論文の内容の要旨

Analysis of growth allometry in the modern avian skull:

implication for evolutionary aspects of cranial ontogeny

（現生鳥類の頭骨における成長アロメトリーの解析：

その進化的側面への示唆）

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The cranial morphology of modern avians has been a prominent subject of evolutionary studies. Although ontogeny of organisms is a pivotal factor that is directly responsible for their phenotypic evolution, our knowledge of avian cranial ontogeny is mostly limited to the period of embryonic development, with available information on postnatal ontogeny of the avian skull remaining very scarce. Furthermore, because there are close relationships between ecology and cranial morphology in extant avians, the postnatal ontogenetic pattern of cranial structures may also be correlated with their diverse life history, suggesting that they potentially provide clues for inferring the growth strategies in non-avian dinosaurs. In order to obtain insight into evolutionary and ecological aspects of cranial ontogeny, this study examined postnatal growth series of extant birds using three-dimensional reconstructions of the cranial skeleton based on images of X-ray computed tomographic scanning. Morphological changes after hatching were quantified through analyses of relative growth. When age information of specimens was available, absolute growth of each cranial structure was also examined to add temporal information to the allometric datasets. The taxa examined here includes four species (*Larus crassirostris*, *Phasianus* *versicolor*, *Coturnix japonica* and *Struthio camelus*) that represent major clades of modern avians (Neoaves, Galloanserae and Palaeognathae). These species provided an opportunity to compare precocial (*P. versicolor*, *C. japonica*, and *S. camelus*) and non-precocial species (*L. crassirostris*), allowing discussion on the allometric patterns and their correlations with the presence of parental care.

First, a wild population of the black-tailed gull (*Larus crassirostris*) breeding on Kabu Island was examined to explore relationships between their growth strategies and ontogenetic changes in the cranial shape (Chapter 2). By examining growth series covering a major part of the postnatal ontogenetic period, it was clarified that the typical form of the adult larid skull was produced through dynamic proportional changes among cranial structures after hatching. In addition, cranial structures related to the oral capacity and deglutition exhibited positively allometric growth in the early nestling phase followed by a period of negative allometry in the later growth phase. Because nestlings mainly feed on foodstuffs supplied by their parents, previous studies suggested the possibility that siblings within a nest compete for food resources. Under this scenario, early acquisition of swallowing abilities, as indicated by the allometric patterns of relevant cranial structures, may be adaptive for nestlings.

Some avian taxa show a prominent variation in the cranial size and shape even among closely related species. Identification of the proximal cause that contributes to such a morphological variation requires clarification of an ontogenetic variation among organisms. The present study focused on the speciose family Phasianidae, which exhibit a remarkable variation in the somatic growth rate and duration. Because some phasianid species show prominent sexual differences in multiple biological characteristics, it was expected that the cranial growth patterns may also be sexually dimorphic. This study examined relative and absolute growth of the cranium of the green pheasant (*Phasianus versicolor*), a sexually dimorphic phasianid bird (Chapter 3). The growth rate of the endocranial volume relative to the skull volume was statistically discriminated between females and males, with the latter characterized by a lower relative growth rate. Such an allometric difference resulted from a much more rapid absolute growth rate of the skull volume in males than in females, combined with nearly identical absolute growth rates of the endocranial volume between them. Whereas skeletal growth in males is likely accelerated by sexual selection favoring a larger body size, the brain size may be lagged behind because its growth can hardly be accelerated likely due to its expensive cost of production. These results suggest the necessity of taking sexual differences into account in interspecific comparative studies of the growth in the cranium, especially the endocranial volume. Based on the above results, postnatal cranial ontogeny in *Phasianus versicolor* was compared with that in the smaller phasianid *Coturnix japonica* to evaluate the interspecific variation within the Phasianidae (Chapter 4). The slopes of the allometric growth lines of facial structures relative to the overall cranial volume were not statistically different between the two species. Furthermore, phasianid evolutionary allometry of facial structures against the overall cranial size was similar to ontogenetic allometry of both *P. versicolor* and *C. japonica*. This result suggests that a large part of evolutionary diversification in facial structures among phasianid birds can be explained by a simple extension or truncation of similar ontogenetic trajectories. On the other hand, the allometric lines of the endocranial volume against the cranial volume were dissociated between the two species, and both were also statistically different from the line of evolutionary allometry. This result suggests that the prenatal, not postnatal, ontogenetic processes is more responsible for a variation in the relative endocranial sizes among phasianids. In conclusion, the relationships of ontogenetic changes to evolutionary variation were apparently different between the facial region and the braincase. Such a dichotomy in the ontogenetic patterning within a skull is consistent with the previously-proposed hypothesis that the facial region and the braincase comprise two separate modules from embryological, functional and evolutionary viewpoints.

Finally, the allometric data obtained from the *Larus crassirostris*, *Coturnix japonica*, *Phasianus versicolor* and *Struthio camelus* were compared in order to find common cranial growth patterns shared among modern avians (Chapter 5). There was a possibility that significant cranial shape changes similar to that found in *L. crassirostris* do not take place during the postnatal growth period in the more precocial species. However, the obtained allometric relationships suggested that the precocial

P. versicolor and *S. camelus* also underwent significant cranial transformation during the postnatal growth period. The cranial proportion in the precocial *C. japonica* did not largely change, probably due to its small size and the narrow range of the cranial size increase. Interspecific differences in the pattern of morphological transformation are apparently associated with the modification in the range of size increase rather than variations in the allometric relationships among cranial structures. These results suggest that evolutionary conservativeness of cranial growth allometry is a key factor that produces cranial evolutionary allometry widely found among extant avians. On the other hand, non-linear growth of cranial structures involving orolingual functions was found unique to *L. crassirostris* among the three examined neognath species. This result is consistent with the hypothesis that non-linear growth exhibited by the oral and hyoid structures in the skull of *L. crassirostris* reflects the functional demand in its life history. However, more phylogenetically and ecologically comprehensive studies are required to fully test this hypothesis.

The present study shed light on the association between postnatal cranial ontogeny and morphological adaptation, evolution and diversification in modern avians. In addition, ontogenetic information obtained herein also bears paleobiological significances. The comparison between precocial and non-precocial species provided a novel example that strongly suggests the parallelism between growth strategies and cranial ontogenetic patterns in extant avians. Because possible ecological and behavioral similarities between extant avians and extinct dinosaurs are often discussed by paleobiologists, future studies that compare postnatal cranial ontogeny among extant and extinct dinosaurs will contribute to proposing and testing hypotheses on life history of extinct dinosaurs. Furthermore, allometric datasets in the present study include age information of examined specimens, which is fundamental for discussion concerning heterochronic evolution of the avian skull. With similar information on extinct archosaurs available through osteohistological observations, integration of age and allometric information in bird-line archosaurs (Avemetatarsalia) is expected to be a fruitful attempt that will clarify how heterochronic mechanisms have contributed to cranial evolution in this linage.