



MESOWEAR ANALYSIS OF *TAUBATHERIUM PAULACOUTOI* (LATE OLIGOCENE, TREMEMBÉ FORMATION), SÃO PAULO STATE, BRAZIL

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ABSTRACT – Despite the benefits of the mesowear analysis method for dietary reconstruction, it has rarely been applied to notoungulates. We here apply traditional mesowear and a mesowear angle approach to an assemblage of the leontiniid *Taubatherium paulacoutoi* from the Late Oligocene (Deseadan SALMA), Tremembé Formation, Taubaté Basin, Brazil. Using both methods, we find support for a browsing diet hypothesis low in abrasive vegetation, which matches predictions from ecomorphology. However, we found differences between the traditional mesowear signal of *Taubatherium*, and any modern ungulate species analyzed. We suggest that this supports the use of mesowear angles in notoungulates for dietary reconstruction, given the lack of modern representatives.

Keywords: mesowear, *Taubatherium*, Brazil, Taubaté, Late Oligocene.

RESUMO – Apesar dos benefícios da técnica do *mesowear* para reconstrução dietética, ela raramente tem sido aplicada em notoungulados. Aplicamos aqui o *mesowear* tradicional e uma abordagem de ângulo de *mesowear* a uma população do leontinídeo *Taubatherium paulacoutoi*, Formação Tremembé, Bacia de Taubaté, Neo-Oligoceno (SALMA Deseadano), Brasil. Usando ambos os métodos, encontramos suporte para uma dieta de pastagem, pobre em vegetação abrasiva, que corresponde às previsões de ecomorfologia. No entanto, encontramos diferenças entre o sinal tradicional de *mesowear* de *Taubatherium* e qualquer espécie moderna de ungulados analisada. Sugerimos que isto apoia o uso de ângulos de *mesowear* em notoungulados para reconstrução dietética, dada a falta de representantes modernos.

Palavras-chave: *mesowear*, *Taubatherium*, Brasil, Taubaté, Neo-Oligoceno.

INTRODUCTION

Various approaches can be used to infer the diet of extinct taxa, including microwear analysis (DeSantis, 2016; Green & Croft, 2018), isotope ratios (Higgins, 2018), ecomorphology (Andrew Barr, 2018) and mesowear analysis (Fortelius & Solounias, 2000; Saarinen *et al.*, 2015; Green & Croft, 2018; Ackermans, 2020). Each method has both benefits and disadvantages, but in combination can offer a comprehensive view of the diet of a particular population. Mesowear reflects the balance of abrasion vs attrition over the course of the life of a particular individual (Fortelius & Solounias, 2000) and, relative to other methods, has the advantage of being fast, cost-effective, and simple, with no equipment required. Compared to microwear, mesowear reflects diet over longer periods of time, with microwear only revealing the “last meal” (Grine, 1986) of a particular organism. However, compared to ecomorphology, it has the advantage of revealing actual diet, rather than the diet the organism is adapted for. For example, an herbivore which is hypsodont may still consume browse (Janis, 1988; Damuth & Janis, 2011).

Despite this, mesowear analyses have rarely been used for South American herbivores. Saarinen & Karme (2017) introduced a new methodology to measure mesowear angles in sloths, whilst there have been only two mesowear studies for the South American Native Ungulates (SANUs). Croft & Weinstein (2008), who used the methodology for the notoungulates of Salla, Late Oligocene of Bolivia, found a generally mixed diet for the ungulates there, which supported an open woodland environment. Wilson *et al.* (2024) applied mesowear angles to toxodontids in Venezuela but did so without any modern comparative materials.

Salla is a relatively well-studied locality from the Late Oligocene (Deseadan South American Land Mammal Age/SALMA) (Macfadden *et al.*, 1985, 1994; Kay *et al.*, 1998; Croft & Weinstein, 2008; Billet *et al.*, 2009; Croft, 2016), but represents only one of at least ten throughout the continent (Pujos *et al.*, 2021). The Deseadan was a time of significant change in the fauna of South America between 29.4–24.2 Ma (Dunn *et al.*, 2013), with the diversification of sloths and many groups of hypsodont notoungulates, which has been suggested to be a response to expanding open habitats and climatic cooling (Woodburne *et al.*, 2014).

One of the few Paleogene assemblages in Brazil is found at the Deseadan locality of Taubaté (Tremembé Formation), São Paulo State, Brazil, which is the easternmost Deseadan locality in South America (Pujos *et al.*, 2021). It preserves a lacustrine environment (Torres Ribeiro, 2004) with a diverse vertebrate assemblage (Carmo *et al.*, 2024), including at least 11 mammal species (Paula-Couto, 1956; Paula-Couto & Mezzalira, 1971; Soria & Alvarenga, 1989; Vucetich *et al.*, 1993; Oliveira *et al.*, 1997; Vucetich & Ribeiro, 2003; Alvarenga *et al.*, 2005; Couto-Ribeiro *et al.*, 2005; Couto-Ribeiro, 2015; Carmo *et al.*, 2024). Palynological analysis from Taubaté suggests that the vegetation ranged from aquatic forms and hot and humid adapted plants in the valley surrounding the lake to more cold-adapted forms at higher levels. At the lake shore, the plant communities were dominated by Pteridophyta, Cyperaceae, and Typhaceae (Melo, 2003).

The lithology suggests a depositional environment with little transport, and therefore that the taxa have been found there likely lived in close association with the lake (Melo *et al.*, 2007). The most abundant mammal within the assemblage is *Taubatherium paulacoutoi*, a long-necked leontiniid notoungulate, weighting between 150–200 kg, and supposedly gregarious (Soria & Alvarenga, 1989; Couto-Ribeiro, 2015; Nelson *et al.*, 2023). Melo *et al.* (2007) suggested that the brachydont dentition and tapering rostrum of *Taubatherium* is indicative of a non-abrasive diet, probably mainly composed of soft vegetation and fruit, but no quantitative analysis of the diet of *Taubatherium* has been carried out yet.

We applied mesowear analysis to the assemblage of *Taubatherium paulacoutoi* from Taubaté to quantitatively assess their diet. We used both traditional mesowear and mesowear angles, discussing the potential implications of our results for applying mesowear studies to other notoungulates as well as for paleoenvironmental reconstruction of the Deseadan assemblage at Taubaté.

MATERIAL AND METHODS

All specimens analyzed here are housed in the Museu de História Natural de Taubaté Doutor Herculano Alvarenga (MHNT), Taubaté, Brazil. We examined all upper molars in an intermediate stage of wear, therefore excluding very young and very old individuals. Where multiple teeth were present, M2 was chosen (Fortelius & Solounias, 2000; Saarinen *et al.*, 2016).

The modern rhino specimens were studied in the following collections: Finnish Museum of Natural History (MZH), Helsinki, Finland; Kenya National Museums (KNM), Nairobi, Kenya; Natural History Museum London (NHMUK), London, UK; Royal Museum of Central Africa (RMCA), Tervuren, Belgium; University Museum of Zoology (UMZC), Cambridge, UK. A single specimen of *Diceros bicornis* was also studied in the field station of Tsavo East, Kenya.

Mesowear coding

Upper molars were coded for two characteristics, relief and cusp shape (Fortelius & Solounias, 2000; Croft & Weinstein, 2008; Saarinen *et al.*, 2016). Cusp shape could either be sharp (1), rounded (2), or blunt (3). When the two cusps differed in shape, the sharpest one was chosen (Fortelius & Solounias, 2000). Following Croft & Weinstein (2008), given the absence of modern analogues, we used three different relief scenarios (Figure 1). Scenario 1 is a selenodont/equid scenario, scenario 2 is a rhinoceros scenario, and scenario 3 is a hyracoid scenario. Relief was coded as high (1), or low (3) depending on whether the inter-cusp angle was more significant than or less than the threshold angle. These codings matched those of modern herbivore taxa taken from Saarinen *et al.* (2016). The mean across all eight *Taubatherium* specimens was taken for cusp shape and relief.

Discriminant analysis

Using the *MASS* (Venables & Ripley, 2002) package for R 4.1.1 (R Core Team, 2021), we performed a linear discriminant analysis (LDA) to predict the diet of *Taubatherium* under each relief scenario. The model used average cusp shape and relief as input data to predict dietary categories (browser, mixed feeder, or grazer). This model was then applied to *Taubatherium* under each relief scenario.

Hierarchical cluster analysis

Hierarchical cluster analysis was performed using the *mclust* R package (Scrucca *et al.*, 2023), which uses maximum likelihood criteria to cluster continuous data for Gaussian mixture models (Fraley & Raftery, 2002). Here, we used the default model, VVV, which is unconstrained. The input data for the clustering were the average values for the relief and cusp shape from the extant taxa and *Taubatherium* for the three different relief scenarios.

Mesowear angles

In some taxa where the traditional mesowear approaches (*e.g.*, Fortelius & Solounias, 2000) have not been possible, ‘mesowear angle’ methodologies have been developed (Saarinen *et al.*, 2015; Saarinen & Karne, 2017; Wilson *et al.*, 2024). The mesowear angle approach uses a principle that has been applied to other mesowear techniques: that occlusal wear in herbivore molars is related to the balance between attrition and abrasion (*e.g.*, Butler, 1972; Fortelius, 1981, 1985; Fortelius & Solounias, 2000); but it measures this balance through angles, either of dentine valleys or of wear facets. It is similar to some forms of mesowear analysis that have been developed (*e.g.*, Mesowear III; Solounias *et al.*, 2014), but using a measured angle, rather than a scoring scheme. In addition to the advantage of being applicable to taxa with different dental morphologies, these angles theoretically offer finer resolution between specimens, and parametric methods can be applied to them for statistical differentiation (Schap & Samuels, 2020).

For each of the *Taubatherium* molars that were scored for traditional mesowear, we also measured the buccolingual angle of the ectoloph occlusal surface relative to the grinding surface of the tooth when viewed in a mesiodistal direction,

following the methodology applied in toxodontids by Wilson *et al.* (2024) (Figure 2). This was done from 3D scans that were produced using the Polycam 3D scanning application v.3.2.27 (Polycam Inc., 2023), using the photogrammetry

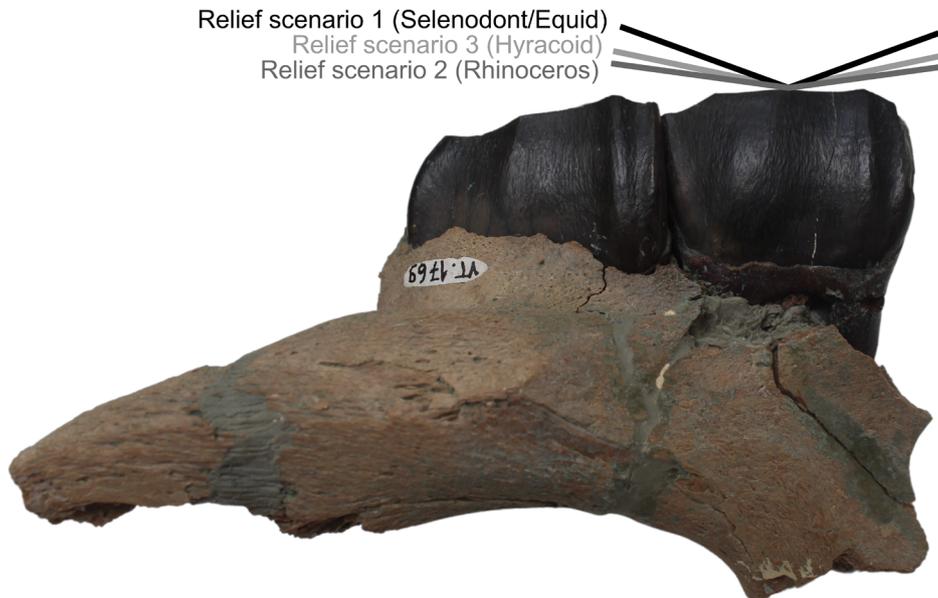


Figure 1. Threshold angles for the three different relief scenarios: Scenario 1 is a selenodont relief scenario; scenario 2 a rhinoceros relief scenario; and scenario 3 a hyracoid scenario. Intercusp angles steeper than these threshold values are coded as high relief (1) and those shallower than these thresholds are coded as low relief (3). The *Taubatherium paulacoutoi* specimen (MHNT-VT-1769) here would be coded as low relief (3) for all scenarios. Not scale.

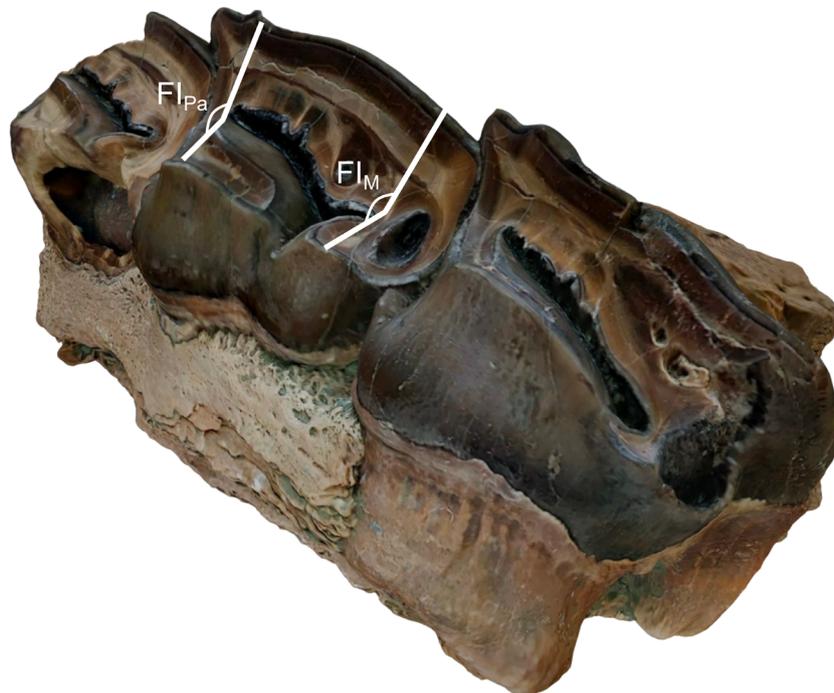


Figure 2. Demonstration of the facet inclination measured in upper molars of *Taubatherium paulacoutoi* (MHNT-VT-1403), shown here in oblique view. **Abbreviations:** FI_{pa} , Facet inclination at the level of the paracone; FI_M , Facet inclination at the level of the metacone. Average facet inclination (FI) then converted to mesowear angles (MA) using the equation ($MA = 180 - 2 \times FI$). Not scale.

mode on an iPhone XR. These scans were exported to Blender v3.1.0 (Blender Online Community, 2022), where angles were measured manually.

We measured the inclination of the wear facet of the ectoloph at the level of the paracone and metacone. Mean wear facet inclination (FI) is the average of these two values. We then converted these FI values into mesowear angles that are comparable to those that have been used in other taxa (Saarinen *et al.*, 2015; Saarinen & Karme, 2017; Wilson *et al.*, 2024). To find this final mesowear angle, we followed Saarinen & Lister (2023), where:

$$\text{mesowear angle} = 180 - 2 \times \text{FI}$$

We applied the same methods to modern rhinos, a group with very similar dental morphology. In modern *Ceratotherium* specimens, the occlusal surface in the region of the ectoloph forms a dentine valley rather than an inclined wear facet. In these cases, we measured the mesowear angle from the base of the valley to the tips of the enamel ridges, following Saarinen *et al.* (2015), at the level of the paracone and metacone, and took the mean mesowear angle from these two values. The dietary ecology of these modern rhinos uses categories taken from Saarinen *et al.* (2016).

While mesowear angles have largely been applied to taxa where traditional mesowear cannot be used (Saarinen *et al.*, 2015; Saarinen & Karme, 2017), the non-analogue nature of the mesowear signal in notoungulates supports the use of multiple approaches. Our preliminary observations suggest that this angle is variable in notoungulates throughout South America in the Cenozoic. With no living representatives for calibration, we do not use any threshold values between dietary categories here. Figures were made using the *ggplot2* R package (Wickham, 2016).

RESULTS

Raw mesowear scores

A bivariate plot of mean relief and mean cusp shape for the extant herbivores reveals that there are differences between the different dietary categories, with grazers having higher scores for both relief and cusp shape (reflecting blunt, flat cusps).

The most remarkable differences between categories seem to be in mean cusp shape. However, there is still substantial overlap in the hulls for these categories, particularly between browsing and mixed feeding. Interestingly, regardless of the relief threshold applied, *Taubatherium* falls outside the convex hulls of any of the dietary categories, with a high proportion of individuals having low relief, sharp cusps (Table 1, Figure 3), suggesting a mesowear signal distinct from all modern herbivores analysed so far. This matches the results of Croft & Weinstein (2008), who also found a high proportion of notoungulates with sharp cusps and low relief.

Linear discriminant analysis

The LDA correctly predicted the dietary category for 64.0625 % of modern ungulates. Prediction errors related to mixed feeding, with 11 browsing taxa misclassified as mixed feeders, five mixed feeders as browsers, five grazers as mixed feeders, and a single mixed feeding taxon (*Cervus duvauceli*) classified as a grazer. This taxon is known to consume mostly grasses in some areas of its range while being a mixed feeder in others (Tewari & Rawat, 2013), which reflects that classifying even modern ungulates into these three dietary categories is challenging.

Applying the model to *Taubatherium* gave different results depending on the relief scenario (Table 2). For relief scenarios 1 and 3, *Taubatherium* was assigned to the grazing category, with a posterior probability of 0.641. For relief scenario 2, it was assigned to the browsing category, with a posterior probability of 0.465. Croft & Weinstein (2008) suggested that the relief scenario with the highest overall posterior probability should be chosen, which means that, in this case, *Taubatherium* would be considered a grazer.

Hierarchical cluster analysis

Largely, the cluster analysis was able to separate the different dietary categories (at least between browsers and grazers) using the cusp shape and relief. The mixed feeders were somewhat more spread between clusters, although their distribution broadly represents a continuum from browse-dominated to graze-dominated mixed feeders. For example, *Tragelaphus imberbis*, a browse-dominated mixed feeder

Table 1. Mesowear scores for each *Taubatherium paulacoutoi* specimen studied, including the relief state for each threshold angle: high relief (1), low relief (3) and the cusp shape: sharp (1), rounded (2), blunt (3).

Specimen	Relief state			Cusp shape
	Threshold 1	Threshold 2	Threshold 3	
MHNT-VT-981	3	3	3	1
MHNT-VT-916	3	3	3	1
MHNT-VT-1435	3	1	3	2
MHNT-VT-1434	3	3	3	1
MHNT-VT-2207	3	3	3	1
MHNT-VT-1769	3	3	3	1
MHNT-VT-1407	3	1	3	1
MHNT-VT-1403	3	3	3	1

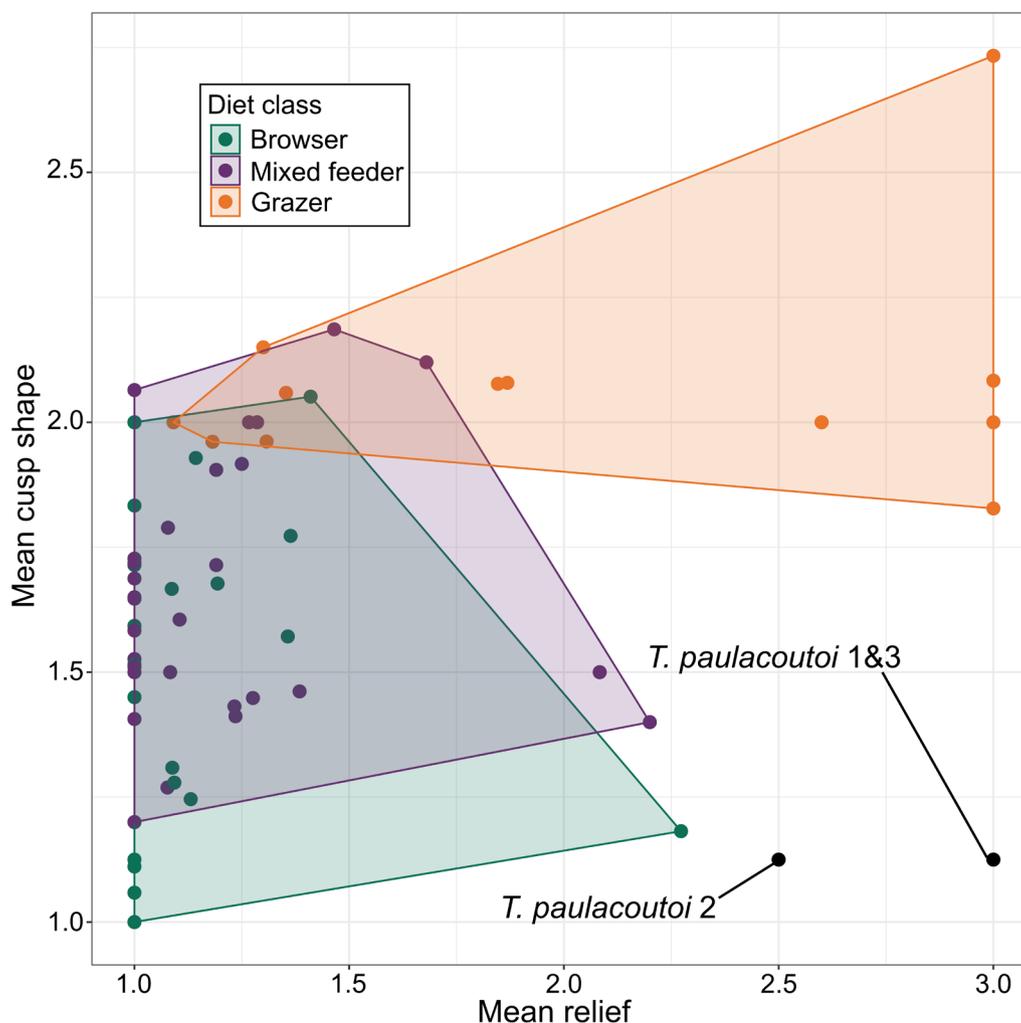


Figure 3. Bivariate plot for mesowear in modern ungulates and *Taubatherium paulacoutoi* showing the differences in mean relief and mean cusp shape between different dietary categories. Numbers next to *Taubatherium paulacoutoi* show the alternative relief thresholds.

Table 2. Results of linear discriminant analysis (LDA) showing the posterior probability for different dietary categories for *Taubatherium paulacoutoi* using the three different relief thresholds. The highest posterior probability for each relief threshold is highlighted in bold.

Relief threshold	Posterior probability		
	Browser	Mixed feeder	Grazer
1	0.19034586	0.16915368	0.64050046
2	0.46535433	0.36032844	0.17431723
3	0.19034586	0.16915368	0.64050046

(Castelló, 2016), is clustered with mostly browsing taxa. For all three relief scenarios, *Taubatherium* clustered with the shrub-browsing taxa, *Heterohyrax brucei*, *Procavia capensis* and *Saiga tartarica* (Figure 4). This cluster is sister to a group of grazing taxa including *Bison bison*, *Damaliscus lunatus*, *Equus grevyi*, *Equus burchelli* and *Ceratotherium simum* but it does not contain any extant grazers itself. These three taxa have been noted to have a somewhat unusual mesowear

signal before, and in the case of the hyraxes, this might be due to their small body mass (they have been included in a group called minute abraded brachydonts, MABRA, Fortelius & Solounias, 2000; Saarinen *et al.*, 2016), though this is not the case for saigas or *Taubatherium*.

Mesowear angles

The angles we observed in modern rhinos are consistent with the known diets of each taxon studied. The three browsing taxa, *Dicerorhinus sumatrensis* (n = 4), *Diceros bicornis* (n = 7) and *Rhinoceros sondaicus* (n = 2) has mean mesowear angles under 90° (75°, 77.3° and 79° respectively). The grazing *Ceratotherium simum* (n = 6) has a mean mesowear angle of 131.6°, while *Rhinoceros unicornis* (n = 4), which is a mixed feeder, had an intermediate mean mesowear angle of 120.4°.

The mesowear angles from the *Taubatherium* specimens suggest a very sharp ectoloph relative to the grinding occlusal surface, with a mean mesowear angle of 78.6° (Figure 5). In other taxa, a mesowear angle of 90° or less is indicative of a diet consisting of largely non-abrasive vegetation *e.g.*, browse

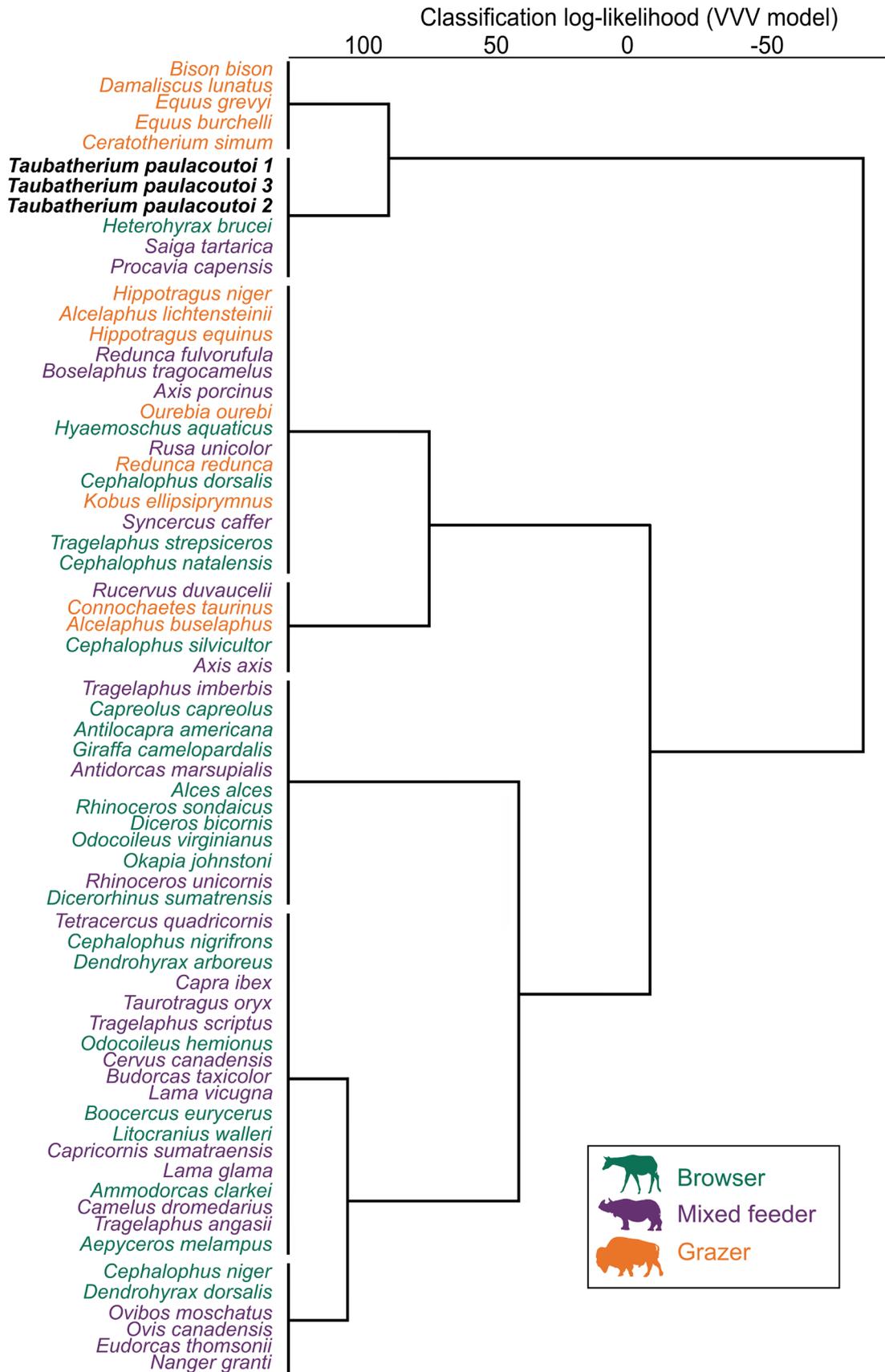


Figure 4. Hierarchical clustering dendrogram of mesowear scores for extant ungulates and *Taubatherium paulacoutoi* based on the mean relief and mean cusp shape. Extant taxa are coloured according to dietary categories (browser, mixed feeder or grazer). Silhouettes for *Okapia johnstoni* (T. Michael Keesey), *Rhinoceros unicornis* (Christophe Mallet) and *Bison bison* (Tracy Heath) from phylopic.org (all CC0 1.0 UNIVERSAL).

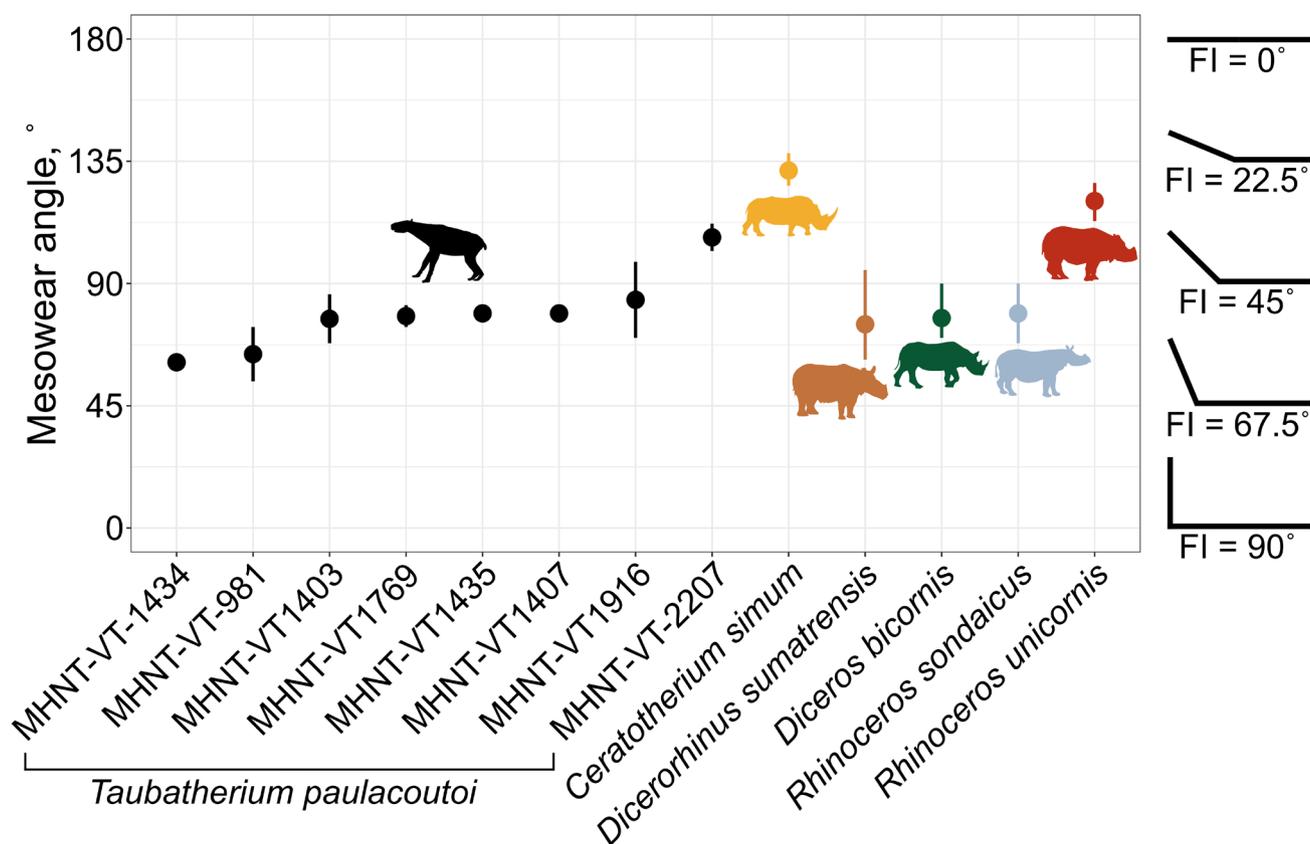


Figure 5. Mesowear angles (based on sharpness of the ectoloph occlusal surface) for the individual *Taubatherium paulacoutoi* specimens analysed here. Threshold values between different dietary categories are not included here in the absence of modern calibration data. Points represent the mean angle for each tooth, while bars show the maximum and minimum angle in each case. Also shown are the mesowear angles for the five modern rhino species for comparison. Schematic diagrams of the relative sharpness of the ectoloph occlusal surface are shown for different mesowear angles. These diagrams are schematic representations of the occlusal surface of the ectoloph relative to the two transverse lophs in a right M2 when viewed from a mesiodistal direction and with the occlusal surface orientated upwards. **FI** = Facet inclination. Silhouettes for *Ceratotherium simum*, *Dicerorhinus sumatrensis*, *Diceros bicornis*, *Rhinoceros unicornis* (Christophe Mallet, CC0 1.0 UNIVERSAL) and *Taubatherium paulacoutoi* (Zimices (Julián Bayona), CC BY-NC 3.0) from phylopic.org. Silhouette of *Rhinoceros sondaicus* made using image by J. Wolf (1876).

(Saarinen *et al.*, 2015; Saarinen & Karme, 2017; Saarinen & Lister, 2023). For seven of the eight specimens measured here, the mesowear angle was less than 90°, suggesting very limited abrasive component to the diet in *Taubatherium*. While the mean angle of MHNT-VT-2207 is still relatively low (107°), it has the same traditional mesowear coding as many of the other specimens, which might suggest that there is potential for differentiation at a finer resolution than with traditional mesowear.

DISCUSSION

Diet in *Taubatherium*

In general, the mesowear signal from *Taubatherium paulacoutoi* is consistent with the expectations from dental and cranial morphology. Using hierarchical clustering analysis with traditional mesowear scores, we reconstruct *Taubatherium* as a browser, although the clustering showed *Taubatherium* associated with three taxa that have an unusual mesowear signal (*Procapra capensis*, *Saiga tatarica* and

Heterohyrax brucei), which in all these species reflects a browse-dominated diet that includes tough, dry-adapted shrubs and herbs (Fortelius & Solounias, 2000; Saarinen *et al.*, 2016). Using discriminant analysis, we found that *Taubatherium* was most likely a grazer, though the results strongly depended on the relief threshold applied, with the lowest threshold (the rhinoceros-type) predicting *Taubatherium* as a browser.

The unusual combination of predominantly low relief but predominantly sharp cusps is most similar to the extant hyraxes *Procapra capensis* and *Heterohyrax brucei*. Although the mesowear signal of *Taubatherium* is non-analogue to any extant ungulate in having nearly 100% low relief and nearly 100% sharp cusps, the closest modern analogue in terms of highest proportion of low relief in combination with the highest proportion of sharp cusps is the bush hyrax (*Heterohyrax brucei*), a browse-dominated feeder in savanna and shrubland environments that has an average dietary composition comprising <10% grasses (Hoeck, 1975; Girmay *et al.*, 2016). In the case of *Taubatherium*, the unusually high

proportion of low relief for a browse-dominated feeder may reflect high chewing pressure required for feeding on tough plants, by the analogy with *Heterohyrax*, although indeed another possibility is inclusion of tough wetland plants such as reeds and sedges or fresh grasses in diet, as suggested for *Taubatherium* before (Melo *et al.*, 2007). The sample of extant taxa from Saarinen *et al.* (2016) that was used here does not contain any species that predominantly consumes aquatic or wetland vegetation, *e.g.*, *Tragelaphus spekkii*. Further investigation of the mesowear signals of such taxa should be considered to understand the ecology of fossil ungulates.

The Middle Miocene leontiniid *Huilatherium pluripicatum*, from La Venta, Colombia has been considered as semiaquatic, and therefore likely consuming aquatic vegetation, based on $\delta^{18}\text{O}$ ratios (Hoerner, 2017). However, comparable mesowear analyses have not been performed for *H. pluripicatum* yet, and dietary analyses of other Deseadan leontiniids have been limited. Further studies on the mesowear signals of other leontiniids, particularly well-known taxa like *H. pluripicatum*, alongside those from an expanded sample of extant ungulates, will help to test the hypothesis of a diet of aquatic vegetation in leontiniids such as *Taubatherium*.

The measured mesowear angles illustrate a very sharp wear facet of the ectoloph occlusal surface relative to the rest of the tooth, which is consistent with a diet composed mainly of low-abrasion vegetation, possibly with a high proportion of very tough plant material like twigs and branches (Popowics & Fortelius, 1997). While we do not apply threshold values here, given the absence of modern representatives, angles of 90° or lower suggest a browsing diet in other taxa (Saarinen *et al.*, 2015; Saarinen & Karme, 2017; Saarinen & Lister, 2023). The mesowear angles in *Taubatherium* are very similar to those of the browsing rhinos measured here, which may suggest that they were similarly browsing. The diets of *Dicerorhinus sumatrensis*, *Diceros bicornis* and *Rhinoceros sondaicus* generally consist of leaves, shoots and twigs (Groves & Kurt, 1972; Hillman-Smith & Groves, 1994; Groves & Leslie, 2011; Hullot *et al.*, 2019) and we think it is likely *Taubatherium* had a similarly browse-dominated dietary ecology. Further application of this method, both in SANUs and in other modern ungulates, will help to determine whether any modern taxa have dietary strategies analogous to those of *Taubatherium* and other SANUs.

Mesowear in notoungulates

Mesowear analysis has largely not been applied to notoungulates since its original use in the group by Croft & Weinstein (2008). We here provide further evidence for the challenge of using mesowear in notoungulates, given that the results for *Taubatherium*, regardless of relief threshold, lie outside the ranges of modern ungulates. It is possible that studying more modern ungulate taxa (especially associated with freshwater environments) will reduce this problem, although the prevalence of low-relief, sharp-cusped individuals observed by Croft & Weinstein (2008) suggests that this might be a widespread signal in Deseadan notoungulates. Our preliminary observations in other notoungulates suggest that

this signal is present in other periods and in other families too, and appears unrelated to hypsodonty or hypselodonty, but it is unclear why this should be the case.

We here propose an alternative approach, by applying the mesowear angle methodology to notoungulates. Though there are no modern representatives for calibration, the mesowear angles support a low-abrasion diet, through comparison with modern rhinos, which have a similar ectolophodont dentition. With only five modern species to use for comparison, and only few specimens for each species considered here, we do not aim to provide thresholds for differentiating diets in notoungulates based on rhinos. Nevertheless, the results from modern rhinos match the pattern observed in other taxa with a high proportion of grasses in the diet showing a higher mesowear angle. *Rhinoceros unicornis* was found to be intermediate between the browsing and grazing rhinos, matching the expectation that it should be a mixed feeder (Laurie *et al.*, 1983), however the recorded mesowear value was much closer to the value for *Ceratotherium simum* (and that of other grazers with a different molar morphology), which is consistent with an interpretation of *R. unicornis* as a variable grazer (Hullot *et al.*, 2019). The variability identified in modern rhinos suggests that there is potential to apply the ectoloph facet mesowear angle method in other ectolophodont taxa, including SANUs.

The continuous nature of the mesowear angle offers greater resolution than the ordinated mesowear values that are traditionally applied and have been shown to work well for dietary reconstruction in other taxa where traditional mesowear methods are inapplicable (Saarinen *et al.*, 2015; Saarinen & Lister, 2016, 2023; Saarinen & Karme, 2017; Schap & Samuels, 2020; Xafis *et al.*, 2020). For instance, the angles of MHNT-VT-2207 revealed a less steeply inclined ectoloph wear facet than the other individuals, though there was no difference observed in the ordinated mesowear scores. While marginally more labour-intensive, the mesowear angles remain faster and less destructive than other alternatives, including microwear and stable isotope analysis.

In lophodont ungulates, like rhinos and notoungulates, the degree of facet development reflects the balance between abrasion and attrition (Butler, 1972; Fortelius, 1981, 1985; Fortelius & Solounias, 2000). Wear facets are formed between the occlusal surface of the ectoloph and the enamel crests of the lower molars through attrition. Consumption of abrasive vegetation (*e.g.*, grasses) causes destruction of these wear facets and decreases the sharpness of the occlusal surface of the ectoloph as the dominant cutting structure, while consumption of less abrasive material will drive attritional wear, and therefore generate more prominent wear facets. Popowics & Fortelius (1997) suggested that facet sharpness reflects this balance and that the differential consumption of abrasive plants in *Ceratotherium* and *Diceros* drive the different sharpness of the ectoloph wear facet in these taxa, which is also observed here. These authors also suggested that particularly tough plant material like twigs and branches would cause re-sharpening of the facets through increased attritional wear, and it is possible that this is an explanation

for the very sharp angles seen in *Taubatherium* too. This would be consistent with its postcranial morphology, as the elongated neck might allow access to high branches (Couto-Ribeiro, 2015).

In extant rhinos, a more steeply inclined ectoloph facet angle is found in browsing species, e.g., *Diceros bicornis*, *Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*, whilst *Ceratotherium simum* (a grazer) has a flat occlusal surface (Fortelius, 1985). The ectoloph facet angle in *Taubatherium* is much more similar to browsing rhinos (Figure 5, Supplementary Material 1). Given the similarities between the overall molar morphology (if not necessarily traditional mesowear signal) in notoungulates and rhinos, we suggest that the same should be the case in this group (as well as other lophodont SANUs, like astrapotherians), and further work should continue to test the utility of the method.

CONCLUSIONS

A combination of traditional and novel mesowear methods suggest that the Deseadan leontiniid *Taubatherium paulacoutoi* probably had a diet that was dominated by non-abrasive foods, and that this taxon should be considered a browser. The traditional mesowear signal in *Taubatherium* is markedly different to that of any extant herbivore previously assessed. In consequence, we suggest that mesowear angles offer a potential mechanism to analyse diet in notoungulates, a group with no modern representatives. Future studies should investigate how to apply threshold values between dietary categories to these mesowear angles.

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