## 論文の内容の要旨

## Morphometrical study of the avian brain and its possible application in paleoneurology

(鳥類の脳に関する形態計測学的研究とその古神経学的応用)

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Although many studies on Aves have uncovered the relationships between brain morphology and biological characteristics, such as intelligence, integration ability, functional ability, studies thus far have often focused on volumetric analyses of avian brain or brain regions. It is evident that volumetric analyses only capture one of the multiple aspects of the structure. Three-dimensional (3D) exploration of brain shape in Aves is necessary for a better understanding of avian brain morphology. Furthermore, fossil specimens provide only external morphological information of the avian brain; understanding the brain shape is critical for further discussion about brain evolution in Aves. Hence, the aim of this study was to investigate the differences or similarities between extant avian brain shapes and to derive new information regarding extinct birds based on the brain morphology findings of extant species.

Extant avian brain models, which were reconstructed by computed tomography (CT) and magnetic resonance imaging (MRI), were analyzed from many directions using 3D geometric morphometrics and linear measurements. Factors responsible for the variation in shape of the avian brain were first revealed. Results demonstrated that change in size is a dominant factor for creating variations in brain shape. With increasing brain size, the telencephalon tends to shrink and the posterior part of the brain rotates caudodorsally. Shrinking of the telencephalon and ventral rotation of the posterior part of the brain is observed during posthatch chick ontogeny. The change in shape leads to rotation of the foramen magnum plane, and the direction of the neck turns dorsally. The rotation of the foramen magnum angle, which cannot be explained by size, correlates with foraging techniques of birds. In addition, the relationship between cranial base angle and relative brain size or eye size was assessed. A significant negative correlation was observed between the cranial base angle and relative brain size, as in mammals. On the other hand, a positive correlation was observed between the cranial base angle and relative eye size. Orbital shape is another factor responsible for shape variation in the avian brain. Three-dimensional multivariate analysis revealed that upwardly tilted concave brains tend to have rounder orbits, while narrower and more anteriorly inclined brains tend to have

anteroposteriorly elongated orbits. Thus, size and orbital shape are factors that cannot be ignored when considering avian brain morphology or avian head position.

As stated above, brain size is important when assessing avian brain morphology. Therefore, a method to measure brain volume would be a powerful tool, particularly in paleontology, where measuring brain volume from damaged fossil specimens is difficult. Because the temporal bones are fairly robust parts of the avian skull, they are relatively well-preserved in many avian fossil specimens. The largest brain width corresponds to the temporal bones, and thus, maximum brain width was the focus of the study. The correlation between absolute brain volume and maximum brain width was confirmed. Brain width significantly correlated with brain volume, demonstrating that brain volume can be estimated only from brain width.

Characteristics related to phylogeny were distinguished by function or lifestyle. The width of the cerebellum and floccular lobe exhibits considerable variation among water birds, and their relative sizes are likely to become characteristics for distinguishing Procellariiformes and Sphenisciformes from Ciconiiformes, Pelecaniformes, and Suliformes. On the other hand, cerebellar shape changes according to the degree of dependence on aquatic foraging. Change in cerebellar shape might correspond with the change in volume of the cerebellar folia.

Using knowledge acquired through analyses of the extant avian brain, fossil plotopterid brains were reconstructed to extract maximum information from them. Although the plotopterid specimens were slightly damaged, one retained its dorsal aspect, which allowed measurement of maximum brain width. Thus, plotopterid brain volume was estimated by brain width. Furthermore, based on the ration of floccular lobe width to telencephalon width, the brain morphology of plotopterid birds was concluded to be similar to that of sphenisciform birds.

The results in this thesis suggest that multiple factors such as size, orbital shape, eye size, skull components, phylogeny, and lifestyle have influenced the diversification of brain morphology in Aves. Novel information was acquired by identifying and quantifying the relationships among these factors in extant species. Using the knowledge obtained from analyses of extant species, considerable morphological information was obtained from the brain and head of damaged fossil specimens. The results of this thesis are expected to contribute to further development in paleoneurology.