COMPARATIVE ONTOGENY OF AVIAN LIMB SKELETON: IMPLICATIONS FOR ONTOGENETIC AGEING AND EVOLUTIONARY VARIABILITY, WITH SPECIAL EMPHASIS ON THE EVOLUTION OF AVIAN FLIGHTLESSNESS

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ABSTRACT

Organismal evolution is a continuing process of modifications of ontogeny through phylogeny. Heterochrony, evolutionary changes in timing and rates of developmental events, has long been a central framework in the study of morphological evolution in paleontology. Nevertheless, practical studies of heterochrony have been suffered from terminological confusion that stems from disregard of different conceptual formalizations and the lack of sufficient mass of empirical data. The evolution of flightlessness in birds is a classic example of heterochrony which has attracted much attention from ornithologists and avian paleontologists, but the above mentioned obstacles are particularly relevant for the study on this topic. Quantitative data on ontogeny of avian skeleton, as well as reliable ageing criteria in avian skeletal specimens, were seriously lacking.

This study aims to contribute to the general understandings of morphological evolution through the study of avian skeletal ontogeny and its possible roles in the evolution of avian flightlessness. Ontogenetic series of skeletal specimens consisting of at least 14 individuals of known ontogenetic stages were collected for each of five species of modern birds, *Calonectris leucomelas* (Procellariidae), *Ardea cinerea* (Ardeidae), *Phalacrocorax capillatus* (Phalacrocoracidae), *Larus crassirostris* (Laridae), and *Cerorhinca monocerata* (Alcidae) (Chapter 2). Three ontogenetic stages were recognized; chick, fledgling/juvenile, and adult stages. For *Calonectris leucomelas*, *Larus crassirostris*, and *Cerorhinca monocerata*, absolute ages of most chicks were available.

Ontogenetic variation of macroscopic morphology, skeletal dimensions, surface textures, and histological structures of major limb bones were described in the five species (Chapter 3). It was observed that longitudinal growth of long bones generally ceases before or around the time of fledging, whereas circumferential growth continues slightly thereafter. Rough surface textures were exclusively observed in bones of immature individuals, and are indicative of active circumferential growth. These results confirmed the validity of the textural ageing method in the avian skeletons, which provides a practical means to assess ontogenetic stages of skeletal or fossil specimens of birds.

Based on the above results, the relationship between ontogenetic and evolutionary variation in the skeletal limb proportion in birds was explored through morphometric analyses (Chapter 4). Most data were collected by measuring museum specimens, and ontogenetic data of *Anas platyrhynchos* (Anatidae) were taken from literature. Through the examination of six target families (Anatidae, Procellariidae, Ardeidae, Phalacrocoracidae, Laridae, and Alcidae), it was revealed that 1) major axes of ontogenetic shape change were significantly different in most pairs, 2) evolutionary shape variation was strongly anisotropic, and 3) directions of major axes of evolutionary shape variation were significantly correlated with those of ontogenetic shape change. These results imply that evolutionary variability of the avian limb skeleton is constrained by ontogenetic integration.

The above results support a previous hypothesis, that is, different propensity for flightlessness among avian taxa are due to difference in ontogenetic integration of the limb skeleton. The results highlight the importance of taxon-specific ontogenetic integration in the evolutionary diversification of birds. Data presented in this study can be used to determine ontogenetic polarities of character states for diagnosing heterochrony or to infer evolutionary changes of ontogenetic trajectories for testing heterochronic hypotheses, and thus would be useful in future discussions on the role of heterochrony in the morphological evolution of birds. Accumulation of more empirical data, as well as considerations of multiple aspects of ontogeny, would enrich exploration of the relationship between ontogeny and evolution.