Abstract

Lagomorphs (Lagomorpha), nowdays represented by rabbits, hares (Leporidae), and pikas (Ochotonidae), are one of the oldest groups of the modern mammals (Mammalia). Including their direct ancestors, the beginning of this lineage can be traced to the early Paleocene, so approximately 60 million years ago. Unlike other groups of mammals (e.g., primates or tapirs), their morphology did not significantly changed from that time. Due to their conservative skeletal morphology, similar adaptations appeared in the evolution of lagomorphs many times, independently in different groups. Therefore, it is hard to determine the characters resulting from the convergent evolution from the features restricted to individual lineages. Their conservative morphology also affects the view of their phylogenetic relationships with other groups of mammals. For years, Lagomorphs were considered rodents (Rodentia, including, e.g., mice, squirrels, beavers or porcupines). Some authors considered Lagomorpha as a separate, monophyletic lineage, but this question was discussed for a long time. Finally, the molecular analysis provided at the beginning of the XXI century determined the position of lagomorphs in the family tree of mammals, clearly indicating their separation from rodents. Although the relationships of lagomorphs with other mammals are now known, the affinities within the group itself are still unclear. Many of extinct species present a mixture of features characteristic of the two main lagomorph lineages, Leporidae and Ochotonidae, so only an extensive and multi-faceted study of Lagomorpha can provide a reliable reconstruction of their evolutionary history. Fossil lagomorphs are known mainly from tooth remains, so this study is focused on the dental features: the changes during evolution in the enamel microstructure and morphology of the teeth.

Sections of the incisors and cheek teeth from 19 lagomorph species were obtained in order to follow the changes in their enamel microstructure. The enamel of the incisors shows that during the evolution of lagomorphs the strengthening the enamel occurred at least in two ways: (1) through complication of the interlacing of the prisms building single-layered enamel, or (2) through subdivision of the enamel into two layers and complication of the prisms within the layers. The presence of single-layered enamel is a plesiomorphic condition which occurs in the leporids, the diet of which does not contain hard plant material. This contrasts with the ochotonids, in which the diet includes dry and hard plants, so strengthening of incisor microstructure to prevent cracking was important for intake of hard food. The cheek teeth always have double-layered enamel, in which the outer layer

tends to become thicker and the prisms building it get arranged into decussating bundles forming irregular enamel, characteristic for modern forms. The appearance of this type of enamel is associated with strengthening of its structure and happens also in other plant-eating mammals. It makes the teeth more resistant to the abrasive effects of silica and plant fibers. Along with irregular enamel, the presence of high-crowned, and rootless teeth (hypsodonty) is also correlated with the adaptation to such food. Although the hypsodonty appeared in lagomorphs already in the middle Eocene, it do not co-occurred with the appearance of irregular enamel. Moreover, it seems that within the Lagomorpha the hypsodonty appeared a few times independently in various species, dependent on their inhabited environment. A structure resembling irregular enamel appeared in early Miocene in the leporid lineage and in the middle Miocene in the ochotonid lineage. The irregular enamel appeared at least two times in the evolution of lagomorphs, independently in the lineage of Ochotonidae and in Leporidae.

The abundance of fossilized lagomorph teeth offered an opportunity to study a large-scale diversification of the cheek teeth. The shape analysis was performed for 7 041 teeth, including extinct and extant lagomorphs. The analysis contains 40 genera of lagomorphs, which comprise a statistically significant sample to analyze the diversity of lagomorphs in Europe form the Oligocene to Holocene. The analysed sample includes also duplicidentates from Asia and North America, what gives an insight into the shape variability also on the other continenst from Eocene to Holocene. The amount of variation in extinct Lagomorpha exceeds that seen in the recent genera (*Lepus*, *Oryctolagus*, and *Ochotona*). The greatest morphological disparity can be noticed in the Miocene of Asia and Europe. The range of morphological variation in recent taxa is also far smaller in comparison to extinct species. For all the teeth, the Eocene taxa occupy a different morphospace than the recent genera. The shape changes in the cheek teeth, enamel microstructure, and hypsodonty appear to be correlated with the vegetation changes resulting from global climate changes. In the Eocene, the warmest Cenozoic epoch, subtropical forests with broad-leaved plants were dominant in the Northern Hemisphere. At the Eocene/Oligocene boundary the progressive cooling of the climate resulted expansion of xerophytic shrublands in East Asia and warm-temperate coniferous forests and sclerophyll woodlands in Europe, but in North America the warm-temperature mixed forests and subtropical forests were not replaced. Thus, the lagomorphs in Asia developed secondary shearing blades as an adaptation for feeding on hard pland material, and due to expansion of such arid areas in the Northern Hemisphere, the ochotonids spread in the early

Miocene to Europe, North America and Africa. However, in the early Miocene the first grasslands appeared and expanded in the late Miocene after the middle Miocene extinction peak, which caused the decrease of lagomorph diversity: extinction of species with rooted teeth, preferring softer plant material, and decrease of the ochotonid diversity, the diet of which is restricted to hard plants, not herbs in open areas. In the late Miocene, when the grasslands expanded, the leporids, which favored open spaces, migrated from North America to Asia and Europe and differentiated the in the Plio-Pleistocene.

Extinct lagomorphs are usually poorly represented in large-scale phylogenetic analyses of Glires (the group including both the Lagomorpha and Rodentia), giving an incomplete view on the relationships within the Lagomorpha. The phylogenetic tree including 53 lagomorph species is the first attempt at a comprehensive reconstruction of their interrelationships and evolution. The phylogenetic tree suggests a new classification of Lagomorpha, so a revision of the recently used taxonomical groups of lagomorphs is also provided. It shows that the commonly used wastebasket taxon ‘Palaeolagidae’ is invalid and the species which were classified within this taxon belong in fact to the Ochotonidae, Leporidae, or the stem. Also, a few genera turn out to be paraphyletic, indicating that a revision of few lagomorph genera is still needed. The results casts a new light on the understanding of the relationships and diversification of Lagomorpha from Eocene to the end of the Miocene.