EXAMINING DIETARY DIVERSITY IN A PALEOGENE HYRAX (AFROTHERIA, MAMMALIA) FAUNA FROM THE FAYUM DEPRESSION, EGYPT USING MESOWEAR ANALYSIS

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Abstract

With most ungulates absent from Africa until the Miocene, the morphologically diverse hyraxes were a major component of the Eocene-Oligocene community at Quarry L-41 (~34 Ma) in the Fayum Depression, Egypt. However, their foraging strategies are poorly understood. This study focuses on four extinct hyraxes: *Thyrohyrax meyeri*, *Thyrohyrax litholagus*, and *Megalohyrax eocaneus*, all expected to be grazers; and *Saghatherium bowni*, previously described as a browser.

Mesowear can place extinct herbivores on a spectrum from grazer to browser based on the abrasiveness of their lifetime diets. Crown height, tooth length, and cusp angle were measured for the first lower molars (M1) in these four hyrax species. Specimens were categorized into Wear Classes (WC), which correspond with developmental age. WC ranged from 1, first adult molar fully erupted, to 8, all molars extremely worn with significant dentin exposure.

Change in mean crown height and cusp angle across different wear classes was not significantly different. Nonetheless, apparent trends suggest compositional differences in diet. Change in mean crown height for *Sagbertherium* indicates that it incorporated more graze than browse because M1 wear occurred in earlier WCs and increased throughout life. In contrast, less wear for WC 1 through 4 in *Thyrohyrax* indicates that it incorporated more browse. This agrees with recently collected carbon isotope data, which suggests that *Saghatherium*'s diet included more graze than *Thyrohyrax*'s. These data are consistent with the description of *Thyrohyrax* as an arboreal browser. The change in mean crown height for *Megalohyrax* also suggests a less abrasive diet, although sample size for *Megalohyrax* was smaller. The browse-biased diet for *Megalohyrax* is surprising, as isotope values suggest a more open environment. Browsing in salt-stressed environments, forest canopies or forest edges could explain these combined data. *Megalohyrax* could have foraged in a wider variety of environments than the other taxa because its larger size enabled a wider range.

By reconstructing the diets and niche partitioning among morphologically diverse hyraxes at L-41, we hope to gain insights about the ecosystem represented by L-41 near the Eocene-Oligocene Boundary. This locality represents a time of ecological dynamism when many mammalian communities were dramatically restructured, though the impact of the EOB on African mammal communities remains poorly understood.

Introduction

In this study mesowear was measured for the first molars in specimens of *Thyrohyrax meyeri*, *Thyrohyrax litholagus*, *Saghatherium bowni*, and *Megalohyrax eocaneus* from Quarry L-41 (~34 Ma) in the Fayum Depression, Egypt, to infer dietary preferences among contemporaneous hyrax species near the Eocene-Oligocene Boundary (see Figure 1).

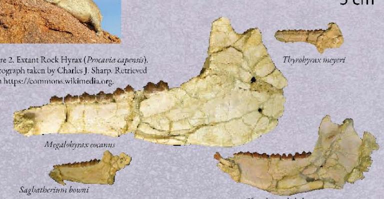
- Mesowear is collected by measuring how crown height, tooth length, and crown angle change between different developmental stages which are based on tooth eruption series. This measures attrition and abrasion over time which correlate with diet.
- This study follows Schap and Samuels (2020). They employed a similar method to measure mesowear in *Tapirus polkensis*.
- Today, Hyracoidea only includes five relatively small extant species. The community at Quarry L-41 represents a morphologically diverse fauna (Rasmussen and Gutiérrez, 2010).
- This study focuses on four species in three genera: *Thyrohyrax meyeri*, *Thyrohyrax litholagus*, *Megalohyrax eocaneus* and *Saghatherium bowni*.
- *T. meyeri* and *Saghatherium* were small-bodied hyraxes. *Megalohyrax* is thought to have approached 1.5 meters in length (Rasmussen and Gutiérrez, 2010). See Figure 4 for relative sizes based on jaw length.

Figure 1. Map of the location of Locality 41 in the Fayum Depression, Egypt. L-41 is located in Jebel Qatrani Formation and is dated to ~34 Ma and the latest Eocene. EOB is Eocene-Oligocene Boundary.

Taxa Used in This Study

Figure 2. Extant Rock Hyrax (*Procavia capensis*). Photograph taken by Charles J. Sharp. Retrieved from https://commons.wikimedia.org.

Figure 3. Mandibles of included taxa printed at actual size.



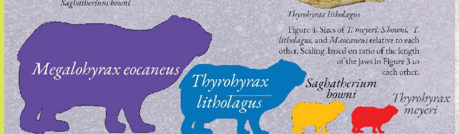


Figure 4. Sizes of *T. meyeri*, *S.bowni*, *T. litholagus*, and *M.eocaneus* relative to each other. Scaling based on ratio of the length of the jaws in Figure 3 to each other.

Methods

- All specimens are from the Duke Lemur Center Museum of Natural History. Specimens were arranged into seven Wear Classes based on visible tooth eruption and wear (Figures 8 and 9). Occlusal photographs were also taken to verify Wear Class (Figure 7).
- Where possible, ten specimens were photographed for each Wear Class for each genus. If fewer than ten suitable specimens were found for any given Wear Class, every suitable specimen was photographed.
- Measurements were collected from digital lingual photographs (Figure 5) and included:
  - Molar length: points were identified on the most anterior and most posterior sediment-free points on each tooth (Figure 6).
  - Molar height: the perpendicular distance between the line used for molar length and the highest point of the crown..
  - Cusp angle: the angle between three points—the anterior point used for molar length, the posterior point used for molar length, and the highest point on the crown (Figure 6).
- To account for differences in determining the points needed for measuring, two investigators independently measured all three values for each tooth. The independent results were averaged within each Wear Class for each genus.

Figure 5. Lingal view with scale bar.

Figure 6. Cusp angle measured in tooth.

Figure 7. Occlusal view with scale bar.

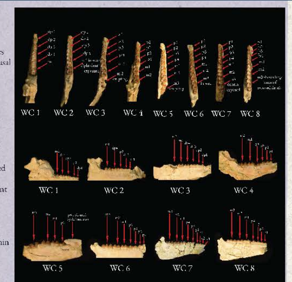


Figure 8. Photographs of *Saghatherium* specimens of each Wear Class from occlusal view and buccal view. In Wear Class 3 and Wear Class 5, the second or third mandibular molar is visibly erupting but has no wear (exposed dentin). The fossil shown in the occlusal view is not necesarily the fossil shown in the buccal view.

Wear Class	Description	Diagram
I*	Deciduous premolars are fully erupted and may be worn. M_1 is fully erupted, but unworn.	dp_1 dp_2 dp_3 dp_4 M_1
II	Deciduous premolars and M_1 are slightly worn. However, no adult premolars or the M_2 are erupted yet.	dp_1 dp_2 dp_3 dp_4 M_1
III	M_1 is worn, and the M_2 and/or adult premolars are exposed but not fully erupted.	P_1 P_2 P_3? P_4? M_1 M_2
IV	P_2-P_3 are fully erupted. P_4 may be exposed but not fully erupted; if not, dp_4 is extremely worn. M_2 is fully erupted.	P_1 P_2 P_3 P_4 M_1 M_2
V	P_4 and M_2 are worn. The M_3 is exposed, but not fully erupted.	P_4 M_1 M_2 M_3
VI	The M_3 is fully erupted, but is not worn yet.	M_3
VII	The M_3 is worn.	M_3
VIII	The M_3 is extremely worn, with the occlusal surface covered by <10% enamel.	M_3

Diagram Key: Erupting; In wear; Worn; Extremely worn

Figure 9. Table with description of critera for inclusion in each Wear Class.

Results

- Within all three genera, change in mean crown height and tooth angle across different wear classes was not statistically significant using Levenes and KW test with Wilcoxon post hoc.
- The change in mean crown height for *Saghatherium* indicates that it ate more graze than browse because wear was present in earlier Wear Classes and increased throughout life at a fairly constant rate (Figure 10).
- The change in mean crown height for *Thyrohyrax* indicates that it ate more browse because change in mean crown height mainly appeared later in life between Wear Class 4 and Wear Class 5 (Figure 11).
- *Megalohyrax* shows a pattern of change in mean crown height that is similar to *Thyrohyrax*. This indicates that it ate more browse than graze. For *Megalohyrax* the larger change occurs between Wear Class 5 and Wear Class 6. (Figure 12).

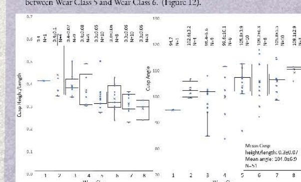


Figure 10. Mesowear for *Saghatherium*. Kruskall wallis for angle: p=0.1, test stat=11.2. Levene's test for homogeneity: p=0.4, test stat=1.1. For height: p=0.2, test stat=10.0. levene's p=0.7 stat=0.7.

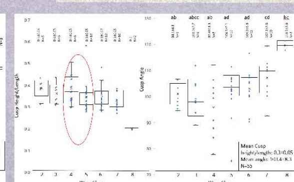


Figure 11. Mesowear for *Thyrohyrax*. Kruskall wallis for angle: p=0.02, test stat=14.5. Levene's test for homogeneity: p=0.2, test stat=1.6. For height: p=0.7, test stat=11.5, levene's p=0.02, test stat=1.6. The change in mean crown height characteristic of a browser is circled.

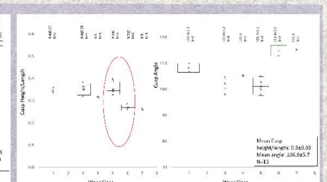


Figure 12. Mesowear for *Megalohyrax*. Kruskall wallis for angle: p=0.02, test stat=14.5. Levene's test for homogeneity: p=0.2, test stat=1.6. For height: p=0.7, test stat=2.8, levene's p=0.03, test stat=5.3. The change in mean crown height characteristic of a browser is circled.

Discussion

- While the results of this study were not statistically significant, the results can be interpreted. They suggest that *Saghatherium* incorporated more graze than browse while *Thyrohyrax* and *Megalohyrax* incorporated more browse than graze.
- These conclusions agree with recently collected carbon isotope data from co-author Simpson's on-going dissertation (Simpson et al., 2023). Isotope data suggests that *Saghatherium*'s diet included more graze than *Thyrohyrax*'s. It also suggests that both species incorporated both graze and browse, but they appear to have differed in their respective ratios.
- Sample size for *Megalohyrax* was smaller, therefore more caution is needed in interpretation of results. Wear suggests that *Megalohyrax* ate a less abrasive diet (browse).
- Isotope values suggest L-41 represents a more open environment for *Megalohyrax*. A salt-stressed environment (such as a coastal region), a forest canopy, or a forest edge could produce the recorded isotopic signature (Simpson et al., 2023). The large size of *Megalohyrax* may eliminate forest canopies as a possibility. Its larger size may have enabled a larger geographic range and thus foraging in forest edges as well as coastal regions.
- Past literature describes *Thyrohyrax* as an arboreal browser (Rasmussen & Simons, 1988; Rasmussen & Simons, 1991; Barrow et al., 2010). This is consistent with mesowear and isotope data. Past literature describes *Megalohyras* as a generalist (Rasmussen & Simons, 1988). Isotope data is not inconsistent with grazing, and mesowear data suggests browsing.
- Changes in hyrax diet over time could reveal how this fauna adapted to ecological changes across the Eocene-Oligocene boundary in Africa, and offer insights into their extinction in the early Neogene.

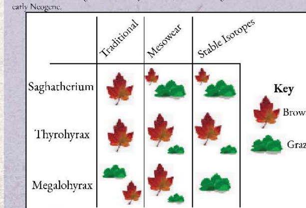


Figure 13. Table showing the tradtional interpration of diet, the diet according to mesowear data, and the diet according to stable isotope data in the three species (Rasmussen & Simons, 1988; Rasmussen & Simons, 1991; Clementz et al., 2008). Sizes of browse and graze symbols are exagerrated for clarity.

Acknowledgements

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References