論文内容の要旨

Morphological Variation in the Mammalian Skull: Function, Ontogenesis, and Evolution

哺乳類頭部の多様性進化に関する機能形態学的および比較発生学的研究

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Considerable morphological variation is found in the mammalian skull. In this thesis, ecological mechanism underlying mammalian cranial diversity and developmental mechanism that produce mammalian cranial diversity are discussed.

Craniodental morphology of 41 primate species with differing dietary patterns was comparatively analyzed. The subfamily Colobinae was selected for comparison since this taxon encapsulates a wide array of dietary variation and serves as an excellent context for identifying covariance patterns between morphology and diet among primates. Colobine species that feed on resistant seeds are found to exhibit increased leverages of the masticatory muscles for biting, more medially positioned tooth rows, and significantly reduced molar rows compared to the primates which rarely exploit resistant food. In particular, the reduction of distal portion of the molar row is suggested to be related to be a trade off with increased mechanical leverage, preventing the distal molars from being pushed into the posterior region of the mandible and to keep the midline muscle resultant force enclosed within the triangle of support. In addition, while seed predators show overall increase of masticatory leverages, morphological divergence between mature seed eaters and immature seed predators is also identified. Mature seed eaters show leverage emphasis for postcanine biting, while immature seed predators exhibit higher leverage at the anterior dentition. High leverage at the anterior dentition is suggested to be adaptation for removing the puncture-resistant husks of unripe fruits and gaining access to the immature seeds (sclerocarpic harvesting). Furthermore, I demonstrate that evolution of bite force increase occurred several times in the colobine lineage and that such bite force increase is clearly related to the increased emphasis on seed eating. Thus, the craniodental variation found in colobine primates is suggested to reflect adaptation for differing diet.

Using three closely related squirrel species, I comparatively analyzed the craniofacial divergence of sympatric species and tested whether such variation can be linked to ecological difference of these species. Results show that species which extensively feed on hard seeds and tough tree bark possesses a greater mechanical advantage of the masseter and temporalis muscles for chewing, and a more robust zygomatic arch, compared to species which feed mainly on softer food items. Thus, species that feed on resistant food is capable of generating greater bite force at a given muscle force at the cheek teeth, and its zygomatic arch is more resistant against the stresses generated by the masseter muscle. In addition, I tested the hypothesis that orbital orientation is related to arboreality and terrestriality. While arboreal species were indicated to have more convergent orbits, terrestrial ones exhibited more divergent and more dorsally oriented orbits. More convergent orbits will facilitate binocular vision, and thus a better stereoscopic depth perception. On the other hand, rather than more convergent orbits, more divergent orbits will be advantageous for terrestrial animals since it will provide wider visual field and increase the chance of predator detection. There have been various debates on whether orbital orientation is associated with the degree of arboreal or terrestrial lifestyle, but my results give support to the hypothesis that more arboreal species should have more convergent orbits and that more terrestrial species should exhibit more laterally oriented orbits. Although some authors have interpreted convergent orbits as a tradeoff with having larger eyes in nocturnal species, results provided here does not support this model since it cannot explain the orbital differences among the three squirrel species which are all diurnal species. I also suggest that not only divergent but also dorsally positioned orbit may be the key feature of terrestrial small mammals, since the ground dwelling rodents can detect predators approaching from dorsal direction more easily with their dorsally positioned obits.

To investigate the role of ontogenesis in producing adult morphological diversity, the most comprehensive analysis to date on osteogenesis of 22 cranial elements in 34 species of mammals was conducted, spanning over nine orders across mammals with various life history. Results demonstrate that mammals are characterized by the delayed onset of pterygoid relative to other bones compared to the sauropsid outgroups. Given the evolutionary fact that the pterygoid bone has experienced a relative size reduction in mammals from the condition of early synapsids, it is suggested that the late shift of the pterygoid is linked to the evolutionary reduction of this bone in mammals. In addition, I find that the moles (family Talpidae) are characterized by the extremely early development of the bones that constitute the vomeronasal complex (nasal, vomer, palatine, frontal, and pterygoid). Since the vomeronasal complex is relatively enlarged compared to those of the moles' close relatives, shrews and hedgehogs, and since vomeronasal complex plays an important role in the moles, I suggest that the early developmental shift of vomeronasal bones in moles may reflect their ecological emphasis on this morphological complex. In addition, I detect the pattern of step-by-step early shifts of the occipital bones (supraoccipital, basioccipital, and exoccipital) in human evolution. Basioccipital moves earlier in Euarchontoglires, supraoccipital shifts earlier in Primates, exoccipital moves earlier in Catarrhini, and exoccipital shifts further earlier in *Homo sapiens*. Other major heterochronies that have occurred in the mammalian evolution are: the late shifts of the vomer and supraoccipital in Placentalia when splitting with Marsupialia, the late shift of the pterygoid in Marsupialia when splitting with Placentalia, and the late shifts of the presphenoid and alisphenoid in Chiroptera when splitting from Pegasoferae. Although previous study on much more limited species sampling proposed that the sequence of cranial ossification is quite conservative and that few heterochronic shifts have occurred along the mammalian evolution, my comprehensive study on cranial ossification sequence reveals that numerous sequence heterochronies have occurred along the evolution of mammals and suggests that sequence heterochrony may have played a significant role in shaping the evolution of the mammalian skull.

The results presented in this thesis suggest that ecological factors, such as dietary and locomotive patterns, have driven the diversification of cranial morphology in mammals. It is clear that the developmental sequence of the cranium have changed dramatically along the mammalian evolution. It is possible that the timing of initiation of an organ in the embryo may affect its final size at maturation and that such heterochrony in the relative developmental schedule plays a significant role in producing the morphological diversity found in organisms.