Ontogenetic and life history trait changes associated with convergent ecological specializations in extinct ungulate mammals

Helder Gomes Rodrigues^{a,b,1}, Anthony Herrel^b, and Guillaume Billet^a

^aSorbonne Universités, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, UMR CNRS 7207, CP 38, Muséum National d'Histoire Naturelle, 75005 Paris, France; and ^bMécanismes Adaptatifs et Evolution, UMR CNRS 7179, Bâtiment Anatomie Comparée, CP 55, Muséum National d'Histoire Naturelle, 75005 Paris, France

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Investigating life history traits in mammals is crucial to understand their survival in changing environments. However, these parameters are hard to estimate in a macroevolutionary context. Here we show that the use of dental ontogenetic parameters can provide clues to better understand the adaptive nature of phenotypic traits in extinct species such as South American notoungulates. This recently extinct order of mammals evolved in a context of important geological, climatic, and environmental variations. Interestingly, notoungulates were mostly herbivorous and acquired high-crowned teeth very early in their evolutionary history. We focused on the variations in crown height, dental eruption pattern, and associated body mass of 69 notoungulate taxa, placed in their phylogenetic and geological contexts. We showed that notoungulates evolved higher crowns several times between 45 and 20 Ma, independently of the variation in body mass. Interestingly, the independent acquisitions of ever-growing teeth were systematically accompanied by eruption of molars faster than permanent premolars. These repeated associations of dental innovations have never been documented for other mammals and raise questions on their significance and causal relationships. We suggest that these correlated changes could originate from ontogenetic adjustments favored by structural constraints, and may indicate accelerated life histories. Complementarily, these more durable and efficient dentitions could be selected to cope with important ingestions of abrasive particles in the context of intensified volcanism and increasing aridity. This study demonstrates that assessing both life history and ecological traits allows a better knowledge of the specializations of extinct mammals that evolved under strong environmental constraints.

dental ontogeny | hypsodonty | abrasion | notoungulates | South America

An understanding of the life history of mammals in their ecological context is essential to predict how these animals may have coped with past environmental and climatic variations. The life history of mammals reflects behavioral, physiological, and anatomical adaptations that have a direct impact on survival and reproductive success (1). Life history traits are in turn directly influenced by size and lifestyle, reflecting the adaptations of mammals to their environment (2, 3). However, life history parameters such as fecundity, the age at sexual maturity, longevity, or mortality often cannot be quantified precisely in extinct species. Estimations of body size (or mass) alone do not allow accurate inferences on life history traits because of intrinsic variations depending on ecological factors (2, 4). For these reasons, bone histology is frequently used in extinct species for physiological inferences (5, 6).

Dental growth measured using crown height can, however, provide data on both ecology and longevity (7–9). Moreover, studying dental replacement, especially the timing of postcanine eruption, can give insights into the pace of life or ecology (10–12). The late eruption of molars compared with permanent premolars can for instance be associated with a slow pace of growth in some mammals

(e.g., humans, hippos, rhinos) (11). However, this relationship, previously summarized under Schultz's "rule," cannot be generalized to all mammals (12, 13). It has also been suggested that the time of eruption of the first molars is a suitable predictor of the pace of life (e.g., longevity, maturity, weaning period) in some mammals (e.g., primates, ruminants) (10, 12). Consequently, the scrutiny of dental ontogenetic patterns may prove very insightful to understand changes in life history and ecology, and therefore to assess the impact of environmental changes on extinct mammals.

During the Cenozoic, the long isolated South American continent underwent drastic geological, climatic, and environmental changes that might have severely affected endemic mammalian faunas (14–17). Among these mammals, the extinct order of Notoungulata was highly diversified taxonomically and consisted of rodent-sized up to rhino-sized taxa (18–20). They exhibited very advanced dental specializations thought to be related to herbivory (21, 22). Interestingly, high-crowned teeth (i.e., hypsodonty) evolved among notoungulates during the Paleogene more than 10 million years before their appearance in the majority of other mammalian groups (17, 21–24). For instance, intense crown height increase occurred during the Middle Miocene–Pliocene period in mammals from northern continents, such as ruminants, and also perissodactyls (e.g., Equidae, Elasmotheriinae) (8, 21, 22, 24), the closest extant relatives of notoungulates (25, 26). Most remarkably, a crown height increase convergently evolved in four distinct notoungulate clades

Significance

Estimating life history traits such as pace of growth or longevity is difficult in extinct mammals. Yet, these parameters could be helpful to better understand how herbivorous mammals adapted to changing environments. We here highlight the insights gained by studying dental growth and eruption in a clade of extinct ungulate mammals. Variation in these traits was assessed in the context of volcanism, cooling, and increasing aridity in South America starting 50 Ma. We show that ever-growing teeth combined with faster molar eruption arose several times during the evolution of these mammals, allowing them to obtain a more durable and efficient dentition in constraining environments. These innovations might represent convergent ontogenetic and physiological adjustments that contributed to their ecological specialization.

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¹To whom correspondence should be addressed. Email: helder.gomes-rodrigues@mnhn.fr.

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(e.g., Toxodontidae, Interatheriidae, Mesotheriidae, and Hegetotheriidae). This repeated innovation was likely selected to withstand high dental wear during mastication (17, 27). It was also assumed to be related to the successive orogenic, volcanic, and erosive phases of the Andean Cordillera starting from the Late Paleocene (approximately 57 Ma) (28), which involved subsequent deposition of abrasive detritic particles on plants (16, 29, 30).

The comparative ecology and life history of the different groups of notoungulates remains, however, poorly understood. Here, we provide data allowing a more complete overview of the convergent crown height increases and associated dental ontogenetic changes in notoungulates to better understand their evolution with respect to environmental variations taking place in South America from the Late Paleocene onwards. For this reason, we studied and compared the evolutionary patterns of dental growth (Fig. 1A) and eruption (Fig. 1B) in different clades of notoungulates along with estimated body mass in the context of a consensual and well-resolved phylogeny. We also put these original data into a geological framework to estimate the variations in ecological and life history traits that may be related to major geological and climatic events during that time.

Results and Discussion

Convergent Increase of Dental Crown Height in Notoungulates. The parsimony reconstruction of character evolution indicates that notoungulates acquired high-crowned cheek teeth at least three times during their evolutionary history (Fig. 2). Specialization toward ever-growing dentitions (i.e., hypselodonty) then convergently spread among the four last-existing monophyletic families of notoungulates (Toxodontidae, Interatheriidae, Mesotheriidae, and Hegetotheriidae). As is evident from the examination of phylogenetic distributions (Fig. 2), there is no significant correlation between crown height and estimated body mass in notoungulates. Such a lack of a significant correlation is exemplified by the Toxodontidae, and most of Mesotheriidae, which show larger body masses than the Hegetotheriidae and

Interatheriidae, whereas they have similar variations regarding crown height. As a result, it can be considered that a crown height increase is not directly influenced by body mass, as was previously suggested for some notoungulates (31) and other mammals (9).

Because they lived in environments on which soil minerals (dust and grit) were likely deposited to an important degree due to volcanic activity (16, 17, 29), high-crowned teeth may have allowed notoungulates to cope with the ingestion of such external abrasive particles that strongly wear teeth during chewing. In the presence of external abrasives, wear rates may have also been enhanced by an increase in the pressure and intensity of chewing, especially given a diet including many fibrous plants with a low nutritive value (e.g., grass and grass-like plants, some shrubs) (27). This increase might also be related with digestive abilities assumed to be less efficient in notoungulates than ruminants, but closer to those of their extant relatives (e.g., horses, rhinos), for which the amount of food intake is higher and the chewing effort greater (17). It is important to point out that the presence of abundant external abrasive particles would have especially affected animals eating a greater proportion of plants close to the soil (i.e., herbaceous to shrubby plants). That may have been the case of some South American mammals, such as notoungulates, small argylagoid marsupials, and ground-dwelling caviomorph rodents, which convergently acquired high-crowned dentitions (17).

Striking Convergent Modifications of Dental Eruption Patterns and Life History Traits. Data on the modes of dental eruption show a very similar distribution to crown height on the cladogram, with a reversal from third molars erupting last to third molars erupting faster than permanent premolars in the four late diverging families (Fig. 2). The details of their eruption sequence slightly differ from one clade to another (Fig. 2). Indeed, in Toxodontidae, the eruption of third molars occurs only before the eruption of the last permanent premolars (P4), as observed in

Fig. 1. Main variations of dental growth and eruption observed in notoungulates. (A) Dental crown height states (*Colbertia magellanica* AMNH49873, *Pseudhyrax* sp. MLP61-IV-9-1, *Paedotherium bonaerense* MNHN.F.MHR45). (B) Dental eruption states (*Trachytherus alloxus* MNHN-BOL-V 009027, *Microtyotherium choquecotense* MNHN-BOL-V 003349). P, premolars; M, molars.

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