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Research paper

Impact of wear and diet on molar row geometry and topography in the house mouse

Sabrina Renaud[a,*], Ronan Ledevin[b]

[a] Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Université Lyon 1, CNRS, 69100 Villeurbanne Cedex, France
[b] UMR5199 PACEA, Université de Bordeaux, Allée Geoffroy Saint Hilaire (Bat. B8), 33615 Pessac, France

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ABSTRACT

Objectives: Dental evolution affects the geometry of the tooth, but the adaptive relevance of these changes is related to tooth sharpness, complexity, and relief (topography). On a set of laboratory mice, we assessed how wear related to age and food consistency affected molar geometry and topography.

Design: Three groups of laboratory inbred mice (C57BL/6J strain) were considered: Four week old mice close to weaning, six month old mice fed on regular rodent pellets, and six month old mice fed on rodent pellets that were powdered and served as jelly. Their upper and lower molar rows were imaged in 3D. The geometry of the surfaces was quantified using a template describing the whole surface of the rows. Topographic indices were estimated on the same surfaces.

Results: The geometry of the molar rows was heavily affected by age-related wear. Food consistency affected mostly the upper molar row, which was more worn and less helical in soft food eaters. Tooth sharpness and relief decreased with age-related wear. Tooth relief was lower in soft food eaters, but only on the upper molar row. Tooth complexity was insensitive to wear.

Conclusion: The primary factor affecting tooth geometry and topography is age-related wear, as wear erodes the molar surfaces. Tooth complexity, however, appears to be insensitive to wear, making this index relevant for comparison of tooth morphology among wild mice of unknown age. Soft food eaters displayed more worn teeth, with less helical molar row occlusal surface, possibly because behavior and jaw morphology were disturbed due to this unusual food resource.

1. Introduction

Efficient food processing is of prime importance for the fitness of an individual and, among the components constituting the feeding apparatus, the dentition plays a key role in achieving the comminution of food particles. Adaptive diversification of tooth geometry into complex multicuspid shapes is thought to be one of the key innovations that led to the mammalian radiation (Wilson et al., 2012). However, different tooth geometry can have similar functional performance (Wainwright, Alfaro, Bolnic, & Hulsey, 2005), especially related to the complexity of the tooth crown (Wilson et al., 2012). Nowadays, geometric morphometrics (Adams, Rohlf, & Slice, 2013) allows the quantification, in 2D or in 3D, of the tooth geometry, providing an insight into its diversification. Additionally, proxies of functional significance, such as tooth relief or complexity, have been developed from 3D data that describe tooth surface (Boyer, 2008; Bunn et al., 2011; Evans, Wilson, Fortelius, & Jernvall, 2007; Santana, Strait, & Dumont, 2011). Tooth complexity appears to be adapted to the mechanical properties of the food preferentially consumed by a species (Boyer, 2008; Santana et al., 2011). Thus, tooth complexity estimates may provide hints about the diet of a species (Boyer, Evans, & Jernvall, 2010). However, these two types of information – geometry and complexity of the tooth – are rarely considered together, despite the fact that they may shed light on the adaptive role of shape differences and how they evolved.

Rodents, and specifically murine rodents (Old World rats and mice) constitute a highly variable group. A part of this success is related to the diversification of their dentition (Misonne, 1969) and how occlusion is achieved (Lazzari, Tafforeau, Aguilar, & Michaux, 2008), which allows them to exploit very different food resources. Diversification of the dentition can even occur within species at the micro-evolutionary level, as has been observed in the house mouse *Mus musculus domesticus* (Ledevin et al., 2016; Renaud, Dufour, Hardouin, Ledevin, & Auffray, 2015). It is tempting to investigate the functional role of such shape differences to provide insight into both their potential adaptive role and how microevolution can shape this intraspecific variation. However, at the scale of population-level variation, the changes caused by wear on

* Corresponding author.
E-mail address: sabrina.renaud@univ-lyon1.fr (S. Renaud).

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tooth geometry may be of the same order of magnitude as, or even be the first order signal overwhelming, any other evolutionary differences (Ledevin et al., 2016). Thus, a prerequisite for applying functional proxies to the mouse tooth would be to better understand the effect of wear on these estimates and on the tooth geometry. However, such studies are primarily conducted in primates (Dennis, Ungar, Teaford, & Glander, 2004; Pampush, Spradley et al., 2016). Furthermore, most studies regard interspecific differences (Godfrey, Winchester, King, Boyer, & Jernvall, 2012; Winchester et al., 2014), rather than addressing whether intraspecific tooth shape variation may be of functional significance in microevolutionary processes.

Thus, we propose a pilot study on the house mouse to assess the effect of wear on tooth geometry and functionality in controlled laboratory conditions. Differences in wear stage related to age were investigated by comparing young and old mice. The potential for specific food material properties to cause differential wear was assessed by comparing mice reared on diets of different consistencies. For these three groups of mice, the geometry of the upper and lower molar rows was quantified using 3D geometric morphometrics (Ledevin et al., 2016). On a larger sample of the same groups, the shape of the first upper molar (UM1) was quantified using an outline analysis (Renaud, Auffray, & Michaux, 2006). Furthermore, the topographic characteristics of the molar rows, presumed to be better estimates of functional performance than shape (Godfrey et al., 2012; Ungar, 2004; Winchester et al., 2014), were estimated on the same molar rows. This allowed us to address the following questions. (1) What is the relative impact of age and food treatment on wear as traced by tooth geometry? (2) Do these geometric changes correspond to differences in tooth topography? (3) What are the perspectives of applications to trace dietary differences in natural populations?

2. Material and methods

2.1. Samples

Female mice from the inbred strain C57BL/6J were ordered from the Charles River Laboratory (Lyon, France). They were three weeks of age when obtained. A cohort of eight mice was sacrificed at four weeks (young group, Y-B6). The other individuals were reared at the PBES (Ecole Normale Supérieure de Lyon, France) until the age of six months. Half were fed a standard hard pellet diet (hard food group, HF). For the other half of the mice, the same pellets were ground to powder and mixed with agar-agar. This mixture was hydrated when given to the mice so that the consistency would correspond to a jelly (soft food group, SF). This resulted in 19 HF and 20 SF.

The mice were sacrificed according to the directive 2010/63/UE of the European Parliament on the protection of animals used for scientific purposes. Breeding conditions in the PBES have the agreement B 69 123 0303–17/02/2009 of the French Ministère de l'Agriculture.

2.2. 2D tooth shape

The first upper molar (UM1) was pictured in 2D, with the occlusal surface manually oriented to the horizontal plane. Then, the outline of the occlusal surface was manually delineated using 64 points at curvilinear equidistance along the outline. This series of points was analysed using a Fourier analysis, which decomposes the outline into successive harmonics that describe the outline in increasing details, after an initial standardisation of the starting point along the long axis of the outline (Renaud et al., 2006; Renaud, Pantalacci, & Auffray, 2011). Each harmonic was described by two Fourier coefficients (FCs). Retaining seven harmonics resulted in an acceptable compromise between information content added by a harmonic and measurement error on this harmonic (Renaud et al., 2011). FCs were standardised by the size of the outline ('zeroth' harmonic), retaining shape information only. The set of 14 FCs (seven harmonics per two coefficients) constituted the set of 2D shape variables to be considered in subsequent multivariate analyses.

2.3. 3D characterization of the upper and lower molar rows

For a subset of mice (three Y-B6, four HF, and four SF), skulls were scanned at a cubic voxel resolution of 20 µm using a microtomograph (µCT) Locus GE at Voxcan (Marcy l'Etoile, France).

The right upper molar row (UMR) was delimited on each slice using a threshold method in Avizo (v. 7.1–Visualization Science Group, FEI Company). Connections with bone were manually closed and the surface generated. Mouse molars are composed of transverse enamel ridges, the cusps of which align to form longitudinal rows that direct the propalinal (antero-posterior) movement during chewing. The upper molars show central, labial, and lingual rows and the lower molars labial and lingual rows (Fig. 1). Describing this complex geometry is challenging because it appears difficult to locate reliable landmarks on such molars and to delineate curves along the ridges (Skinner & Gunz, 2010). Thus, we developed a method of shape description that entirely relies on the description of the tooth surface. On the first mouse of the

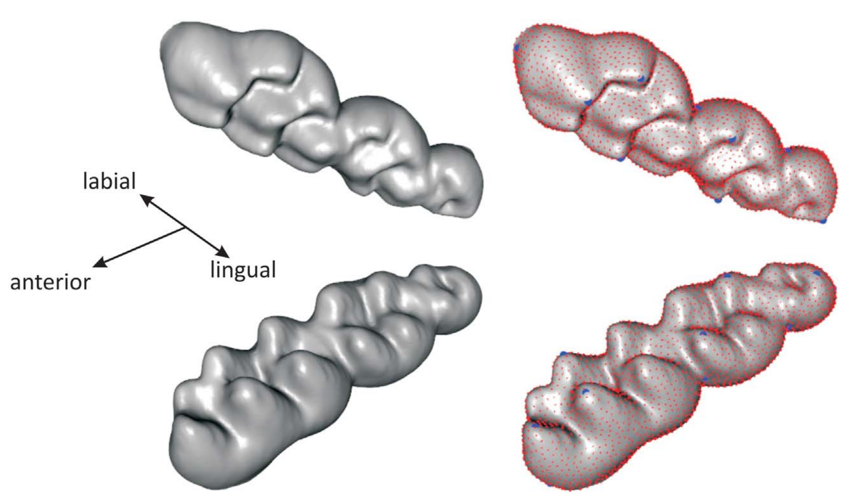

Fig. 1. Upper and lower molar rows of a young C57BL/6J mouse (specimen Y-01) and the associated template with landmarks serving for the initial superimposition of the different specimens. Fourteen fixed landmarks (blue dots) were positioned on each upper molar rows as guide during the registration process of the template, which was composed of 2194 sliding semi-landmarks (red dots) that were analysed using a Procrustes procedure. A similar method was used for the description of the lower molar row, with 14 fixed landmarks and 2213 semi-landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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