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The role of bite force in the formation of orthodentine microwear in tree sloths (Mammalia: Xenarthra: Folivora): Implications for feeding ecology

Robert K. McAfee [a,*], *Jeremy L. Green* [b,1]

[a] *Ohio Northern University, Department of Biological & Allied Health Sciences, 525 S. Main Street, Ada, OH 45810, USA*

[b] *Kent State University at Tuscarawas, Department of Geology, 330 University Drive NE, New Philadelphia, OH 44663, USA*

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ABSTRACT

Objectives: The purpose of this investigation was to explore the role and interplay that bite force has on the formation of microwear features upon the dentition of two- and three-fingered tree sloths (*Choloepus* and *Bradypus*, respectively), with the hypothesis that increasing relative bite force would correlate with an increase in frequency of microwear features.
Design: Microwear patterns were assessed by counting features (e.g. scratches, pits) seen within a standardized field of view on the mesio-labial facets casts of upper molariform series from sloth specimens using Scanning Electron Microscopy. Relative bite force was estimated using a geometric model to quantify the muscular inputs of the temporalis and masseter muscles with respect to the mandible at the centre of each lower tooth.
Results: Although relative bite force increases posteriorly along the toothrow, there is not a significant increase in frequency of scratches or pits in either sloth. Scratch width increases significantly as bite force increases in *Choloepus*.
Conclusions: We reject the hypothesis that higher magnitude of bite force is correlated with an increased number of microwear features in tree sloths. Results here suggest that other endogenous variables (such as chewing direction, manipulation of food during mastication, amount of food ingested) play a more significant role in the formation of microwear in sloths than orthal closure force. This further supports the formation of microwear on teeth as an intricate process that has multiple influences beyond the texture of food particles.

1. Introduction

Studies in the field of dental microwear are steadily advancing and revealing new insights about the feeding ecology of both extinct and extant taxa. Great utility exists in interpreting the various microwear features of scratches, gouges, and pits from extant animals (particularly mammals) to establish patterns that reflect known dietary habits and niches.[1–8] With these as a basis, data obtained from fossil relatives allows for inference

* *Corresponding author*. Tel.: +1 419 772 2762.
E-mail addresses: rkmcafee@gmail.com (R.K. McAfee), jgreen72@kent.edu (J.L. Green).
[1] Tel.: +1 330 308 7563.
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about paleodiet and in some cases may elucidate evolutionary changes in feeding patterns, which could also be correlated with environmental shifts, particularly in the Cenozoic.[6,9–12]

The strength of these studies lays with the properties of the teeth being studied, in particular the relative hardness of enamel. Dental enamel, although durable, is still damaged through the occlusion of teeth and food particles during mastication. This damage comes in the form of microscopic scars, such as scratches and pits (called "dental microwear"), that are visible under magnification.[6,13] Turnover in dental microwear is high (hours to days) so it is interpreted to represent an animal's last meal or last few meals, rather than a life history of diet.[14] Nevertheless, an examination of dental microwear patterns in a large sample of teeth across different mammalian species will generally reveal strict differences in scar patterns. This differentiation in interspecific microwear is useful as a proxy for reconstructing dietary strategies in herbivorous mammals, such as leaf browsing, fruit browsing, mixed feeding, and grazing.

Among mammalian clades, some taxa lack enamel, instead having a relatively softer outer layer of orthodentine. The placental clade Xenarthra, consisting of extant armadillos, anteaters, and tree sloths, as well as extinct taxa such as ground sloths, pampatheres, and glypodonts, is the most outstanding of enamel-less mammals as all of its adult members (with the exception of the extinct armadillo, *Utateus*[15–17] and the edentulous anteaters) bear this derived condition. Extant members also exhibit a wide array of feeding strategies, from strict myrmecophagy to omnivory to obligate folivory.

Independent analyses of microwear on xenarthran teeth have been successful in broadly distinguishing microwear patterns between members of the group (both extant and extinct) that have different feeding behaviours.[1,10,18–21] However, there remains a lack of understanding as to the specific causative mechanism of scar features on orthodentine tooth surfaces (e.g. scratches, pits). Beyond the physical properties of ingested food, it stands to reason that masticatory variables, such as bite force during jaw closure, should influence the formation of microwear on orthodentine. This begs the question as to how important these endogenous characteristics are to the patterns that have been previously recorded. As an effort to begin addressing this gap in our knowledge of orthodentine microwear, we herein investigate the potential correlation between microwear and bite force in tree sloths, the latter component applying a comparative estimation of the input forces associated with orthal closure of the mandible. We hypothesize that as relative bite force increases, there should be a correlated increase in the frequency of microwear features.

2. Materials and methods

2.1. Specimen selection

Fifteen specimens from three taxa (*Bradypus variegatus* [$n = 9$]; *Choloepus didactylus* $n = 4$]; *Choloepus hoffmanni* [$n = 2$]) were examined (Appendix). Specimens came from the mammal collections at the Field Museum of Natural History, Chicago, IL (FMNH). To standardize our sampling of bite force estimation and dental microwear, we only used skulls that contained a complete maxillary and mandibular dental series on the right side. The microwear portion of our analysis focused exclusively on second through fourth right maxillary molariforms (M2–M4[21]), and we only sampled microwear on the mesio-labial facet of each tooth. M2, M3, and M4 occlude directly with the three mandibular teeth from which our bite force estimations were obtained (see below). We analyzed microwear only on maxillary teeth to (1) make our data more comparable to previous SEM studies,[1,10] and (2) to reduce intertooth variation, as significant differences in microwear between maxillary and mandibular teeth exist in some taxa, such as *Choloepus*.[19] These strict sampling criteria reduced our final sample size for *Bradypus* (i.e., *Choloepus* = 6, *Bradypus* = 7), yet helped eliminate potential noise in our microwear signal corresponding to biomechanical differences in mastication across the tooth surface (e.g., to reduce inconsistent averaging of quantitative wear patterns associated with the leading edge versus those associated with the trailing edge of the power stroke).[22]

2.2. Specimen preparation and scanning electron microscopy

Cleaning, moulding, casting, and SEM preparation for microwear analysis followed protocols previously established by one of the authors.[1] All casts were analyzed using an Amray Model 1600 Turbo scanning electron microscope located in McGilvery Hall at Kent State University. Each specimen was screened for ante-mortem microwear features prior to image capture. If microwear was absent on the mesio-labial facet of at least one tooth in the series, the specimen was rejected. Of the original 15 sampled specimens, thirteen had visible microwear on all three right maxillary teeth under study. For each skull, two digital images of microwear on the mesio-labial facet of each tooth (M2–M4) were captured at 500× (with an operating voltage of 20 kV using secondary electrons). This resulted in six total images per skull (78 total images). Each image was resized to 1000 × 800 pixels (118.11 pixels/cm) in Adobe Photoshop CS4. Brightness and contrast adjustments were standardized for each image using the "Levels" feature in the same programme, such that the darkest pixel was black and lightest pixel was white. No additional brightness/contrast adjustments were allowed after this standardized procedure. The analysis area on each image was standardized to a 100 μm × 100 μm digital square that was constructed in Adobe Illustrator CS4 and centred over the area of highest density of visible microwear features, following pre-established protocols.[1,10]

2.3. Microwear analysis

Orthodentine microwear features were quantified using the semi-automated custom software package Microware 4.02.[23] This programme was originally designed to quantify scratches and pits on enamel surfaces in mammals; however, the overall similarity of orthodentine microwear features to those in enamel[1,10,18–21] supports the use of this programme for this study. We maintained a length/width ratio of 4:1 to discriminate