論文内容の要旨

論文題目　The Evolution of Ribcage Anatomy and Breathing Function in the Mesozoic Therepods

（中生代獣脚類における胸郭と呼吸機能の進化）

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The origin and the evolution of birds are represented by major changes of body plan particularly in vertebrate history. To date, it was revealed that birds were derived from the Theropoda, a clade within the Dinosauria, and recent phylogenetic analyses have reached to a consensus about the phylogenetic relationship within the Theropoda including birds (Aves). Therefore, the Theropoda is well suited for the study of the evolutionary process through their changes in the morphology and in the ecology. Moreover, the radiation of birds had occurred in younger ages than that of mammals, thus the fossil record is relative rich in quality and in quantity. However, the evolutionary process of the ribcage in the theropod lineage toward birds has not been explored extensively, although the ribcage architecture of birds is an extreme example in tetrapods.

Extant birds possess a specialized respiratory system aided by airsacs, and consequently they have a better efficiency in breathing and greater tolerence toward the hypoxia than mammals. The airsacs are pulmonary diverticula branched from the lung, but the epithelia of airsacs scarcely contribute to the gas exchange. Instead, the airsacs act as pumps during the ribcage movement, i.e.

costal breathing, and they induce gas flow in the tube-like lung (parabronchi). In other words, the pump and the gas exchanger are functionally separated in the avian respiratory system. As a result, the gas flow and the blood flow always cross each other at right angles (i.e. cross-current system), providing great efficiency in the avian respiratory system.

Existence of airsac is confirmed by the perforation of bones, because the airsacs often penetrate bones. Recently, presence of airsacs was confirmed in the non-avian theropod vertebrae, and it became clear that the non-avian theropods also possessed the airsac system that enables the bird-type ventilation. However, the only evidence that non-avian theropods possessed the basic avian pulmonary design is not sufficient to prove that the non-avian theropods employed the complete bird-type respiratory system.

Ribcage movements play a central role in breathing in most amniotes. Accordingly, it is expected that studies on ribcage anatomy, which have been insufficiently done, would help understanding the evolution of breathing mechanisms. Unlike mammals that have diaphragm, extant birds adopt a unique breathing mechanism, in which the tube-like lung is very robust and the inspired air firstly flows into the caudal airsac system. The ribcage movement determined by morphology of vertebrae and ribs contributes to generating this gas flow. Therefore, studies on ribcage anatomy of theropods are an essential key to rationalize whether these animals achieved the bird-type breathing mechanism or not.

In this study, I investigated comparative anatomy of ribcages in the theropod lineage, with an emphasis on the fossil record. On the basis of these data, I could delineate comprehensive history of the ribcage anatomy, and could present a theoretical model of the ribcage movement of selected non-avian theropods, in order to deduce their breathing mechanisms.

Firstly, I collected data on the ribcage anatomy of 111 theropod species from the Mesozoic, by direct observations on museum specimens (41 species) as well as from literature (70 species). To minimize effects of postmortem deformations, multiple specimens were observed for each taxon whenever possible. On the basis of these data, character evolution was traced on a compiled phylogenetic framework, in which I have collapsed nodes that I consider controversial based on recent published analyses. In addition, I traced the ribcage evolution in the geologic time scale. The results demonstrate that mechanical refinements of the ribcage were accumulated in a stepwise pattern with changes occurring both within and outside Aves, in the following sequence. Firstly, the ossification of sternum occurred. Then, the ossification of sternal rib occurred in the Middle/Late Jurassic. Subsequently, ossified uncinates were polyphyletically acquired during the Neocomian. These findings reveal suggest that gradual changes of costal aspiration mode in theropods. In the extant birds, the *M. rectus abdominis* is vestigial and minor, whereas a part of the Mesozoic birds retained the gastralia, indicating that they retained basic archosaurian abdominal musculature with a major mass of the *M. rectus abdominis* on their bellies. Theropods with the posterior extension of postcranial skeletal pneumaticity firstly appeared in the Late Jurassic, and they evolved polyphyletically. Such taxa gradually increased from the Late Jurassic to the Late Cretaceous.

Secondly, I developed a model for representing the ribcage kinematics in three-dimentional (x-y-z) coordinate space, on the basis of direct measurements on the fossil specimens. In this model, I used the orientations of the rotational axis for the rib and the rib curvatures of the theropods without the ossified sternal ribs. This model enables to quantitatively test the mode of ventilation, whereas the previous studies discussed only morphology of the costovertebral articulations. As a result, models of the ribcage movements in *Tyrannosaurus* (Tyrannosauroidea), *Allosaurus* (Allosauroidea), and *Majungasaurus* (Ceratosauria) were concluded to have performed the greater volumetric changes in the anterior or mid-thoracic regions than in the posterior thoracic regions. Consequently, without other accessory components (e.g., abdominal muscles), these theropods were probably incapable of accomplishing the mode of ventilation seen in the extant birds, where the inspired air flows into the posterior region.

This study presented the detailed evolutionary process of the ribcage anatomy for the first time. These lines of evidence lead to the interpretation that the highly specialized respiratory system seen in the extant birds were not completed at the time of acquirement of the airsacs by some theropods, but after the acquirement of the movable joint between the vertebral and sternal rib (Late Jurassic).