How can we tell the forelimb posture of *Triceratops*?

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We would never see the extinct animals alive. Then, how can we tell how they looked like, and how they stand and walk? There has been a lot of controversy over the reconstruction of forelimb posture in extinct tetrapods, mainly due to our poor knowledge on the relationship between the skeletal morphology and the limb postures even among the modern taxa. Here I introduce some of my studies that tackled the problems in determining forelimb postures of extinct taxa, especially focusing on *Triceratops* (Ceratopsia), one of the most famous quadrupedal dinosaurs.

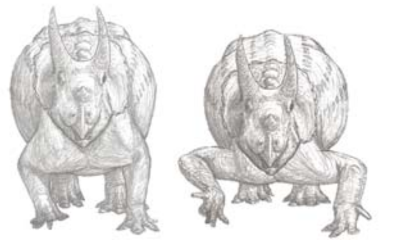

Fig. 1. *Triceratops* reconstructed in (left) upright/sagittal and (right) sprawling forelimb postures.

Topic 1) Upright/sagittal or sprawled?[*1]—It has been difficult to tell whether the extinct animal walked on its forelimb right beneath their trunk like many mammals do (upright/sagittal), splayed out like lizards and salamanders do (sprawling), or creeped on bellies like sloths do (creeping) (**Fig. 1**). Muscle moment arm analyses using 300< modern taxa found that quadrupeds in upright/sagittal, sprawling, and creeping postures emphasize moment arms of the respective anti-gravity muscles of the elbow joint—the elbow extensor, adductor, and flexor muscles, respectively (**Fig. 2**). Therefore, the moment arms of the elbow muscles can be used to discriminate the forelimb posture in extinct forms.

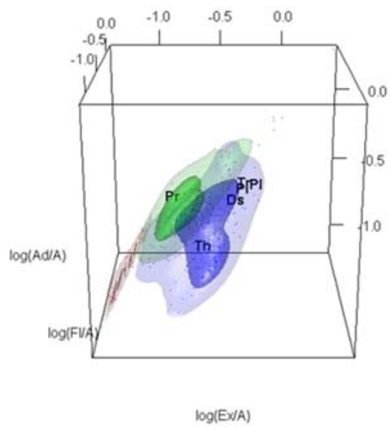

Fig. 2. Kernel density distributions of the moment arm ratios for elbow extensor (Ex/A), flexor (Fl/A), and adductor (Ad/A) in modern (blue) upright/sagittal, (green) sprawling, and (red) creeping quadrupedal tetrapods[*1].

Topic 2) Elbow joint angle in supporting the body[*2–3]—Modern tetrapods are known to maintain the limb joint angles during the support phase within the limited range, although the joint allows larger range of motion. Can we determine the joint angle of stance phase from the bone geometry? According to the study on over 30 modern quadrupedal tetrapod taxa that employ upright/sagittal posture, they were shown to keep the elbow joint at angle where the moment arm of the anti-gravity muscle maximize (**Fig. 3**). The orientation of the muscle attachment from the joint thus could be a powerful tool to estimate the joint angles in stance of the animal.

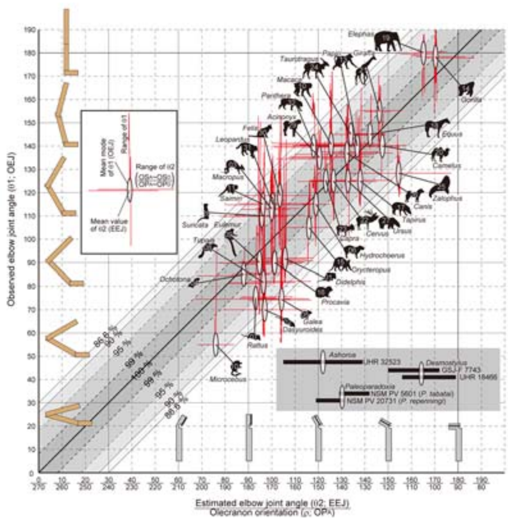

Fig. 3. Relationship between (horizontal) the elbow joint angle where the extensor moment arm maximize and (vertical) the elbow joint angle while supporting the body in modern upright/sagittal quadrupeds[*2].

Topic 3) Scapular position[*4–5]—The scapulae are not directly connected with the ribcage. Therefore, determining the positions of the scapulae in relation to the trunk has been most difficult topic in the skeletal reconstruction of extinct tetrapods. However, all the modern tetrapods that facultatively/obligately support their body on forelimbs share the scapular position near the median, and above the anterior portion of the ribcage. In the support phase of quadrupedal posture, the ribcage is suspended between the scapulae via serratus and rhomboid muscles encountering the gravity. Three-dimensional muscle moment analyses on extant quadrupedal taxa revealed that net-roll, -yaw, and -pitch moments of the trunk caused by the contraction of these muscles and the gravity become negligible, if the scapulae are in the position shared by modern quadrupeds (**Fig. 4**). Furthermore, the ribs beneath the scapulae were shown to have relatively higher strength against the vertical compression among the other ribs in quadrupeds. This is consistent with the function of the specific ribs to support the body against the gravity. These features would together provide a reasonable reconstruction for the scapular position in extinct quadrupeds.

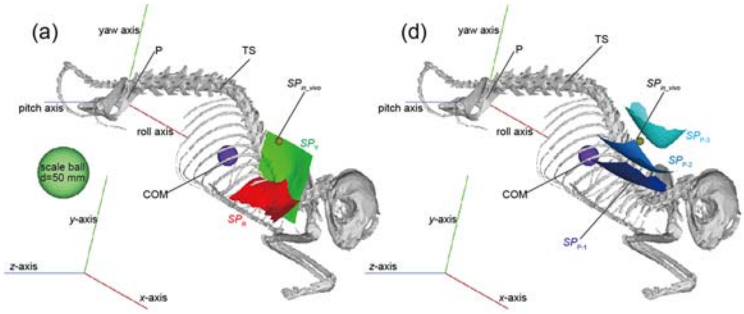

Fig. 4. Appropriate positions of the scapula to prevent net-roll (red), -yaw (green), and -pitch (blue) of the trunk about the hip-joint caused by body weight and contractile forces of anti-gravity muscles connecting the trunk and the scapula in cat (*Felis silvestris catus*). The animal can stay stable in support on the forelimb, if the scapular position satisfies the above three conditions (red, green, and blue zones)[*5].

According to the above-mentioned interpretations, the forelimb postures were indicated to vary among the ceratopsian dinosaurs. Among the ceratopsians, *Triceratops* likely employed upright/sagittal forelimb posture, whereas, *Protoceratops* likely employed sprawling postures, respectively. The elbow angle of *Triceratops* is likely maintained in 130–140° in stance. However, both taxa would share the scapular positions with modern quadrupedal tetrapods.

References:

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*5) **Fujiwara S** (2018) Fitting unanchored puzzle piece in the skeleton: appropriate scapular position for the quadrupedal support in tetrapods. *J Anat* 232: 857–869. DOI: 10.1111/joa.12778.