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## Dental functional morphology predicts the scaling of chewing rate in mammals

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### Abstract

How food intake and mastication scale to satisfy the metabolic needs of mammals has been the subject of considerable scientific debate. Existing theory suggests that the negative allometric scaling of metabolic rate with body mass is compensated by a matching allometric scaling of the chewing rate. Why empirical studies have found that the scaling coefficients of the chewing rate seem to be systematically smaller than expected from theory remains unknown. Here we explain this disparity by decoupling the functional surface area of teeth from overall surface area. The functional surface area is relatively reduced in forms emphasizing linear edges (e.g., lophodont) compared with forms lacking linear structures (e.g., bunodont). In forms with reduced relative functional surface, the deficit in food processed per chew appears to be compensated for by increased chewing rate, such that the metabolic requirements are met. This compensation accounts for the apparent difference between theoretically predicted and observed scaling of chewing rates. We suggest that this reflects adaptive functional evolution to plant foods with different fracture properties and extend the theory to incorporate differences in functional morphology.

### Introduction

A recent study in biophysiology by Viro et al. (2017) highlighted that scaling in mastication and processing of food does not strictly follow fixed laws, but balances between physical, physiological and temporal limits. Ever since the scaling of chewing rates was established for ungulates (Fortelius 1985), a lot of empirical evidence on chewing rates has been gathered to support or clarify the theory (Fortelius 1985, Druzinsky 1993, Shipley et al. 1994, Gerstner and Gernstein 2008, Ross et al. 2009, Ungar 2014, Viro et al. 2017). While the theoretical scaling of chewing rate to body mass is expected to be -0.25, the empirical chewing rates have been found to vary mainly in the range -0.15 to -0.22. The exponents observed thus seem to be systematically smaller, implying faster actual chewing than the theoretical scaling coefficient would suggest. Here we address this disparity.

We propose that the key to resolving this disparity lies in the adaptive relationships between dental morphology and mechanical properties of foods. Even though teeth scale isometrically with body mass (see, e.g., a review by Ungar 2014), the working surface of teeth may scale in different ways depending on their functional morphology. Mammalian molars often have linear structures formed of enamel crests, which work as the primary instruments for breaking food during mastication. Such structures are on the surface, but they are closer to linear than to surficial, and therefore do not necessarily scale directly with area. Therefore, if teeth primarily contain blades the working surface of teeth would be disproportionately smaller than the whole surface accommodating the blades, and the working surface would scale allometrically.

Regardless of dental morphology, animals need to process the amount of food expected from their body mass according to metabolic scaling. Teeth with a smaller working surface could, all else being equal, process the required amount of food by chewing it more times. This would explain

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