Isotopic dietary evolution linking with lineage evolution and interspecific competitions in small mammals, using Miocene rodents as a case study

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Abiotic forces, including climate change, continental drift, and geographic barriers, have been viewed as the major driver of macroevolutionary change in organisms, evidenced by various studies from empirical, ecological, phylogenetic, and paleontological approaches on different time/spatial scales and resolutions. On the other hand, biotic interactions such as predator-prey interactions, interspecific competition for food, density-dependent natural selection has been limitedly recognized as a factor for shaping evolutionary patterns. In vertebrates, biotic interactions can be directly observable in field studies. However, the nature of long generation times in animals makes it difficult to obtain general patterns of biotic interactions apart from seasonal variations in the relatively short-term studies. In vertebrate paleontology, despite the advantage of the long-term time scales, possible morphological diversification and/or constraints due to the presence of competitors or competitive lineages is rarely documented.

In this study, we utilized two paleontological events of small mammals from in the Miocene Siwalik Group of northern Pakistan in order to evaluate isotopic dietary evolution in relation to (1) lineage evolution and (2) interspecific competitions. The first event is that murine rodents (true mice and rats) from the region record the earliest appearance of the group to its diversification into two sympatric lineages (here called *Karnimata* and *Progonomys* lineages), beginning before and continuing through a unidirectional shift from C_3- to C_4-dominated vegetation. The second event is that cricetid rodents (hamsters) were completely replaced by murine rodents (true mice and rats) at least within 5 million years after the earliest appearance of basal murines in Pakistan. Carbon and oxygen isotope values in enamel of first lower molars were obtained by laser-ablation GC-IRMS to infer dietary and habitat preferences, ranging from 15 to 6.5 Ma. Tooth shape of upper first molars was defined by morphometric distance of ecomorphological characters, 2D geometric morphometric analysis of tooth outline, and 3D GIS models.

For the topic of lineage evolution, our dataset demonstrates that murine rodents experienced a remarkable C_3-C_4 dietary shift with the *Karnimata* lineage consuming a greater percentage of C_4 grasses than the *Progonomys* lineage at any given time. In 2D analyses, adaptive change of tooth morphology in the *Karnimata* lineage is more strongly associated with increasing chewing efficiency in the propalinal direction of mastication. However, in both clades, preliminary 3D model analysis shows that more derived (and younger) species have average slopes of cusps directed more anteriorly than more basal (and older) species, which is also related to the propalinal chewing direction. These results indicate that while both clades morphologically adapted to varying contributions of C_4 grasses to their diets, selection pressure forcing dental adaptations was differentially greater in the *Karnimata* lineage.

For the topic of interspecific competition, our initial data suggest that the dietary conservation among the fossil rodents can be detected even in the C_3 plant-dominated region but that change in dietary niche breath could not be observed as the variance. Throughout the 5 million-year range of coexistence, mice have isotope values similar to phylogenetically closer taxa, whose size is smaller than more distant taxa

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that are similar in size to the mice. Although the power of the statistics is still weak due to the small number of the samples, phylogeny is a more important factor than body size in the competition.

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