papio*, 7 *P. mutiwa*, 4 *R. turkanaensis*, 27 *T. brumpti*, 9 T. *oswaldi*, and 5 *Theropithecus* only identified to the genus level (*T.* sp) from the Shungura Formation via mass spectrometer, comparing $\delta^{13}C$ and $\delta^{18}O$ between taxa. Samples of *T. oswaldi* from Shungura were also compared to *Theropithecus* samples in the Omo Group, eastern Africa, and South Africa using existing data (Table 1).

TABLE 1. *Existing records of carbon isotope analysis of Theropithecus*

Publication	Site Location	Taxa Studied	Time Period
Lee-Thorp *et al.*, 1989; Codron *et al.*, 2005	Swartkrans, S. Africa	*T. oswaldi*	1.85 Ma
van der Merwe *et al.*, 2003	Sterkfontein, S. Africa	*T. oswaldi*	2.3 Ma
Fourie *et al.*, 2008	Makapansgat, S. Africa	*T. oswaldi*	2.8 Ma
Cerling *et al.*, 2013	Koobi Fora Formation, Kenya	*T. brumpti* *T. oswaldi*	4.0-3.2 Ma 1.95-1.5, 3.2 Ma
	Nachukui Formation, Kenya	*T. brumpti* *T. oswaldi*	2.0 Ma 1.2 Ma
	Olorgesaille, Kenya	*T. oswaldi*	1.0 Ma
Levin *et al.*, 2015	Woranso Mille, Ethiopia	*T. oswaldi*	3.66-3.33 Ma
Wynn *et al.*, 2016	Hadar, Ethiopia	*T. oswaldi*	3.4-3.0 Ma and 2.35 Ma
Robinson *et al.*, 2017	Middle Awash Valley, Ethiopia	*T. oswaldi*	2.8 Ma
Uno *et al.*, 2018	Olduvai George, Tanzania	*T. oswaldi*	1.70-1.66 Ma
Negash *et al.*, 2020[1]	Shungura Formation, Kenya	*T.* sp	3.58-1.0 Ma

[1]$\delta^{13}C$, $\delta^{18}O$, and age values were compared to overlapping samples from our data and readjusted with a different fractionation factor for to be consistent in our analysis

RESULTS and DISCUSSION

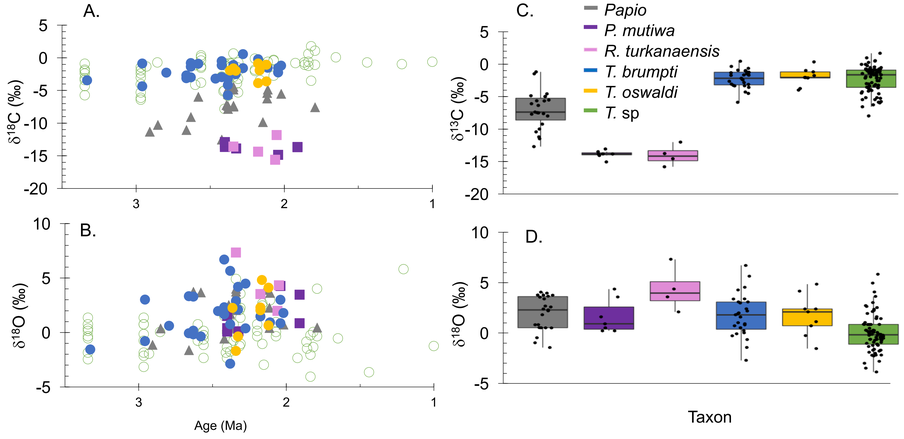
$\delta^{13}C$ and $\delta^{18}O$ values of Omo fossil cercopithecids

- *STRONG DIETARY NICHER PARTITIONING: Theropithecus* had a more C_4- based diet than *Papio* (*p<0.001*), which was more C_4-based than both colobine species (p<*0.001*).
- No difference in oxygen in taxa (ANOVA, *p=0.18*).

TABLE 2. *P-values of Welch's T-test comparing taxa within the Shungura Formation*

	n	(P)	(Pm)	(Rt)	(Tb)	(To)	(Th)	
Papio (P)	23	N/A	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	
P. mutiwa (Pm)	7	0.67	N/A	0.87	**<0.01**	**<0.01**	**<0.01**	
R. turkanaensis (Rt)	4	0.12	0.08	N/A	**<0.01**	**<0.01**	**<0.01**	
T. brumpti (Tb)	27	0.78	0.85	0.09	N/A	0.58	N/A	$\delta^{13}C$
T. oswaldi (To)	9	0.83	0.87	0.10	0.99	N/A	N/A	
Theropithecus[1] (Th)	112	0.93	0.68	0.12	N/A	N/A	N/A	
				$\delta^{18}O$				

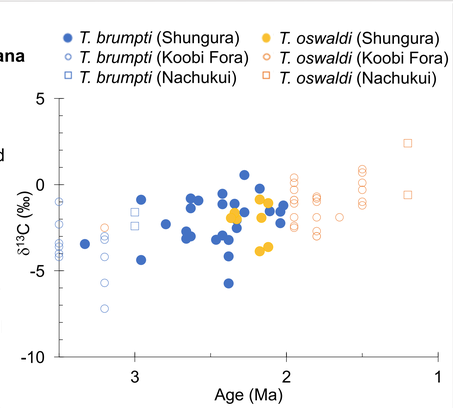
[1] includes all *T. brumpti*, *T. oswaldi*, and *T.* sp samples from the Shungura Formation



◂ Fig. 3. Ratios of carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes in enamel samples of Shungura monkeys. (A) $\delta^{13}C$ and (B) $\delta^{18}O$ of each taxon over time. Filled symbols represent data from this study, open symbols represent data from Negash *et al.*, 2020 (C) $\delta^{13}C$ and (D) $\delta^{18}O$ of each taxon represented in boxplots, including data from Negash *et al.*, 2020. $\delta^{13}C$ values above -2‰ represent C_4-dominated diets whereas $\delta^{13}C$ values below -8‰ represent C_3-dominated diets.

T. brumpti and *T. oswaldi* in the Turkana Basin

- *T. brumpti* had an increasingly C_4-based diet in the Turkana Basin over time, whereas *T. oswaldi* remained consistent in the level of C_4-based food in its diet.
- Overall, *T. oswaldi* had a more C_4-based diet than *T. brumpti*, although **when the two species lived contemporaneously (2.5-2.0 Ma), their diets were not different** (p=0.58).



▲ Fig. 4. $\delta^{13}C$ values of *Theropithecus* in the Turkana Basin. Filled symbols represent data from this study, open symbols represent existing data (Cerling et al, 2013).

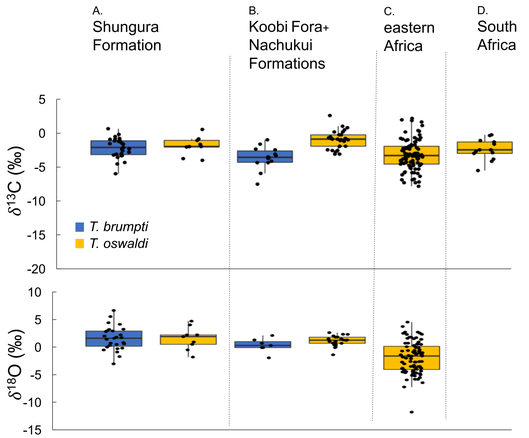
TABLE 3. *P-values of Welch's T-test comparing taxa within the Turkana Basin*

Taxa	n	Taxa	n	$\delta^{13}C$	$\delta^{18}O$
T. brumpti Shungura	27	*T. brumpti* KF+N	14	**0.01**	**<0.01**
T. oswaldi Shungura	9	*T. oswaldi* KF+N	27	0.12	0.17
T. brumpti TB	41	*T. oswaldi* TB	36	**<0.01**	**<0.01**

KF+N = Koobi Fora and Nachukui Formations; TB = Turkana Basin

Trends of *T. oswaldi* in eastern Africa and South Africa

- *T. oswaldi* consistently had a diet specializing in C_4 vegetation.
- Oxygen seems more related to regional variation than diet.



▲ Fig. 5. $\delta^{13}C$ and $\delta^{18}O$ values of *Theropithecus* in (A) the Shungura formation (this study), (B) the Koobi Fora and Nachukui Formations (Cerling *et al.*, 2013), (C) other locations in eastern Africa (Cerling *et al.*, 2013; Levin *et al.*, 2015; Wynn *et al.*, 2016; Robinson *et al.*, 2017; Uno *et al.*, 2018), and (D) South Africa (Lee-Thorp *et al.*, 1989; van der Merwe *et al.*, 2003; Codron *et al.*, 2005; Fourie *et al.*, 2008). $\delta^{18}O$ data was not collected in South Africa so are not included in this figure.

CONCLUSIONS

- Carbon isotopes display **strong dietary niche partitioning among Omo primate genera.**
- This analysis includes the only isotopic analysis of coeval *T. brumpti* and *T. oswaldi* and shows no carbon-based dietary niche partitioning between these two species when they were contemporaneous.
- Though the diet of *Theropithecus* consisted mostly of C_4 vegetation, a small part remained C_3-based. It is possible that the genus preferentially ate C_3 forbs, however isotopic analysis alone cannot differentiate between types of C_3 plants.
  - This distinction would be helpful in reconstructing past vegetation patterns that reflect the intricacies of the diet of *Theropithecus.*

Acknowledgements

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