Dental Topography and Dietary Ecology of the First North American Euprimates

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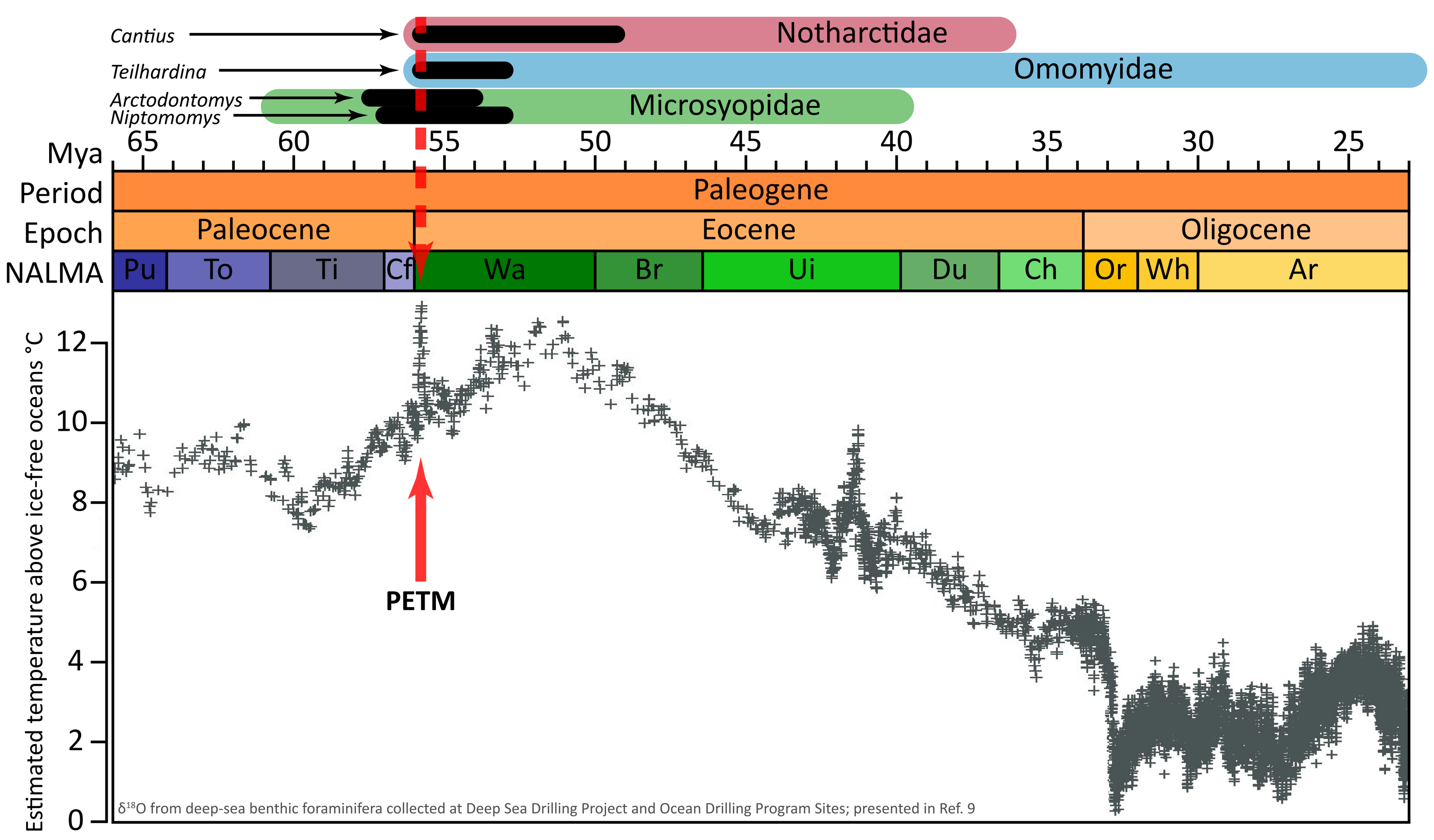
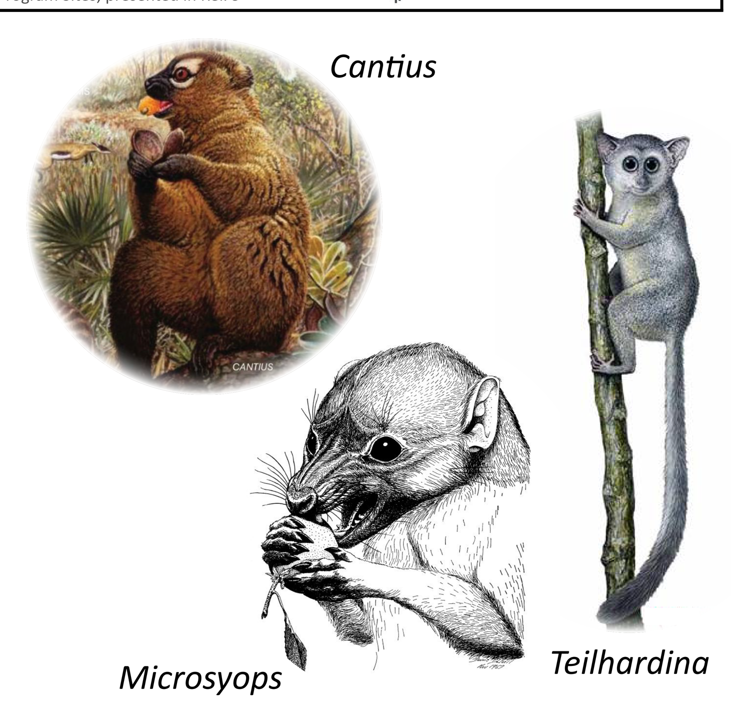
1. Introduction

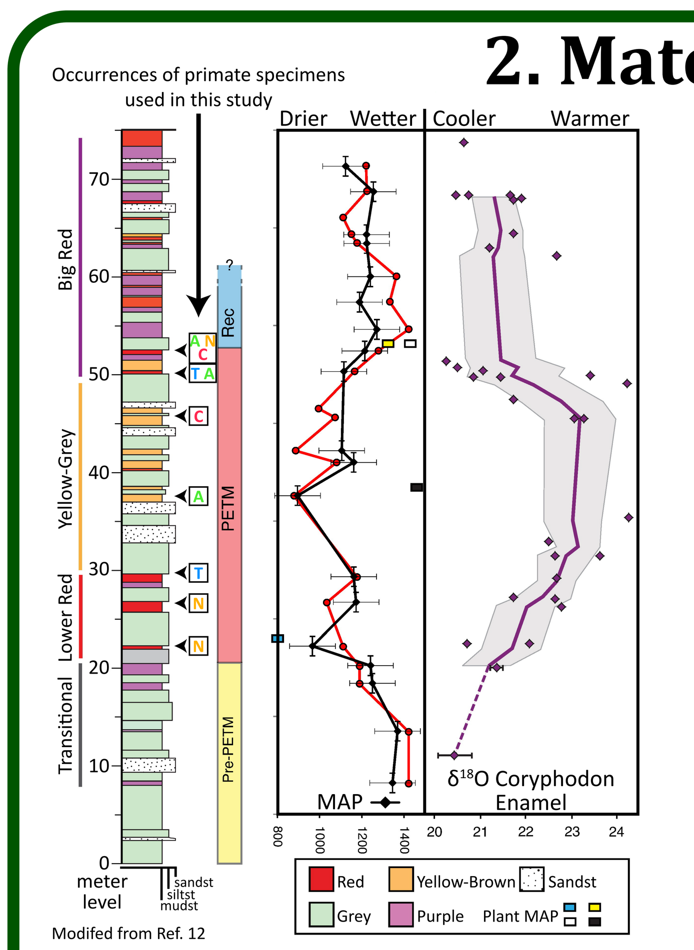
The Paleocene-Eocene Thermal Maximum (PETM) was a significant global warming event that occurred 56 million years ago[1], characterized by an increase of ~5-8 °C in mean annual global temperature[2-4]. Among the panoply of physical, chemical, and biotic effects associated with the PETM, this brief interval (~200 thousand years[2]) marks the first appearance of primates of modern aspect, or 'euprimates.' The first euprimate immigrants to reach North America were the omomyid *Teilhardina brandti* and the notharctid *Cantius torresi*[5-7].

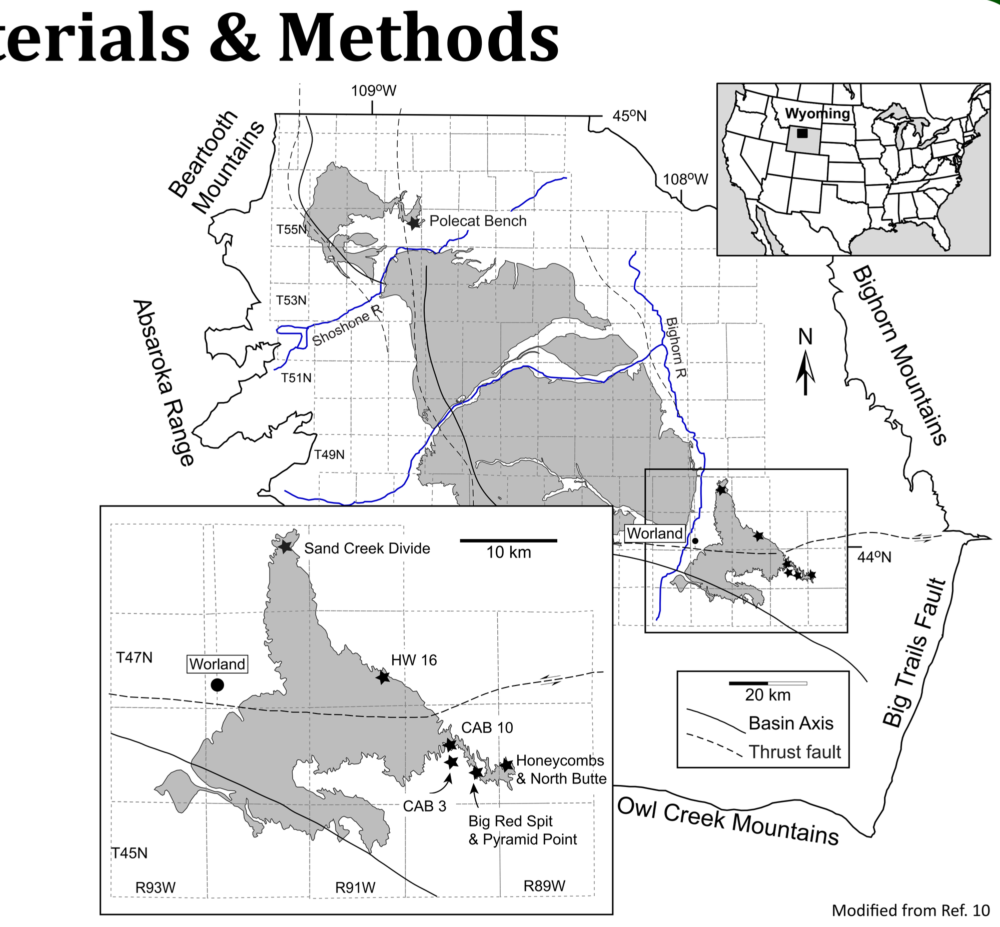


While euprimates immigrated to North America just after the Paleocene-Eocene boundary, plesiadapiform stem primates had already diversified during the Paleocene in North America. One family, the Microsyopidae, is commonly found during the PETM and is represented by *Arctodontomys wilsoni* and the diminutive *Niptomomys doreenae*. These endemic taxa are recovered from the same PETM fossil deposits as euprimate immigrants, are most likely arboreal, are of similar size, and have qualitatively similar tooth crown morphology. These factors suggest the possibility of competition for dietary resources. We used quantitative metrics of dental topography that differ among extant primates[8] to test if primate taxa from the PETM showed evidence of dietary partitioning.



2. Materials & Methods

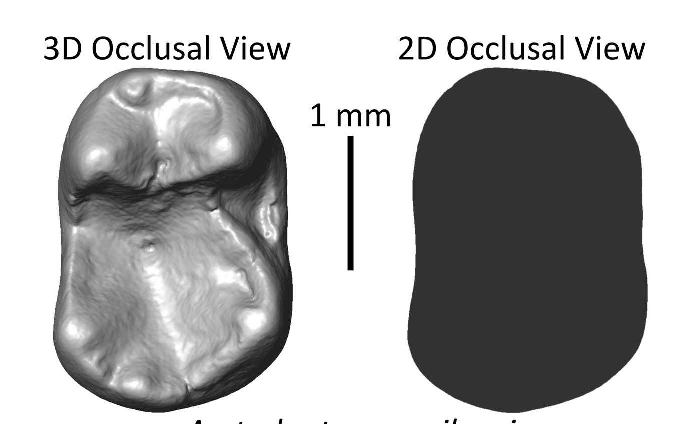




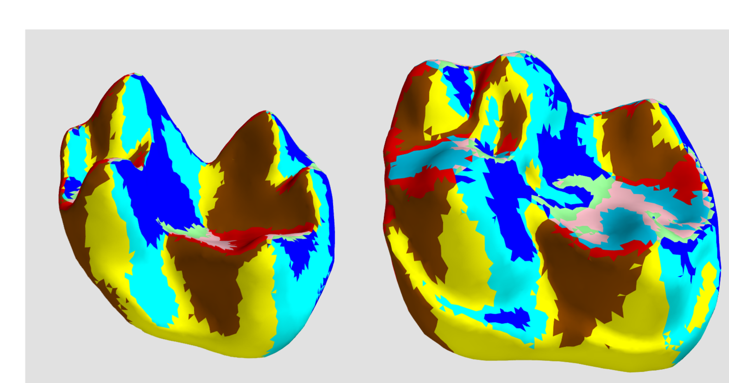
Primate specimens were collected in the Cabin Fork drainage in the southeastern Bighorn Basin of Wyoming. After a decade of fieldwork, this region has produced a collection of ~8,500 PETM fossils, high-resolution integrated chemostratigraphy, lithostratigraphy and biostratigraphy[10], and is the only place where the unique flora of the PETM has been characterized[4]. We used micro-CT to generate high-resolution 3D digital models of primate M_2's recovered from PETM sediments (see Results for summary table) and applied three complimentary quantitative dietary ecology metrics using the free MorphoTester software[11]:

Relief Index (RFI):

- Compares three dimensional surface area to two dimensional surface area of tooth crown
- Performs well at differentiating extant prosimian diets based on the amount of incorporated structural carboyhdrates[13]
- Folivores have higher RFI than frugivores and granivores



Arctodontomys wilsoni



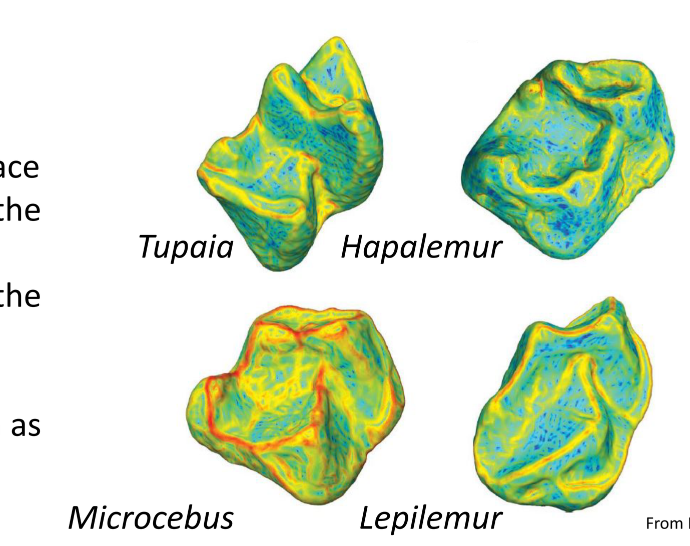
Niptomomys doreenae *Cantius torresi*

Orientation Patch Count (OPCR):

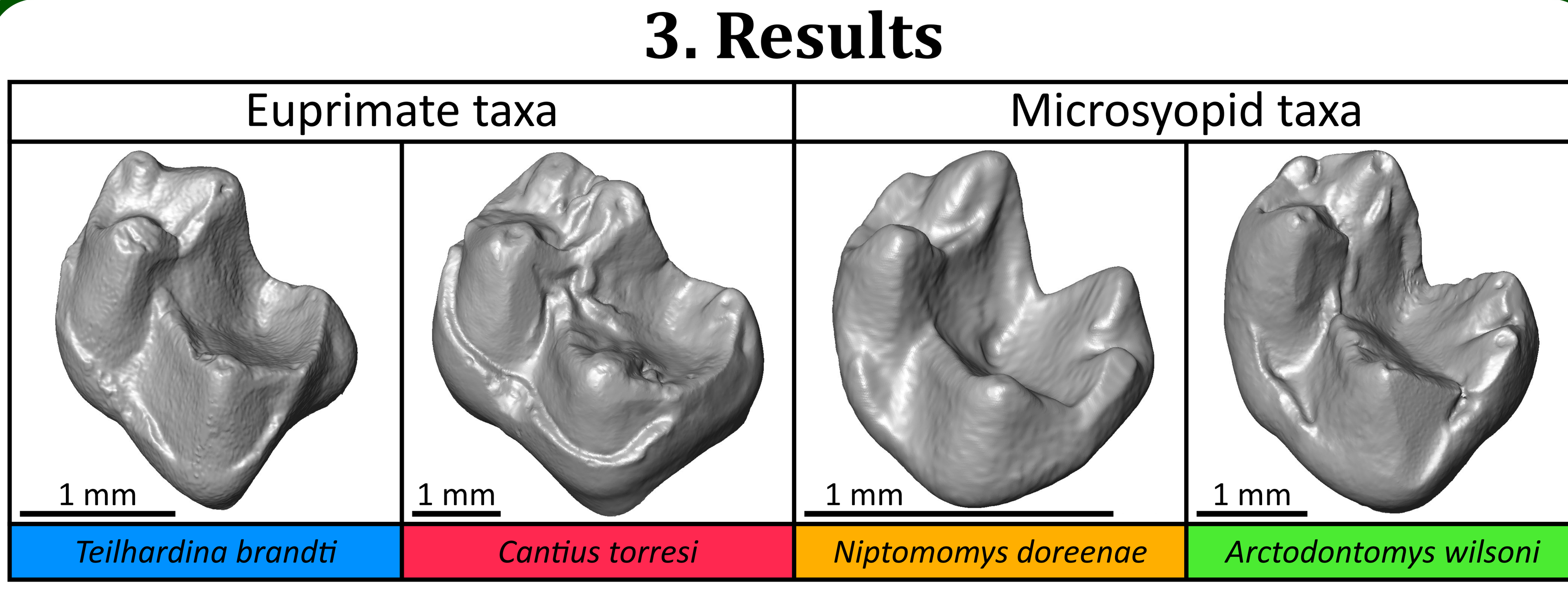
- Groups 'patches' of tooth crown faces based on their shared orientation (minimum # of faces = 3)
- Patch count averaged from eight views of tooth crown
- Differentiates mammals within orders based on the complexity of tooth crown morphology
- Teeth of herbivorous taxa tend to have high OPCR, whereas carnivorous taxa have low OPCR[14]

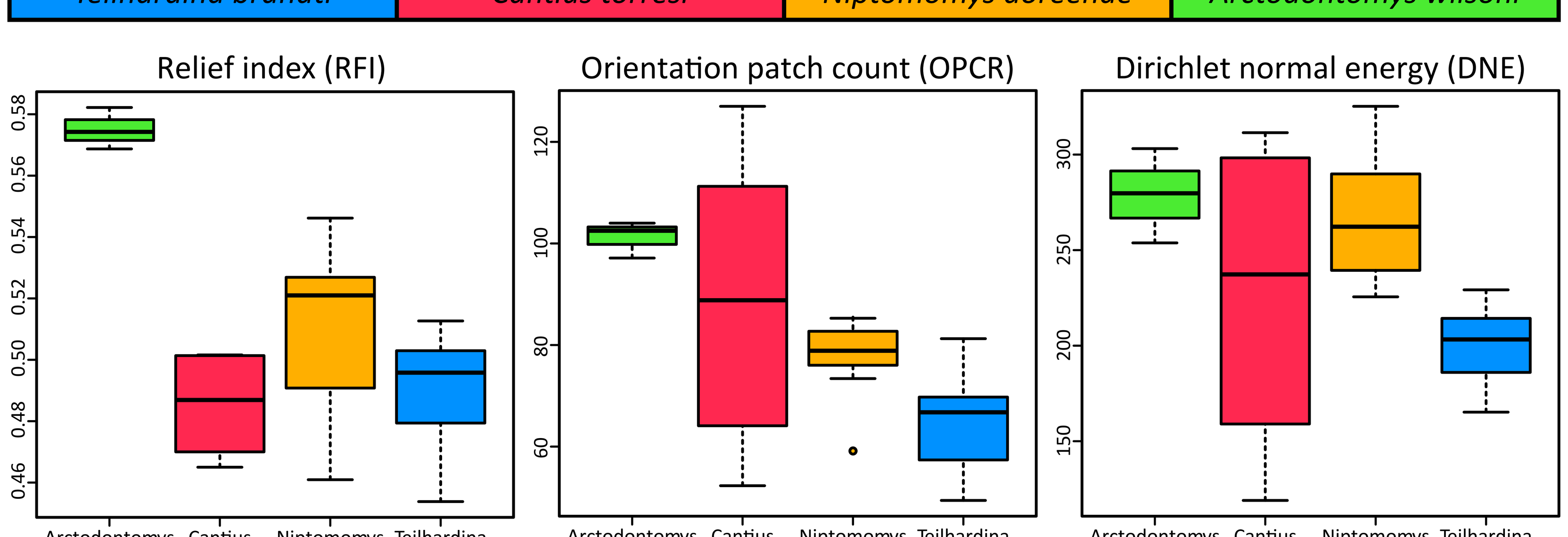
Dirichlet Normal Energy:

- Considers the normal direction of each point on the tooth face
- If normal directions of adjacent points greatly diverge, the normal map between them grows orthogonally
- Calculated as an increase in the Dirichlet energy, capturing the curviness of crown morphology
- Independent of position, orientation, or scale
- Higher in taxa with molar crowns adapted for shearing such as insectivores and folivores[8]



3. Results





- *Arctodontomys* clear outlier for RFI, likely incorporating more structural carbohydrates into their diet than other PETM primates
- Kruskal-Wallis one-way analysis of variance significant for RFI and OPCR, but not for DNE
- Large-bodied taxa (*Arctodontomys* and *Cantius*) not significantly different for OPCR or DNE, but significantly different for RFI by Mann-Whitney *U* test (p = 0.024)
- Small-bodied taxa (*Niptomomys* and *Teilhardina*) not significantly different for RFI or OPCR, but significantly different for DNE by Mann-Whitney *U* test (p = 0.002)

Taxon	Group	N	Est. Body Mass (g)*	$\bar{x}$(RFI)	$\bar{x}$(OPCR)	$\bar{x}$(DNE)
Cantius torresi	Notharctid euprimate	6	530-830	0.49	88.7	227.1
Arctodontomys wilsoni	Microsyopid plesiadapiform	3	120-270	0.58	101.2	278.9
Teilhardina brandti	Omomyid euprimate	6	50-145	0.49	65.2	200.2
Niptomomys doreenae	Microsyopid plesiadapiform	7	10-30	0.51	77.4	267.4

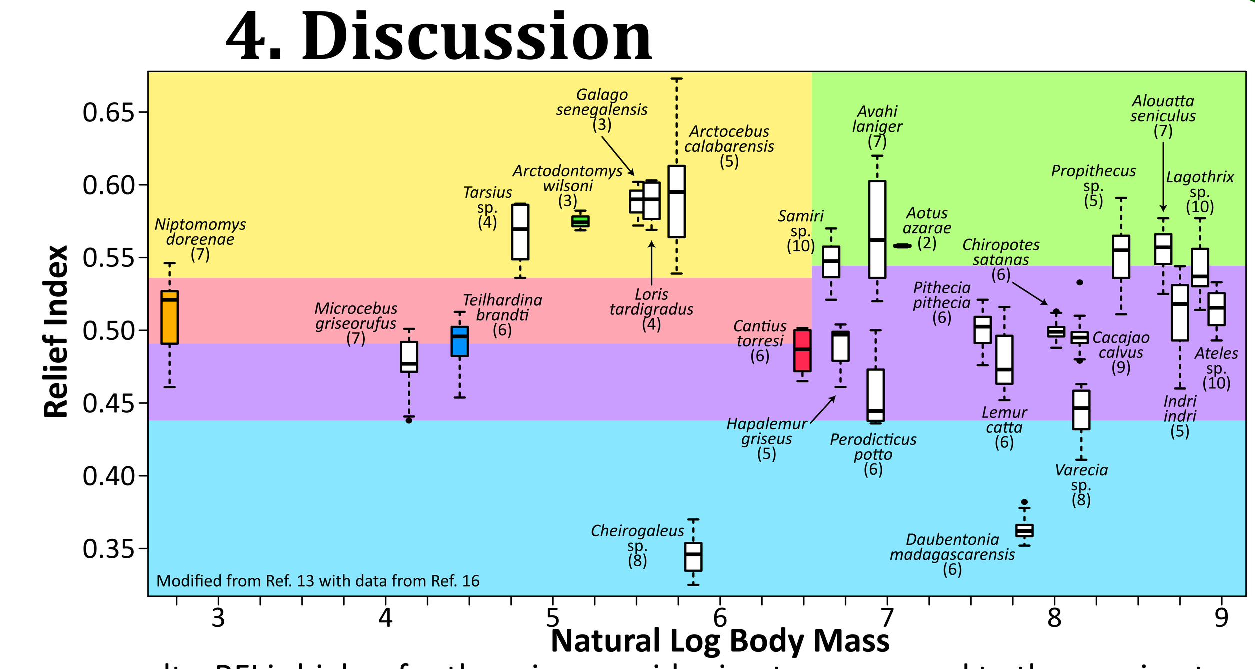
*Body mass estimates based on area of M_1 using Ref. 15, "Prosimian Grade" regression, reported as averaged 95% confidence intervals of full sample

4. Discussion

Relief Index of PETM primates measured in this study compared with extant primates

Dietary Categories:

- Insectivory
- Frugivory
- Folivory
- Omnivory
- Ambiguous



Several trends emerge from our results: RFI is higher for the microsyopid primates compared to the euprimates, but only *Arctodontomys* is a significant outlier. This indicates that *Arctodontomys* may have been incorporating a higher proportion of insects in its diet compared to other PETM primates. The lower DNE of *Teilhardina* relative to the small-bodied *Niptomomys* reflects greater bunodonty in the euprimate and may indicate relatively greater emphasis on fruit eating. The larger-bodied *Arctodontomys* and *Cantius* have more complex crown morphology, as indicated by higher OPCR, which would have made them more adept at processing tough food items such as leaves. Despite marked differences for some taxa in certain metrics, we note that generally the PETM primates are quite similar to one another, especially compared to the wide range calculated for these metrics in extant primates (e.g., see above). Despite non-overlapping body size and potentially sharing the same habitat, either of which could serve to differentiate diet, the teeth of both endemic microsyopids and immigrant euprimates appear adapted to process foods with similar mechanical properties. These early primates may therefore may have competed for food resources during the PETM.

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