Feeding specializations in Rodents

With 11 Figures

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Abstract

The particular pathway of evolution of the mammalian order of the rodents as compared to the other herbivorous mammals is described. In their dentition the most important change consisted in the replacement of the primitive molar plan of the pantotherian ancestors by completely new dental structures. The new evolutionary options acquired by this, are one of the reasons for the particular evolutionary success and the great diversity of niches formed by this group. The newly developed family-specific dental patterns soon became genetically fixed, to the effect that functional optimizations - that means adaptive evolution - could only be realized through allometric change of shape and proportions. This was possible in connection with increasing hypsodonty. New descriptive parameters allowing to characterize the divergent adaptations are defined. Among them the relative amount of enamel within the occlusal surface is the most reliable indicator of feeding specialization. A comparison reveals that the small rodents in their hypsodont evolution mostly diminished the crowding in their dental patterns, whereas in the evolution of several very large mammalian herbivores quite the contrary occurred. The functional reasons for this are discussed. Arguments are brought forward that the morphological optimization of the molar dentitions of rodents can attain degrees not realizable in large hypsodont herbivores.

Key words: Feeding specialization, Rodents, evolution

Introduction

The origination of new morphological structures and gradual change of shape and proportions of these, are two different evolutionary processes. One of the best known examples for this is the formation of the internal bony structure of the fins of the crossopterygians and the many secondary changes this pattern later underwent within the tetrapods under various functional needs. Thereby it revealed that the anatomical structures behaved in a highly conservative manner, whereas shape and proportions varied following particular environmental and adaptive contexts. Largely the same can be said of the evolution of the vertebrate skull. Probably one of the latest incidents of the formation of new morphological structures in evolution is the origin of the molar patterns in the mammalian order of the rodents. Also in this case manyfold secondary change of shape and proportions occurred in the subsequent evolution. Thanks to a good fossil documentation and the existence of many living species the rodent example can be investigated in much detail. Since they are frequently found in fossil sites in great numbers they are particularly suitable for quantitative comparative investigations on a statistical basis. Due to their typically very low body weight, rodents were able to form many different feeding niches, which is reflected in a multiplicity of divergent secondary changes of their molar teeth. In addition to this, in many cases the fossil species are well documented as evolutionary lineages over millions of years so that morphologic changes can be followed step by step. All this makes them particularly appropriate for evolutionary studies. In the following exclusively the herbivorous specializations are...
Degeneration of the inherited molar plan and formation of new dental structures

The primitive molar pattern originally shared by the marsupials and placentals was formed in the Cretaceous during the evolution of the pantotherians. Its characteristic arrangement of cusps and crests is generally called the tuberculosectorial or tribosphenic plan. Check teeth of this type were particularly suitable for breaking up insect food which very probably formed the main pantotherean alimentation source. When the radiation of mammals started, the tribosphenic molar plan revealed to be easily transformable for the needs of carnivorous specializations through rather simple allometries. Not the same can be said, however, as to the formation of vegetarian niches, because the cusps and crests of the plesiomorphic molar morphology were too steep as to allow high pressures between opponent dental surfaces during tooth occlusion. In most herbivores, as for instance the ungulates and New World notoungulates but also the lagomorphs, the original pattern was mainly conserved. Cones got reduced in height and crests became more prominent and only in the upper teeth few morphological elements were added. Therefore the plesiomorphic structure of the molars mostly still discernible in the unworn teeth of even highly specialized descendants. Thanks to these modifications the molars became appropriate for disintegrating leaf material as the most abundant vegetarian food resource of the early Tertiary. Only later, that means in the Neogene, grass became another prevailing dietary basis.

Very different from this mainstream development was the pathway of molar specialization of the rodents. In these the original tribosphenic pattern became largely dissolved to give free way to the formation of new occlusal structures. Looking for an explanation of this particular specialization history, two main reasons can be found. 1) Thanks to the possession of highly modified strong incisors, rodents were able to open up seeds and fruits covered by strong ligneous envelops. The exclusive access to this food resource could provide an essential part of their energy budget, given their typically very low body weight, and brought them a niche advantage not disputed by contemporaries from other groups. 2) As supplement to this, due to their ability of living on trees, further soft and nourishing plant tissues could be acquired, such as burgeons and berries. In order to disintegrate such kind of food, molar surfaces with very low relief were most suitable, because more vertical pressure could be developed between their occlusal surfaces. From an evolutionary point of view such types of molars could easily be acquired through morphological atrophy of the plesiomorphic occlusal elements. As a result, occlusal surfaces with rounded cones and low and strongly variable surface shrinkles were formed, as can be found in many Lower to Middle Eocene representatives of the rodent order. However, with the evolutionary success of rodents and the increasing number of species very capacities of the characterized particular feeding niches were no longer sufficient very soon. As a consequence, increasing selective pressure towards the formation of niches with less restricted alimentary resources arose. This led to the many secondary specializations to more fibrous, less nourishing food. However, for the disintegration of these materials molar surfaces with more relief elements were required. This is why during a phase of secondary structuration new arrangements of crests were formed on the molars. These at the beginning were submitted to considerable variation but with further evolution soon became freezed to the group-specific patterns found in most rodent families since the Upper Eocene. In the following radiation, rodents with very low body weight formed numerous particular feeding niches, many of them not available to larger plantivorous mammals. In these niches the functional requirements for breaking up food were very different and as a consequence many divergent specializations formed. These, however, were not acquired by structural changes of the teeth in a proper sense, because the dental structures had already become genetically fixed in the preceding evolutionary phase. The modifications instead were realized through allometric changes of the tooth crown. This was possible in many groups in connection with a development generally known as increasing hypsodonty.

Text-fig. 1. Hypsodonty as result of exclusive vertical strechening of the base of the tooth crown: example of a lower molar of Issiodoromys limognensis from Pech du Fraysse, Upper Oligocene, Quercy, France. The parameter values were obtained by artificial abrasion of an individual tooth. D: structural density = degree of lobation of the tooth pattern; H: abraded crown height.

Progressive hypsodonty is a means of compensating the increasing rate of abrasion of the teeth during their function. At the same time it opens up the possibility of modifying the proportions of the tooth crown itself. In fact, hypsodonty could be realized in different ways as a result of particular ontogenetic growth programs. A closer look shows that the vertical elonga-