Can Dinosaurs ’Hindlimbs Maintain their Stance Posture Using the Passive Interlocking Mechanism Confirmed in Crocodilian Hindlimbs?

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Abstract: This report addressed the stance mechanism in a non-avian dinosaur *Protoceratops andrewsi* hindlimbs using a robotic approach. Our previous studies demonstrate the passive interlocking mechanism in crocodilian hindlimbs is crucial to achiev- ing their standing motion. We verified the importance of the passive mechanism by implementing artificial musculotendinous systems, following the inference derived from crocodilians, onto a 3D printed physical model of the *Protocereatops* skeleton. The experiments validated the feasibility of achieving the stance posture of *Protoceratops* through the interaction between the artificial musculoskeletal tendinous system and ground reaction forces in a similar manner to crocodilians. This report highlights constructing a physical model with artificial musculotendinous systems is a valuable platform for exploring locomotion in extinct animals.

Keywords: dinosaur; *Protoceratops andrewsi*; musculoskeletal system; passive interlocking mechanism

1. INTRODUCTION

Animals possess a musculoskeletal tendinous system that comprises multiple joints and redundant muscle configurations, resulting in a highly complex multi-degree-of-freedom system. Revealing the essential mechanisms required for animal locomotion proved to be challenging but attracted much scientific attention not only in biology but also in robotics. Merely elucidating how individual muscles generate force might not inherently lead to a comprehensive understanding of overall locomotion. Functional anatomical studies demonstrate that passive interlocking mechanisms achieved by the coordination of multiple muscles, tendons, and bones are vital to producing remarkably smooth limb movements with minimal activation of muscles in horses [1], birds [2, 3], and crocodiles [4, 5]. Reproducing such passive mechanisms by synthesizing robots has been shown to emerge the natural motion of animals in studies [5-10]. These studies underscore the significance of comprehending the intricately connected muscle systems and replicating them through physical models to reveal the underlying mechanisms of animal locomotion.

The approach to understanding locomotion through robotic replications is not exclusive to extant species; it can be extended to those that are extinct. The locomotion and musculotendinous system supporting it were lost through fossilization, and therefore, validating their efficacy through the replication of physical models is highly informative to locomotive strategies of extinct animals. Previous studies have employed computer simulations to analyze the locomotion of extinct species e.g., [11, 12]. However, mathematical models inherently lose information during the modeling process, and there might be numerous aspects that can only be understood through the replication of physical models.

Fig. 1. A reconstructed skeleton of *Protoceratops andrewsi* (cast) at the Museum of Dinosaur Research, Okayama University of Science.

This study, therefore, aims to elucidate and reconstruct the musculoskeletal tendinous systems present in extinct species by establishing a physical model based on actual fossil specimens. This report presents a physical model based on a remarkably well-preserved fossil specimen of a non-avian dinosaur, *Protoceratops andrewsi* (Fig. 1). We emulate the passive interlocking mechanism supported by certain muscles and tendons observed in the hindlimbs of crocodiles, extant relatives of non-avian dinosaurs. Using the physical model with the emulated passive systems, we demonstrate the ability to stand upright and maintain a stance posture in *Protoceratops* through robotic experiments.

2. MATERIALSANDMETHODS

To reconstruct a physical model of a dinosaur, we used a cast of *Protoceratops andrewsi* skeleton with the musculotendinous system for maintaining a stance posture implemented based on the passive interlocking mechanism of the crocodilian hindlimb [5].

2.1. Skeletal model of *Protoceratops andrewsi*

A cast of the nearly complete *Protoceratops andrewsi* skeleton was utilized for this study. This species is a small- bodied quadruped herbivorous ceratopsian dinosaur and is represented by numerous well-preserved skeletons from the Upper Cretaceous Djadokhta Formation in the Gobi Desert, Mongolia [13]. It was collected at Tugrikin Shireh on August 28, 1993, during the Hayashibara Museum of Natural Sciences and the Mongolian Paleontological Center Joint Expedition [14]. The specimen preserves a nearly complete skeleton, lacking only the rostral region of the skull and the tip of the tail. It measures approximately 1.7 meters in length and is estimated to weigh around 106-179 kilograms based on the estimation formula by Campione and Evans [15]. The specimen is minimally deformed by taphonomic processes. The skeleton is now housed in the Institute of Paleontology of the Mongolian Academy of Sciences in Ulaanbaatar, Mongolia, and the specimen number is MPC-D 100/531. The skeletal cast was reconstructed in a standing posture at the former Hayashibara Museum of Natural Sciences in Okayama, Japan (Fig. 1) [16], and later transferred to the Museum of Dinosaur Research, Okayama University of Science. The re- constructed standing posture, including each joint angle, is congruent with that of the independent study of *Protoceratops* locomotion [17]. Three-dimensional digital models of the pelvic girdle and each hindlimb element were created based on the isolated casts of the bones using photogrammetry [18] and X-ray computed tomography (CT) scanning. The photogrammetric models were created using Metashape Standard version 1.7.3 (Agisoft, Russia). The casts were CT scanned using Latheta LCT-200 (Hitachi Aloca Medical, Japan). The obtained CT images were rendered using VGSTUDIO MAX 3.4 (Volume Graphics, Germany) and segmented using 3DSlicer version 5.3 [19].

2.2. Stance mechanism based on the passive interlocking of the musculotendinous system in crocodilian hindlimb

We implemented the musculotendinous system onto the skeletal model of *Protoceratops* based on the passive inter- locking mechanism of the crocodilian hindlimb, maintaining a stance posture. The mechanism achieves a stance posture using the caudofemoralis longus (CFL), the branched tendon of the CFL (CFLT), and the gastrocnemius externus (GE) in crocodilians (Fig. 2A [5]). The CFL, the largest muscle around the hindlimbs, originates from the third to fifteenth caudal vertebrae and inserts into the fourth trochanter on the posterior side of the femur. A thick tendon (CFLT) branches slightly distal to the CFL insertion, connecting to the GE, and forms a Y-shaped junction (Fig. 2B). The GE originates from the lateral femoral epicondyle, descends alongside the tibia, and inserts into the flexor digitrum longus around the metatarsi, which inserts into the ventrodistal aspect of the phalanges [20].

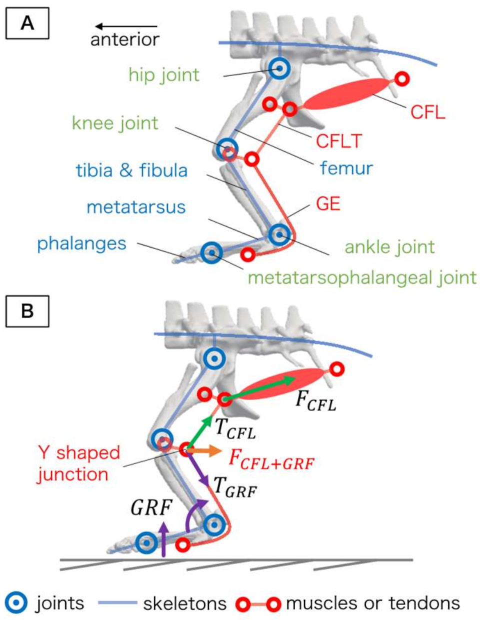

Fig. 2. A. The schematic diagram of the stance posture maintenance mechanism in crocodilian hindlimbs. B. summarized representations of generated forces.

This musculotendinous arrangement is based on our previous anatomical studies of *Crocodylus porosus* [5] and other previous studies of multiple crocodilian species [20, 21]. The mechanism of crocodilian hindlimbs to support weight and maintain a stance posture is performed through the traction generated by the active contraction of the CFL and the ground reaction forces (GRF). The active contraction of the CFL F_{CFL} results in traction of the femur, causing extension of the hip joint, and simultaneously generates the tension of the CFLT T_{CFL} posterodorsally (Fig. 2B). If the hindfoot makes contact with the ground when the CFL is activated, the GRF affects the ankle joint's dorsiflexion, resulting in tension TGRF that pulls the Y-shaped junction posterovenrally along the GE. The active contraction of the CFL F_{CFL} results in traction of the femur, causing extension of the hip joint, and simultaneously generates the tension of the CFLT T_{CFL} posterodorsally (Fig. 2B). At this moment, considering the combined forces acting on the Y-shaped junction formed by the CFLT and GE - T_{CFL} and T_{GRF} - the resultant force $F_{CFL+GRF}$ pulls the Y-shaped junction posteriorly. $F_{CFL+GRF}$ acts as a force that pulls the lateral femoral epicondyle, which is the origin of the GE, posteriorly through the Y-shaped junction, leading to the ex- tension of the knee joint if the foot does not slip. Essentially, upon hindfoot contact with the ground, the stance posture in the hindlimb can be accomplished and maintained solely through the traction exerted by the CFL and the passive joint coordination in crocodilians. This interlocking mechanism within the crocodilian hindlimb musculotendinous system for maintaining a stance posture was verified through robotic experiments in our previous study [5].

3. RESULTS

3.1. Reconstruction of the *Protoceratops* hindlimb musculoskeletal tendinous system

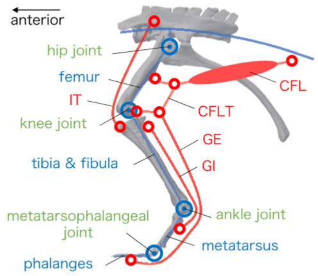

Fig. 3. Reconstructed musculoskeletal tendinous system to achieve a stance posture in *Protoceratops*.

We implemented the musculotendinous system to the *Protoceratops* hindlimb based on that of crocodilians, primarily focusing on the passive interlocking mechanism (Fig. 3). To reconstruct soft tissue structures of extinct animals that are rarely fossilized, paleontologists have utilized inferences from extant relatives (e.g., [22]). The origin and insertion points of the CFL, CFLT, and GE are regarded as consistent among archosaurs, including extant crocodilians, extinct non-avian dinosaurs, and extant birds [8, 11, 23-40]. Therefore, these muscles can be implemented in the *Protoceratops* model with high certainty. Additionally, we introduced the gastrocnemius internus (GI) and the iliotibialis (IT) muscles, which are also consistent among archosaurs, as passively functioning elements (e.g., [11, 23]). The GI originates from the medial surface of the proximal end of the tibia and inserts onto the plantar surface of the metatarsals in crocodilians [20, 21]. In our previous research [5], introducing the GI into the crocodilian hindlimb musculoskeletal model limits ex- cessive dorsiflexion of the ankle joint, avoiding collision be- tween the tibia and metatarsi. Furthermore, we assumed that the addition of the GI to the *Protoceratops* skeleton is essential to maintain the digitigrade posture observed in non-avian dinosaurs by passively restricting the range of dorsiflexion in the ankle joint. Such passive support of the ankle joint by elastic stretch of the muscles was also predicted to have been present in dinosaurs by Bishop et al. [11] and Sellers et al. [12]. The IT in crocodilians originates from the dorsal border of the iliac blade and inserts into the cnemial crest of the tibia [20, 21]. Our previous study [10] revealed that introducing the IT into the crocodilian hindlimb musculoskeletal model results in passive extension of the knee joint, coordinating with the extension of the hip joint. The inclusion of IT is assumed to be critical to maintaining a more upright stance for dinosaurs compared to crocodilians.

3.2. Design of the *Protoceratops* hindlimb robot

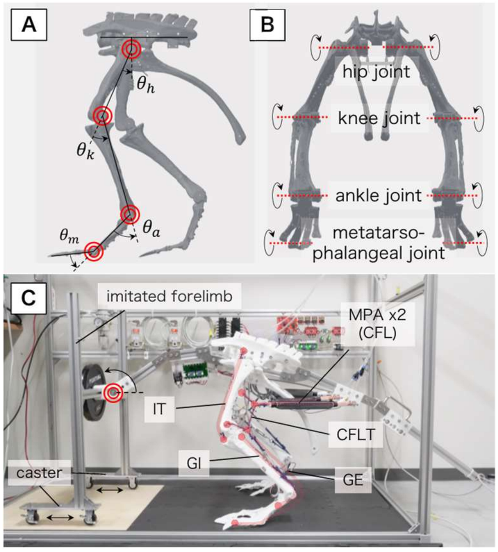

Fig.4. Left lateral view of *Protoceratops* hindlimb region showing the positions of joint axes. B. Anterior view of the hindlimb region. C. Experimental system using the physical model of the *Protoceratops* hindlimb.

We designed the *Protoceratops* hindlimb robot (Fig. 4), combining the pelvic and hindlimb elements with the hip joint, knee joint, ankle joint, and metatarsophalangeal joint (only the second digit) as single-axis rotational joints (Fig. 4B). These joints were equipped with potentiometers to measure the relative angles (Fig. 4A). We fixated the constructed pelvic and hindlimb elements onto the aluminum frames that imitating dorsal and caudal vertebral column. Additionally, a single-axis rotational joint was positioned at the equivalent point of the shoulder joints and connected to imitated forelimbs (Fig. 4C). The imitated forelimbs are equipped with casters to slide on the ground, enabling movement in the horizontal plane. To prevent lift force due to their lighter weight compared to the hindlimbs, we attached 5 kg weights to the forelimbs. We then implemented the artificial musculotendinous system (Fig. 3). The CFL was implemented using two McKibben-type pneumatic actuators (MPAs) arranged in parallel, as it requires an active function. Other passive muscles and tendons were reconstructed using Kevlar lines. The natural lengths of the GI, GE, and IT elements were configured to be adjustable. The dimensions of the robot are approximately 1.6 m in length, 0.7 m in height, and 0.6 m in width, weighing around 16 kg.

3.3. Experiment of upright standing and maintaining the posture

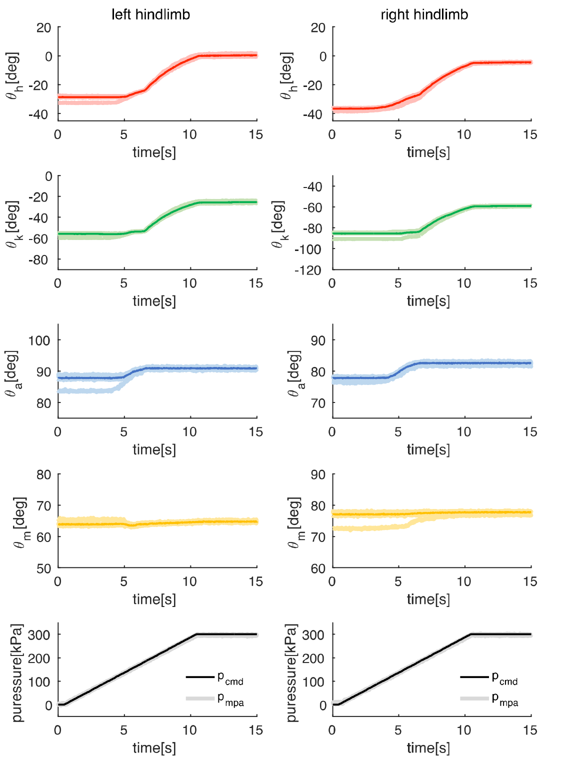

Fig. 6. The relative angle of each joint according to the MPA pressures. The lighter solid lines represent the variations in the relative angles over ten trials, while the darker solid line represents their averages.

The experiments verified that the *Protoceratops* hindlimb robot successfully performs standing-upright motion and maintains the stance posture (Fig. 5). The experiments started from an initial posture resembling a crouched posture with flexed knee and hip joints. The pressure within the MPAs, representing the CFL, was

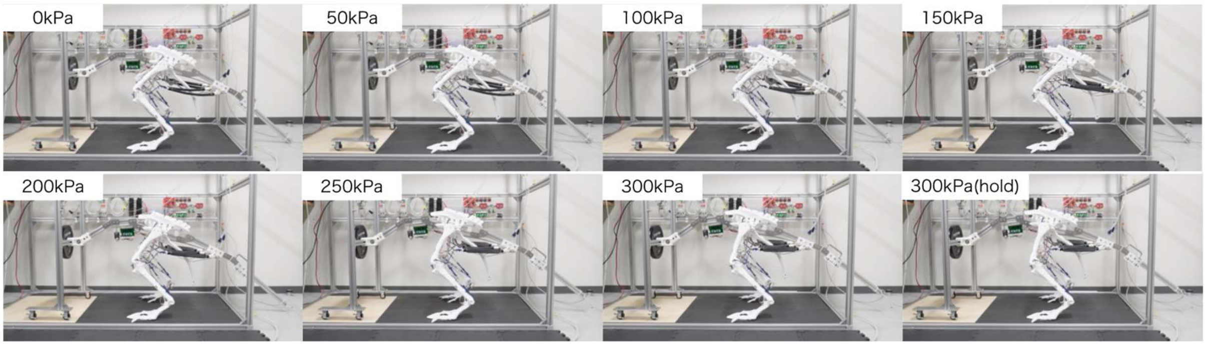

Fig. 5 A sequence of movement of *Protoceratops* hindlimb robot in response to the change of the MPA pressure.

increased at a constant rate from the atmospheric pressure, causing gradual contraction. Around the relative pressure of 200 kPa, the hip and knee joints began extending. At approximately 300 kPa, the posture resembles the stance posture of the reconstructed skeleton, illustrated in Fig. 1. We replicated the experiment ten times and recorded the transition of the relative angles of the joints in the left leg (Fig. 6). The results showed that the robot successfully stood upright and maintained the stance almost identically regardless of uncertainties (e.g., differences in initial condition) in all tests.

4. CONCLUSIONS

This report demonstrates that the implementation of the passive interlocking mechanism, seen in crocodilian hindlimbs, enables *Protoceratops andrewsi* to achieve a stance posture solely by the activation of the CFL with the coordination of the passive musculotendinous structures and GRF. The importance of such passive mechanisms in the study of dinosaur locomotion has been raised but not investigated (e.g., [11,12]). The robotic approaches of this study, in contrast, directly contributed to understanding passive mechanisms in dinosaur locomotion. The measurement of the forces acting upon each muscle and tendon element, as well as ground reaction forces, will facilitate a more thorough investigation into the mechanics behind how dinosaur musculoskeletal systems achieve the stance posture relevant to their locomotion.

Now, we have the *Protoceratops* robot that is capable of standing upright, and the apparatus serves as an effective platform to investigate other musculoskeletal systems to achieve different aspects of locomotion (e.g., walking) in *Protoceratops*. This study highlights that constructing physical models based on original fossil specimens is a highly effective scheme to emulate the locomotion and the underlying musculoskeletal tendinous systems in various extinct species beyond non-avian dinosaurs.

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