論文の内容の要旨

EVOLUTION OF THE INTERNAL LIMB BONE STRUCTURE IN TETRAPODS ASSOCIATED WITH SECONDARY AQUATIC ADAPTATION AND ITS APPLICATION FOR THE PALEOECOLOGICAL RECONSTRUCTION OF FOSSIL TETRAPODS, WITH SPECIAL REFERENCE TO TESTUDINES

（四足動物の二次的水棲適応に伴う長骨内部構造の変化の解明，および化石四足動物の古生態復元への応用－特にカメ類に着目して－）

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The internal bone structure in secondarily aquatic amniotes is modified from their terrestrial ancestries, as recognized as change in sectional compactness profile and bone density. The relationships between bone internal structure and mode of life have been documented in order to establish criteria for reconstructing the mode of life in extinct animals. However, the alternation in three-dimensional internal bone structure and its evolutionary process remains to be only partly understood.

In this study, in order to reveal how the internal limb bone structure of amniotes is modified in association with secondary aquatic adaptation, and to reveal what adaptive characteristics are seen in it, the author conducted a detailed comparison between amniotes living in a variety of environments ranging from dry land to deep sea. For clarification and functional interpretability of structures, the author uniquely categorizes lifestyle. The author focused especially on carnivorans (Mammalia: Carnivora) and turtles (Reptilia: Testudinata), which are promising materials to accomplish the purpose of this study in including plentiful terrestrial, semiaquatic, and aquatic members.

First, a novel method for two-dimensional comparison is established based on ontogenetic model. Since comparison using homologous sectional planes is necessary to discuss about evolutionary process, the author focused on the three-dimensional position of the center of ossification as a homologous point. Assuming that the position where a nutrient canal does not drift within compact bone, the center of ossification is estimated as the inferred origin of nutrient canal using three-dimensionally reconstructed CT data. The sagittal and transverse sectional planes are chosen as passing through the inferred center of ossification. These sectional images and three-dimensional translucent images are described microanatomically and compared interspecifically.

In carnivorans, the humeri of terrestrial taxa show tubular structure in diaphysis with open medullary cavity. In association with the secondary aquatic adaptation, the medullary region becomes filled with spongy bone and the periosteal compact bone is only locally thickened around the center of ossification. This condition is immediately interpreted as the inhibition of internal periosteal resorption in association with the reduction of cursoriarity. Among aquatic taxa, only *Mirounga leonia* shows an extremely spongy diaphysis, which is due to extensive resorption of periosteal compact bone. Epiphyseal and metaphyseal trabecular systems in terrestrial and semiaquatic taxa form orderly oriented architecture, whilst those of aquatic taxa show no preferred orientation.

In turtles, limb bone internal structure is characterized by lack of large open medullary cavity. Terrestrial taxa have tubular compact cortex in stylopodial diaphysis, although its internal region is filled with spongy bone. This pattern of internal limb bone structure is also found in a basal Testudinata *Proganochelys quensteadti* (Upper Triassic, Germany), whose lifestyle is believed to be terrestrial. In stylopodial and zeugopodial bones of semiaquatic to aquatic turtles, the spongy bone is restricted to the region of endochondral bone, resulting in local thickening of hourglass-shaped internal spongy bone. Humerus of a basal testudinate *Mongolochelys efremovi* (Late Cretaceous, Mongolia) with unknown lifestyle also follows this pattern. In Testudinata, *Dermochelys coreacea* have abundant spongy tissue in the region of periosteal origin. Unlike carnivoran mammals, architectural orientation of epi-/metaphyseal trabecular system does not occur in all terrestrial taxa.

The first common pattern found in the relationships between lifestyle in turtles and carnivorans, inhibited of periosteal resorption in semiaquatic to aquatic taxa compared to terrestrial taxa can be functionally interpreted as de-adaptation from terrestrial weight-bearing mode of life, in which the skeletal lightening saves the power required for locomotion. If the reduction of cavities is effective in body ballasting under water in these animals, it is more reasonable to reduce in bone resorption than adding more compact bone. On the other hand, the second common pattern, sponginess in periosteal bone in deep divers is interpreted as cancelation of the reduction in lung volume during diving. Since these ecological differences of three-dimensional internal bone structure depending on lifestyles is generalized among two phylogenetically independent tetrapod groups, it is claimable that the pattern of change in bone microanatomy is applicable for reconstruction of ecological evolution in completely extinct animal group, such as ichthyosaurs, plesiosaurs and desmostylians.

The higher compactness of limb bones in the terrestrial turtles compared to the terrestrial mammals suggests a weaker selection pressure for skeletal lightening, possibly due to the slow limb movements restricted by shells. Lack of architectural orientation of epi-/metaphyseal trabecular system in terrestrial turtles seems to occur also for the weak evolutionary selective pressure for constructing weight-bearing and stress-dispersing system with minimal bone mass.