論文内容の要旨

New biomechanical models of the forelimb postures of extant and extinct tetrapods

（力学的手法に基づく現生~~および~~及び絶滅四肢動物の前肢姿勢に関する研究）

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Reconstructing postures and locomotion of tetrapods are one of the most important issues in the evolutionary studies of vertebrates. Postures and locomotion are highly correlated with the skeletal morphology. One of the most difficult and unsolved questions in reconstructing a skeleton of extinct tetrapods is how the positioin of the shoulder and forelimb area are determined. The shoulder and forelimb do not directly articulate with the axial skeleton. Thus, there have been quite a number of different forelimb reconstructions suggested even for a single species of extinct tetrapods. I hereby propose a new method to securely identify the craniocaudal position of the scapula on the presacral ribs. I would also like to suggest a new method to identify the angle of the elbow joint at its propulsive phase based on the orientation of an olecranon process.

Determining of scapular position is a major issue in reconstructing the skeletal system of extinct quadruped archosaurs and mammals, because the pectoral girdle has no direct skeletal joint with the axial skeleton. In standing or walking, the trunk of quadrupeds is suspended between the forelimbs by the *m. serratus ventralis*, which originates from the lateral sides of the "thoracic" ribs and inserts to the proximal portion on the costal surface of scapula. Therefore, the “thoracic” ribs are subjected to a static or dynamic vertical compression between the lifting force from the muscle and the gravity force from the vertebral column. To elucidate the body support function of the ribs, I analyzed the mechanical strength of the ribs of extant tetrapods by the finite element method, and compared their degree of strength through their craniocaudal scapular positions. The result of this simulation showed that the “thoracic” ribs of quadrupeds, to which the serratus muscle attaches, have relatively high strength against compaction than the other ribs. In bipeds, however, I could not find such a significant correlation between the strength of ribs and the serratus muscle. It suggested that the location of robust ribs is associated with the arrangement of the serratus muscle, and provides a probable candidate for the scapular position, not only for extant quadruped amniotes but also for extinct quadruped archosaurs and mammals. The correlation between the mechanical strength of ribs and the position of craniocaudal position of scapula is proposed here the first time in this study.

Deciphering the angles of limb joints is another difficult task in the skeletal reconstructions of extinct vertebrates. It is mainly because each joint has a wide range of rotation in the forelimb. Several forelimb reconstructions have been suggested for Oligocene-Miocene desmostylian mammals such as *Desmostylus* and *Paleoparadoxia*, and Late Cretaceous ceratopsian dinosaurs, such as *Leptoceratops*, *Centrosaurus*, *Anchiceratops*, and *Triceratops*. This study also proposed a new method to reconstruct the elbow joint angle, which is formed by the humeral shaft and forearm in quadruped tetrapods with prominent olecranon processes. In the study, orientations of olecranon process to the long axis of forearm were measured in dried skeletons of 25 genera of extant mammals, and the results were compared with the elbow joint angle during locomotion of the living animals. In most cases the olecranon process and the shaft of the humerus are oriented nearly perpendicular to each other in the propulsive phase. By keeping the angle of the olecranon process and the humeral shaft almost perpendicular, major extensor muscles can maximize the lever arm at the elbow joint. Orientation of the extensor lever arm, such as olecranon process, can be used to reconstruct the forelimb posture for quadruped mammals, regardless of taxonomic attritions and body sizes.

According to this model, *Desmostylus* is considered to have had more upright forelimb, with elbow joint angle of approximately 160 degrees, whereas *Paleoparadoxia* with elbow joint angle of 130 degrees. The difference of elbow joint angles between these two genera may suggest a difference of stance and gait of these animals. Some ceratopsian dinosaurs, including *Leptoceratops* and ceratopsids, such as *Centrosaurus*, *Anchiceratops*, and *Triceratops*, also possessed the prominent olecranon processes. These animals were supposed to keep their elbow joints in approximately 140 degrees.

Crocodilians do not have the ossified epiphyses nor the prominent olecranon processes at their elbow joints. These animals do not keep their elbow joint angles by relying only on the leverages of olecranon processes. According to an anatomical observation of the bodies and kinetic analyses of three crocodilian species, including *Alligator mississippiensis*, *Tomistoma schlegelii*, and *Crocodylus siamensis*, their elbow joints were suggested to have restricted mobility which is due to surrounding soft tissues. The elbow joint extensions of crocodilians were restricted by skin, muscles, stiff tendons around the joint, and the hooking mechanism on the epiphyses between the cartilaginous olecranon fossa and anconeus process which are firstly reported in this study. Their elbow joint flexions were limited by the skin and muscles around the elbow joint, and the displacement of the radius.

The support mechanisms of forelimbs of ceratopsian dinosaurs are considered as fairly different among taxa. Within the ceratopsian dinosaurs, *Psittacosaurus* and *Protoceratops* did not possess the prominent olecranon process. Insertional tendons of triceps muscles of these animals were suggested to be bent along the caudal surfaces of their humeri at the propulsive phases. In contrast to the other ceratopsian dinosaurs with prominent olecranon processes, such as *Leptoceratops* and ceratopsids, *Psittacosaurus* and *Protoceratops* did not rely on the leverage of the olecranon processes.