

Doctoral Dissertation (Censored)

博士論文 (要約)

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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ABSTRACT

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 (Aves + Archosauria) is expected to be a fruitful attempt that will clarify how heterochronic mechanisms have contributed to cranial evolution in this lineage.

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CHAPTER 1

General Introduction

The origin and diversification of modern avians

Modern birds comprise Aves, a clade of endothermic tetrapod vertebrates, characterized by numerous apomorphies such as toothless beaks, an enlarged brain, wings, feathers, a high metabolic rate and a four-chambered heart (Gill, 2007). Phylogenetic analyses based both on molecular and morphological data have recognized two basal subdivisions of modern avians: Palaeognathae containing the tinamous and flightless ratites, and much more diverse Neognathae containing all other modern avians (e.g., Livezey & Zusi, 2007; Hackett et al., 2008; Prum et al., 2015; Fig. 1 on the following page). Neognathae is further divided into Galloanserae containing chickens, ducks and their allies and Neoaves containing all other neognaths (e.g., Livezey & Zusi, 2007; Hackett et al., 2008; Prum et al., 2015; Fig. 1). Although deep phylogenetic branching patterns within Neoaves have hardly been resolved due to the explosive divergence early in their evolutionary history (Poe & Chubb, 2004; Chojnowski et al., 2008), interordinal relationships within this clade have been resolved to some extent based on molecular phylogenetic analyses using large, multilocus datasets (e.g., falcons and parrots are successive sister groups to passerines; Hackett et al., 2008; Prum et al., 2015).

The origin of birds has been one of the most enduring and fascinating problems in evolutionary paleontology. Last four decades have witnessed a major accumulation of evidence supporting the hypothesis that avians descended from maniraptoran theropod dinosaurs (e.g., Xu et al., 2014). Although modern avians have numerous characteristics unique among extant vertebrates (e.g., feathers), there are many anatomical, physiological and behavioral resemblances between avians and other

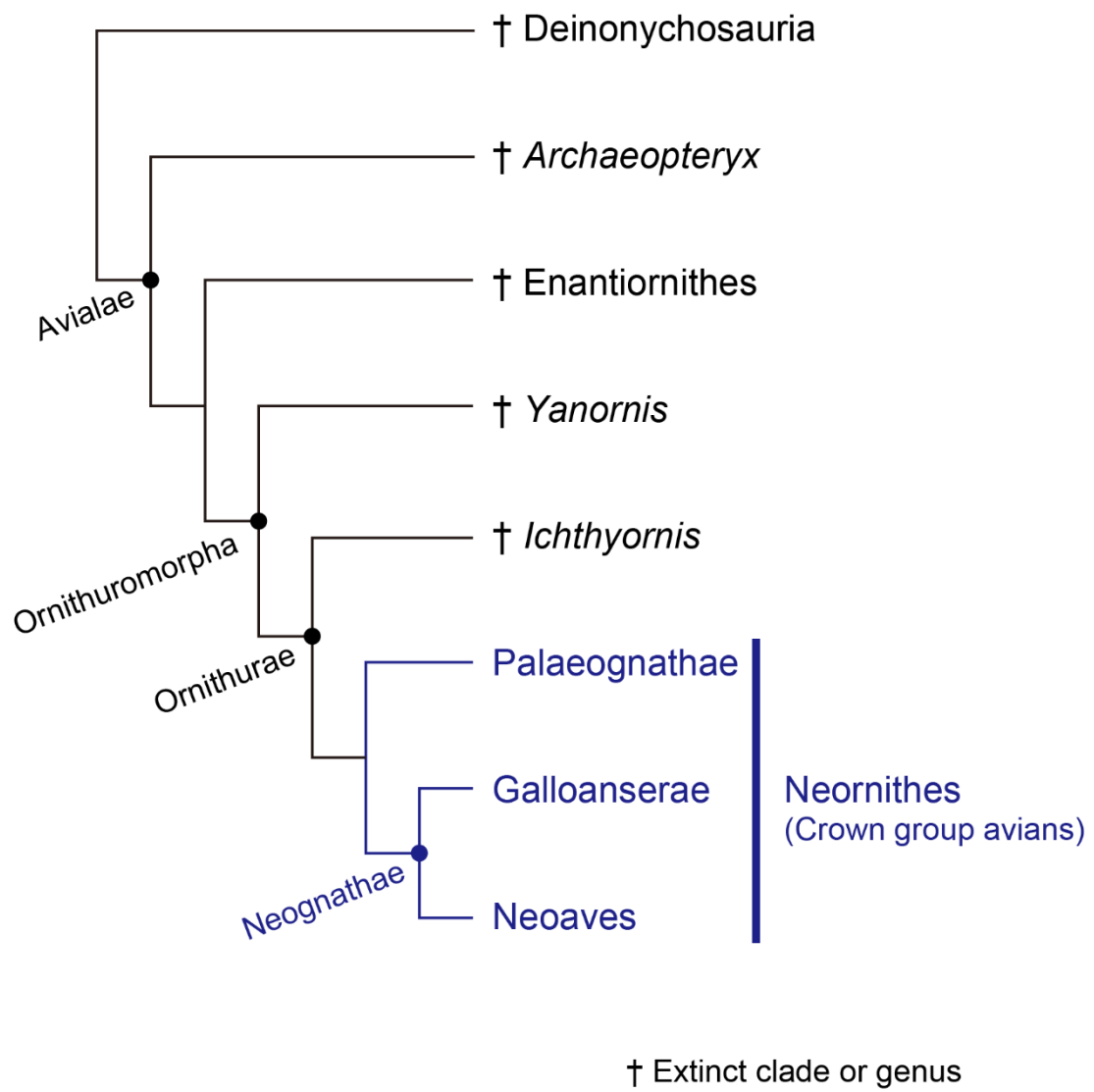


Figure 1. Simplified phylogeny of Neornithes (or crown group Aves) and their extinct relatives.

dinosaurs (e.g., Fastovsky & Weishampel, 2012; Xu et al., 2014). For example, the presence of primitive feathers is documented in numerous non-avian theropods such as *Sinosauropteryx* and even in some ornithischians (Chen et al., 1998; Godefroit et al., 2014). Examination of highly pneumatic skeletons in *Majungasaurus* and *Aerosteon* suggested that those non-avian theropods had a complex air-sac system and bird-like respiration (O'Connor & Claessens, 2005; Sereno et al., 2008). Fossilized nests suggest brooding and parental care behavior in non-avian dinosaurs similar to those observed in modern avians (e.g., Horner and Makela, 1979; Horner, 1984; Varricchio et al., 1997; Erickson et al., 2007). Numerous phylogenetic analyses strongly support the hypothesis that avians are phylogenetically nested within theropod dinosaurs (e.g., Gauthier, 1986; Holtz, 1998; Clark et al., 2002; Livezey & Zusi, 2007; Xu et al., 2014).

The oldest fossil record definitely placed within the crown group avians (Aves or Neornithes) is the anatoid anseriform *Vegavis iaai* coming from the Maastrichtian of Antarctica, implying that the several basal divergences of Neornithes had occurred by the latest Cretaceous, producing at least Palaeognathae, Anseriformes, Galliformes and Neoaves (Clarke et al., 2005). Early members of neornithines survived the mass extinction event at the end of the Cretaceous and their descendants achieved a global-scale adaptive radiation during the Cenozoic (Clarke et al., 2005; Jetz et al., 2012, 2014; Prum et al., 2015; Larson et al., 2016; Field et al., 2018). Today, Neornithes is composed of approximately 10,000 living species, showing extraordinarily diverse morphology, physiology, ecology and behavior (Gill, 2007; Gill & Donsker, 2019).

Growth and development in modern avians

Living birds are characterized by remarkable growth strategies unique among vertebrates. For example,

their maximum growth rates are much greater than those of non-avian reptiles and marsupial mammals of the same body size (Case, 1978; Erickson et al, 2001). The explosive growth of altricial birds stand out among growth patterns of all vertebrates including eutherian mammals (Case, 1978). Avian growth rates are so rapid that the transition from the hatchling to adult takes only a few to several weeks in many species (Stark & Ricklefs, 1998; Gill, 2007). The timing of reproductive maturity also characterizes the life history of modern avians. Whereas non-avian reptiles including non-avian dinosaurs reach reproductive maturity before reaching the adult body size, sexual maturity in modern avians occurs well after growth cessation (Erickson et al., 2007; Lee & Werning, 2008).

Modern avians show a broad spectrum of development modes (Gill, 2007). Hatchlings of various species differ markedly in the relative degree of maturation of many aspects of their behavior, physiology and anatomy. The variation in the developmental mode among extant avians is called the altricial-precocial spectrum, which ranges from passerines and parrots whose chicks hatch in an almost embryo-like state and are dependent on their parents, on the one extreme, through megapodes whose hatchlings can fly and are highly self-sufficient, on the other (Starck & Ricklefs, 1998). Paleontologists have been examining fossil evidence trying to identify the ancestral mode of development in Neornithes. Whereas both altricial and precocial species are known in non-avian dinosaurs (e.g., Horner and Makela, 1979; Horner, 1984; Horner & Weishampel, 1988; Bo et al., 2016), Enantiornithes, extinct clade closely related to Neornithes, is considered highly precocial (Zhou & Zhang, 2004; Xing et al., 2016, 2017). Basally-diverging members of Neornithes (i.e., Palaeognathae and Galloanserae) also exhibit a precocial developmental mode, suggesting that precocity is an ancestral mode of development in Neornithes (Gill, 2007). The altricial mode, on the other hand, would have evolved after the divergence of Neoaves, occurring independently in multiple lineages within this clade (Gill, 2007).

Evolutionary aspects of the avian skull

The remarkable taxonomic diversity of modern avians is reflected by a great variety of their cranial morphology. Their diverse rostral morphology has been considered as a textbook example of ecological adaptation to various diets (e.g., Grant & Grant, 1993; Zusi, 1993; Gill, 2007; Tokita et al., 2017). The beak shape determined by the premaxillary bone and the keratinous sheath appears to be a key target of natural selection related to trophic niches (Grant & Grant, 1993, 2002; Cooney et al., 2017; Yamasaki et al., 2018), and evolutionary flexibility of the beak shape has enabled rapid radiation of some clades (e.g., Galápagos finches and Hawaiian honeycreepers; Grant & Grant, 1993, 2002; Tokita et al., 2017; Abzhanov, 2017). An enlarged braincase that characterizes the avian skull has also been a prominent subject of evolutionary studies. The degree of encephalization differs among avian taxa, and the volume of the braincase (i.e., brain size) relative to the body size is correlated with the altricial-precocial spectrum of developmental modes (Starck & Ricklefs, 1998; Iwaniuk & Nelson, 2003; Gill, 2007). The endocranial shape, which reflects the brain shape rather accurately in birds, is also diverse among modern avians, with differences in brain dimensions reflecting species-specific cognitive capacities and behavioral repertoires (Iwaniuk et al., 2005; Kawabe et al., 2013; Marugán-Lobón et al., 2016). Marugán-Lobón and Buscalioni (2004) compared cranial shapes among all known modern avian orders by using two-dimensional geometric morphometrics (GM). They found a major variation in the rostral length and the degree of flexion between the rostrum and braincase. Klingenberg and Marugán-Lobón (2013) examined the morphological diversity of the braincase and facial region excluding the rostrum, taking phylogenetic relationships among the examined taxa into account. Mapping of the shape data onto the molecular phylogenetic tree revealed that there is a significant phylogenetic signal in the skull shape of modern avians.

Functional differences between the facial region and the braincase suggest that they may evolve divergently as two separate modules. A module is a morphological unit that is relatively independent from other such modules in genetic, developmental, functional and evolutionary contexts (Klingenberg, 2008). The hypothesis that the avian beak is a target for natural selection independent of the rest of the skull assumes the modular nature of the cranium. Indeed, the avian facial skeleton exhibits more diverse morphology than the braincase (Bright et al., 2016). Even within a single avian species, the braincase is conservative in shape whereas facial morphology exhibits a remarkable variation (Liu et al., 2010). However, GM studies revealed that cranial elements of modern avians are evolutionarily integrated (Klingenberg & Marugán-Lobón, 2013; Bright et al., 2016) and that the beak and braincase evolve in a coordinated manner (Bright et al., 2016). Morphological integration refers to a coordinated variation among morphological traits, caused by their interrelationships at genetic, developmental, functional, and evolutionary levels (Olson & Miller 1958; Cheverud, 1996; Goswami, 2006). Allometry patterns prevalent across phylogeny is regarded an important contributor to morphological integration in the evolutionary context (Klingenberg, 2008). In modern avians, the skull shape exhibits a significant evolutionary correlation with the skull size, indicating the allometric nature of the avian cranial morphology (Klingenberg & Marugán-Lobón, 2013; Bright et al., 2016; Tokita et al., 2017). Analyses incorporating dietary information found evidence against the belief that the avian beak shape can easily respond to natural selection (Bright et al., 2016; Navalón et al., 2019). These findings suggest that evolution of the avian cranial morphology is more significantly constrained evolutionarily than previously expected. The explosive diversification of Galápagos finches and Hawaiian honeycreepers may be exceptional cases that have broken the strict morphological correlation between the beak and braincase (Bright et al., 2016; Abzhanov, 2017).

Evolutionary developmental biology in the modern avian skull

Modifications of ontogenetic processes are pivotal factors responsible for phenotypic evolution (Webster & Zelditch, 2005). In the past decade, the progress in evolutionary developmental biology shed new light on macroevolution of the avian skull morphology (e.g., Bhullar et al., 2012, 2015; Young et al., 2014; Hu et al., 2015; Fabbri et al., 2017; Smith-Paredes et al., 2018). The embryological study by Young et al. (2014) revealed that the embryonic facial regions of modern amniotes including avians share a period of a reduced shape variance (putative ‘phylotypic stage’; e.g., Hall, 1997). The authors further found that, after a period of such a reduced shape variance, the developmental trajectory of the avian facial region diverged from that of other amniote faces and led to the typical avian facial shape, which consists of an enlarged premaxilla and a reduced maxilla (see Fig. 4 in Young et al., 2014). Smith et al. (2015) compared the avian facial developmental trajectories after such divergence from other amniotes and revealed that more closely related species (*Gallus gallus* and *Coturnix japonica* belonging to Galliformes) shared a similar facial morphology for a longer time during development whereas *Anas platyrhynchos* (Anseriformes) diverged earlier from those galliforms. These studies suggest that (1) the facial morphology unique to modern avians starts appearing earlier than in other amniotes and that (2) more distantly related species are also more divergent in the developmental trajectory.

In amniotes including birds, bony elements of the braincase are derived from paraxial mesoderm, whereas those of the facial region are derived from neural crest cells (Noden & Trainor, 2005). Such a difference in the developmental source in the skull is one of the theoretical bases of the hypothesis that the facial region and the braincase are two separate modules that can evolve in a semi-independent manner (e.g., Liu et al., 2010; Young et al., 2017; Felice & Goswami, 2018). Although some studies pointed out a high degree of evolutionary integration of the overall cranial shape in modern

avians (Klingenberg & Marugán-Lobón, 2013; Bright et al., 2016), recent analyses provided new evidence for divergent modification among avian cranial elements (Felice & Goswami, 2018; Yamasaki et al., 2018; Felice et al., 2019). For example, the GM study by Yamasaki et al. (2018) revealed that, if there is a selective pressure, the beak shape in corvids can flexibly evolve by deviating from the trend of allometry and integration. In summary, evolutionary modularity and integration in the avian skull remains actively debated and thus requires further inspections based on novel evidence.

Whereas developmental studies on the avian skull have contributed to our understanding of its evolutionary patterns, previous studies have predominantly focused on the period of embryonic development (e.g., Gussekloo & Bout, 2002; Noden & Trainor, 2005; Maxwell, 2008, 2009; Young et al., 2014; Bhullar et al., 2015; Hu et al., 2015; Fabbri et al., 2017; Smith-Paredes et al., 2018), leaving available information on its postnatal ontogeny very scarce (Klingenberg & Marugán-Lobón, 2013). Several factors have hampered analyses of postnatal cranial ontogeny in modern avians. Firstly, it is difficult to obtain carcasses of immature birds from wild populations because many avian species have specific breeding periods and their hatchlings accomplish a major part of somatic growth in only a few weeks or months (Stark & Ricklefs, 1998; Lee & Werning, 2008; Gill, 2007). Secondly, some parts of cranial elements are not fully ossified or fused together in hatchlings, making specimens of intact, dried skulls very rare.

The few previous studies on postnatal cranial ontogeny in avians are listed in Table 1 on the following page. Dodson (1975a) examined growth of the bony crest in cassowaries (*Casuarius*) and showed that the crest grew in positive allometry against the skull length after attainment of 65 to 80% of the adult skull length. Although adults are characterized by a prominent crest, juveniles have no or

Authors	Examined taxa	Study subjects
Dodson (1975a)	<i>Casuarius</i>	Development of the bony crest
Genbrugge et al. (2011)	<i>Geospiza fortis</i>	Cranial shape changes reflecting the dietary shift
Bhullar et al. (2012)	<i>Gallus gallus</i> <i>Struthio camelus</i>	Heterochronic evolution of the skull in bird-line archosaurs
Atterholt (2015)	<i>Zenaida macroura</i> <i>Calypte anna</i> <i>Pyhurra molina</i> <i>Aphelocoma californica</i> <i>Carpodacus mexicanus</i> <i>Falco sparverius</i> <i>Buteo jamaicensis</i> <i>Elanus leuculus</i> <i>Tyto alba</i> <i>Bubo virginianus</i> <i>Larus occidentalis</i> <i>Callipepla californica</i> <i>Struthio camelus</i>	Role of development in avian cranial evolution

Table 1. Previous studies that examined postnatal cranial ontogeny in modern avians and analyzed species.

incipient ones. The growth pattern of the crest found in cassowaries was consistent with the hypothesis proposed by Dodson (1975a) that smaller hadrosaurid dinosaurs lacking any crests (*Prochenosaurus*) are juveniles of the larger, crested hadrosaurid *Corythosaurus*. Genbrugge et al. (2011) described development of the skull in the medium ground finch (*Geospiza fortis*) and discovered that large changes in the skull shape took place between the nestling and juvenile phases. Reorientation of the premaxilla and the orbit and formation of well-developed processes and cristae for muscle attachment are likely related to the dietary shift after juveniles leave the nest. Bhullar et al. (2012) compared cranial ontogenetic trajectories of various archosaurs including fossil species and extant avians by two-dimensional GM. The authors showed that the cranial shape of early avialans (e.g., *Archaeopteryx*) was similar to that of embryonic or juvenile non-avian archosaurs, suggesting that enlarged braincase and orbit characterizing the avian skull evolved through paedomorphosis from the ancestral archosaurian form. In an unpublished dissertation, Atterholt (2015) examined postnatal cranial shape changes in 13 avian species and discussed the relationship between postnatal developmental patterns and macroevolutionary morphological changes in avians. She mainly examined the facial region of the skull and found general developmental patterns including (1) an increase in the length and ventral curvature of the beak; (2) moderate anterior elongation of the external nares; (3) substantial widening of the dorsal surface of the cranium; (4) a decrease in the orbit size relative to the skull size and its lateral reorientation due to a mediolateral broadening of the face; and (5) the braincase shortens anteroposteriorly and dorsoventrally. Atterholt (2015) suggested that the developmental patterns of the cranial shape were conservative and included little phylogenetic signal in modern avians.

Whereas the previous works reviewed above have shed new light on the avian cranial diversity from the viewpoint of postnatal ontogeny, there are many problems remaining to be solved. Firstly,

some previous studies were conducted on very small sample sizes and did not fully consider possible sources of intraspecific variations such as sexual dimorphism (e.g., Genbrugge et al., 2011). Furthermore, a majority of postnatal ontogenetic processes in Aves remains unclear, because some studies examined ontogenetic shape changes merely by comparing discrete two stages, i.e., hatchlings and adults (Bhullar et al., 2012; Atterholt, 2015). Finally, although temporal information is essential in strict discussion on heterochronic evolution (Klingenberg, 1998), specimens examined in the previous studies lack age information and thus absolute growth has rarely been analyzed.

Modifications of postnatal ontogenetic trajectories can directly lead to a morphological variation found among closely related species (e.g., Mitteroecker et al., 2004; Watanabe & Slice, 2014; Evin et al., 2017; Watanabe, 2018; Gray et al., 2019; Morris et al., 2019). In addition, because natural selection can operate across the ontogenetic process (e.g., Gould, 1977; Klingenberg, 1998; Frankino et al., 2005), the process of postnatal ontogeny is expected to reflect ecological demands that growing individuals experience (Carrier & Leon, 1990; Genbrugge et al., 2011; Iijima, 2017). In this context, a large diversity and adaptive aspects of the modern avian skull serve as an ideal target of evolutionary investigation.

Paleontological significance of cranial ontogeny in modern avians

The diverse ecology and behavior of modern avians provide us significant implication for life history in non-avian dinosaurs (e.g., Farke et al., 2013; Tanaka et al., 2018). It is expected that recently increasing findings of immature specimens of non-avian dinosaurs will enhance significance of data on extant avian ontogeny. The last two decades have witnessed great progress of our knowledge on ontogeny in non-avian dinosaurs, thanks to an increasing number of nearly complete immature

specimens (e.g., Kobayashi & Lü, 2003; Evans, 2010; Risz et al., 2010; Tsuihiji et al., 2011; Farke et al., 2013; Zhao et al., 2013; Currie et al., 2016) and great advance of histological studies (reviewed by Erickson, 2014). Well-preserved skull specimens of immature individuals have provided implication in their ecology such as ontogenetic dietary shifts (Whitlock et al., 2010; Tsuihiji et al., 2011, Woodruff et al., 2018). Farke et al. (2013) compared growth of cranial ornamentation between ornithischian dinosaurs and modern cassowaries (*Casuarius*) and showed that ornithischians initiated development of cranial ornamentation at a relatively younger age and a smaller size than in *Casuarius*. The authors considered that, if cranial ornamentation played at least some role in sexual selection and/or species recognition, the precocious development mode of such ornamentation may reflect reproductive maturity preceding somatic maturity in ornithischians. Ecological and behavioral information of modern avians can be obtained by direct observations of their life. If parallelism between postnatal cranial ontogenetic patterns and diverse life history is widely found in modern avians, comparison of postnatal cranial ontogeny between modern avians and non-avian dinosaurs will be able to offer novel clues for inferring life history in the latter.

Concept of allometry and its analytical methodology

There are two classic concepts in ontogenetic changes in morphology: relative growth and absolute growth. Relative growth describes allometric changes involving a covariation among sizes of two or more morphological traits whereas absolute growth describes growth by contrasting age and trait sizes (Klingenberg, 1998). In this study, allometry means the pattern of covariation among measurements of several morphological traits (Huxley, 1932; Klingenberg, 1998). Allometric analyses can address variations at three levels: static allometry—individual variation within an identical growth stage of a

population; ontogenetic allometry—variation in a single species as a result of growth; and evolutionary allometry—variation between taxa as a result of evolution (Klingenberg, 1998). Allometry can be described by examining relative growth of two morphological traits, being expressed by a simple equation $y = bx^k$, where x and y are trait sizes (e.g., Huxley, 1932; Imbrie, 1956; Klingenberg, 1998; Shingleton, 2010). The x and y variables are log-transformed so that the above equation can be expressed as $\log y = \log b + k \log x$. This transformation allows the covariation between x and y to be expressed as a linear relationship, where $\log b$ is the intercept of the line on the y -axis and k is the slope of the line, also known as the allometric coefficient (e.g., Huxley, 1932; Imbrie, 1956; Klingenberg, 1998; Warton et al., 2006; Shingleton, 2010). If two or more body parts increase their sizes at the same rate and thus the proportions among those parts remain constant during growth, relative growth among those parts is termed isometry ($k = 1$). On the other hand, if those traits increase in size at different rates, relative growth among those parts represents allometry ($k \neq 1$), which leads to proportional changes of organismal form during growth (Huxley, 1932; Klingenberg, 1998; Shingleton, 2010; Brown & Vavrek, 2015). If $k > 1$, y is called *positively allometric* with respect to x , indicating that y increases in size faster than x . Conversely, $k < 1$ means *negative allometry* of y against x , indicating y increases in size slower than x . As long as the ratio of growth rates of the two traits (k) is constant throughout growth, the resulting allometric plot will be linear on a log-log scale (Klingenberg, 1998). The equation of relative growth is derived directly from multiple measurements of a single individual throughout its growth period (i.e., longitudinal studies: several observations of the same individuals over a period of time). However, the equation can be also estimated from samples consisting of multiple individuals at various stages of ontogeny (i.e., cross-sectional studies: comparison of different individuals at a single point in time).

Reduced (Standardized) Major Axis (RMA or SMA) has been used for fitting a line to a bivariate allometric plot and estimation of allometric parameters b and k (Imbrie, 1956; Warton et al., 2006). Imbrie (1956) and Hayami and Matsukuma (1970, 1971) introduced statistical methods to analyze the allometric parameters. Allometry and isometry can be discriminated by the statistics termed z calculated by the following equation:

$$z = \frac{a - 1}{a \sqrt{\frac{1 - r^2}{N}}}$$

where a is the slope of RMA, r is the correlation coefficient, and N is the sample size. If $|z| \leq 1.96$, the slope cannot be confidently discriminated from 1.0 (isometry) at a 5% significance level, whereas if $|z| > 1.96$, non-isometric growth of two traits would be suggested. The difference of the slopes of two RMAs can be tested using an alternative form of z calculated by the following equation:

$$z = \frac{a_1 - a_2}{\sqrt{\sigma_{a_1}^2 + \sigma_{a_2}^2}}$$

where a_1 and a_2 are the slopes of two RMAs, σ_{a_1} and σ_{a_2} are the standard errors of the slopes of two RMAs (Imbrie, 1956; Hayami & Matsukuma, 1970, 1971). If $|z| \leq 1.96$, the difference of slopes is not significant at a 5% significance level, and if $|z| > 1.96$, the slopes of two lines can be significantly discriminated. However, this method of discrimination can be confidently used only in the case where the sum of the sizes of two samples is 35 or more (Imbrie, 1956). This requirement is hardly satisfied in studies of vertebrates, especially fossil species, because the sample sizes are usually very limited (Brown & Vavrek, 2015).

Recent studies of allometry in vertebrates utilize 95% confidence intervals (CIs) of the slopes to determine allometric trends or to discriminate two allometric lines (e.g., Evans, 2010; Brown & Vavrek, 2015; Iijima, 2017; Iijima & Kubo, 2019). Relationships of x and y variables are considered

either negatively or positively allometric when the 95% CIs of RMA slopes does not include the expected isometric slope ($k = 1.0$). The allometric slopes are discriminated when their 95% CIs do not overlap with each other. The function for estimating 95% CIs of the slope is implemented in R package SMATR (Warton et al., 2012) and freely available to the public. This method is applicable to analyses suffering from sample size limitation. However, it should be noted that, when the sample size is too small, the null hypothesis (e.g., isometry) is rarely rejected even if an alternative hypothesis (e.g., allometry) is true (Brown & Vavrek, 2015).

Allometric plots effectively visualize differences or similarities of ontogenetic trajectories representing multiple samples. However, allometric plots do not suggest which morphological trait, x or y , is responsible for the difference of two allometric lines. For example, in the case where two different allometric lines originate from the common initiation point (Fig. 2 on the following page), the allometric plot only tells that the relative growth rate of y against x is larger in the sample A than in the sample B. Therefore, it is not necessarily true that y in the sample A grows faster than y in the sample B. The concept of relative growth does not take temporal information (i.e., age) into account, and thus the absolute rate and timespan of growth cannot be discussed in this framework.

A full understanding of ontogenetic differences between samples requires temporal information, which is an essential parameter for analyzing absolute growth. Absolute growth is usually represented by a sigmoidal growth curve. Although allometric plots and growth curves describe different aspects of the same ontogenetic sequence (see Fig. 1 in Klingenberg, 1998), morphometric studies examining both relative and absolute growth are very rare. It is expected that combination of these two classes of ontogenetic analyses would provide fundamental information for discussing evolutionary phenomena such as heterochrony.

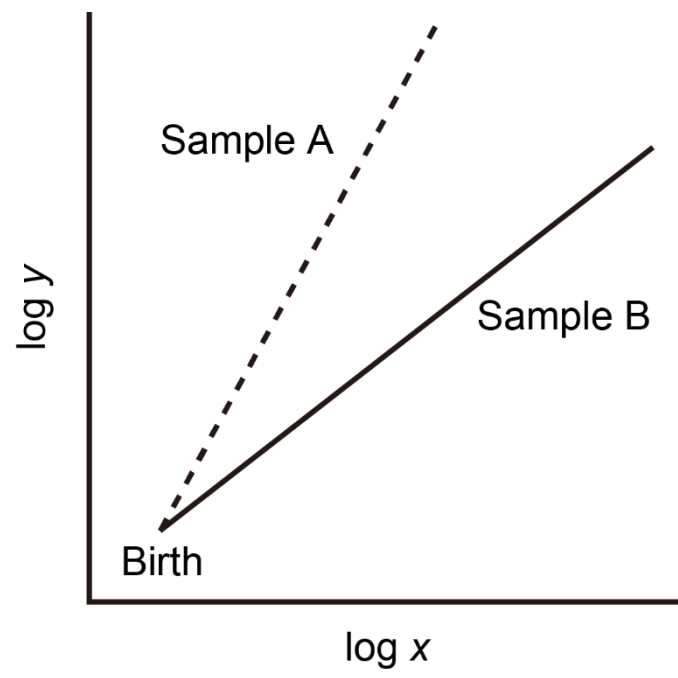


Figure 2. Schematic plot showing two allometric lines.

General goals of this dissertation

The ultimate goal of the present study is to clarify the processes of postnatal ontogenetic changes in cranial morphology in multiple avian species and to gain new insight into the adaptive aspects of cranial ontogeny as well as the relationship between morphological evolution and ontogeny. In order to achieve this goal, this study conducted quantitative analyses of morphological changes of the skull through postnatal growth in avians.

Although data were obtained based on three-dimensional skulls segmented on computed-tomographic (CT) images of heads, analyses were conducted by using bivariate analysis of relative growth in this study because it has several advantages in quantifying allometric growth of the avian skull. Allometric analyses can also be performed by GM placing points (landmarks) at locations anatomically homologous among all specimens (e.g., Klingenberg & Marugán-Lobón, 2013; Kawabe et al., 2015; Bright et al., 2016; Marugán-Lobón et al., 2016; Tokita et al., 2017). However, the braincase in modern avians lacks distinct anatomical features suitable for landmarks, making it difficult to quantify the braincase morphology by GM (e.g., Klingenberg & Marugán-Lobón, 2013; Atterholt, 2015; Tokita et al., 2017). In analyses of relative growth, on the other hand, the size of braincase can be incorporated by measuring its volume. In addition, even when significant deformation of specimens hampers precise analyses by three-dimensional GM, analyses of relative growth using linear measurements may be conducted more accurately. Accordingly, because fossilized skulls almost always suffer deformation to various degrees, analyses based on linear measurements are expected to be advantageous in including fossil taxa in future studies.

In Chapter 2, a growth series of the black-tailed gull (*Larus crassirostris*) obtained from the wild population on Kabu Island are examined to analyze the relationship between cranial ontogeny and

life history. Because *Larus crassirostris* breeds colonially on the ground, numerous carcasses at different growth stages can be collected for studies on ontogeny. In addition, its breeding behavior and ecology have been well documented in previous studies (e.g., Tomita et al., 2018), providing a rare opportunity for approaching ecomorphological aspects of cranial ontogeny in wild birds. In Chapter 3, the potential sexual differences in cranial ontogeny are examined in a sexually dimorphic species (the green pheasant *Phasianus versicolor*) to evaluate their significance in evolutionary studies. Based on the results of Chapter 3, the relationship between ontogeny and evolutionary diversification of cranial morphology is explored in Phasianidae in Chapter 4. Although phasianid birds exhibit a wide spectrum of the cranial size and shape, ontogenetic mechanisms that have yielded diverse cranial morphology are not well understood. In Chapter 5, general patterns of cranial ontogenetic allometry are compared among four species representing three major clades of modern avians (Palaeognathae, Galloanserae and Neoaves) to discuss the cranial ontogenetic variation in relation to developmental modes, sizes and phylogeny. Finally, implications for avian evolutionary biology and dinosaur paleobiology, as well as a future direction of the study on avian cranial ontogeny, are discussed in Chapter 6.

CHAPTER 2

Postnatal cranial ontogeny and growth strategies in the black-tailed gull *Larus crassirostris*

breeding on Kabu Island, Aomori, Japan

本章については、5年以内に雑誌等で刊行予定のため、非公開。

CHAPTER 3

Sexual dimorphism in cranial growth dynamics and allometry

in the green pheasant *Phasianus versicolor*

本章については、5年以内に雑誌等で刊行予定のため、非公開。

CHAPTER 4

Interspecific variation of cranial ontogeny and its evolutionary significance in phasianid birds

第3章に関する内容を含むため、非公開。

CHAPTER 5

Interspecific comparison of cranial growth allometry among four extant avian species

第2章と第3章に関する内容を含むため、非公開。

CHAPTER 6

General Discussion:

Evolutionary and Paleontological Implications

第2章と第3章に関する内容を含むため、非公開。

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