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MORPHOFUNCTIONAL CHARACTERISTICS OF THE LOWER HINDLIMB AND FOOT MUSCLES OF BORNEAN ORANGUTAN (*Pongo pygmaeus*)

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ABSTRACT

This research aims to study the morphofunctional characteristics of the lower hindlimb and foot muscles of Bornean orangutan and its relation to the type of locomotion and daily behavior. This research was conducted on the right leg of a male orangutan by observing the morphology of the lower hindlimb and foot muscles and observing the behavior of the Bornean orangutan through video observations. The results showed that digital flexor muscles are more developed than plantar flexor muscles as an adaptation towards arboreal activities that require finger flexor movements such as gripping tree branches. Orangutans have rudimentary hallux, which is related by the less developed intrinsic muscle and indicated by the way orangutan grips tree branches dominantly using digits II-V. At a certain time, male Bornean orangutans are active on terrestrial that causes the digital extensor muscles to have more developed as an adaptation to terrestrial activity. It can be concluded the morphology of the lower hindlimb and foot muscles is in accordance to its function and behavior adaptation in arboreal and terrestrial.

Key words: arboreal, Bornean orangutans, foot, lower hindlimb, terrestrial

ABSTRAK

Penelitian ini bertujuan mengetahui karakteristik morfofungsi otot-otot daerah betis dan telapak kaki orang utan kalimantan dan kaitannya dengan tipe lokomosi dan perilaku hariannya. Penelitian ini dilakukan terhadap kaki kanan seekor orang utan jantan dengan cara mengamati morfologi otot-otot daerah betis dan telapak kaki serta mengamati perilaku orang utan kalimantan melalui pengamatan video. Hasil penelitian menunjukkan otot-otot flexor digit lebih berkembang dibandingkan otot-otot flexor plantar sebagai adaptasi dari aktivitas arboreal yang membutuhkan gerakan flexor digit seperti saat mencengkeram cabang pohon. Orang utan memiliki digit I yang rudimenter sehingga otot-otot intrinsik digit I kurang berkembang, ditunjukkan dengan cara orang utan mencengkeram cabang pohon yang dominan menggunakan digit II-V. Pada waktu tertentu, orang utan jantan dewasa aktif di teresterial yang menyebabkan ukuran otot extensor digit relatif lebih berkembang sebagai bentuk adaptasi terhadap aktivitas teresterial. Morfologi otot betis dan telapak kaki orang utan sesuai dengan fungsi dan adaptasi perilakunya di arboreal maupun teresterial.

Kata kunci: arboreal, orang utan kalimantan, telapak kaki, otot betis, teresterial

INTRODUCTION

Orangutans are the only great apes that live arboreally in the tropical rain forests of Borneo and Sumatra that are closely related to other great apes such as gorillas and chimpanzees. Anatomical differences in each animal species are adaptations to their functions and natural habitats (Cartmill 2010). Orangutan locomotion type is generally semi-bipedal (Oishi *et al*. 2009), compared to other great apes which have dominant terrestrial behavior with a quadrupedal locomotion type namely, knuckle-walking (Zihlman *et al*. 2011).

Orangutans undergo specific adaptations in both arms and legs (Vereecke *et al*. 2005). The development of both leg muscles of orangutans is due to the influence of locomotor function and manipulative movements. Their feet are less active in manipulative functions than the arms, but they still have strong muscles to grip tree branches when they are moving arboreally (Tuttle 1972).

The locomotor structure influences the locomotion patterns, habits, or behavior of primates (Ankel-Simons 2007). It is important to research the structure of the muscles of the lower hindlimb and foot of the Bornean orangutan (*Pongo pygmaeus*) to estimate the effect of locomotion type and arboreal behavior on muscle structure as an active locomotion apparatus. In addition, this study can be used to distinguish the type of locomotion and behavior of orangutans from other great apes such as gorillas and chimpanzees.

MATERIALS AND METHODS

A set of right-leg of a five years old male Bornean orangutan (*Pongo pygmaeus*), which had been preserved in 10% formalin was used in the present study. The cadaver was obtained from the Division of Pathology, Department of Veterinary Clinic Reproduction and Pathology, School of Veterinary Medicine and Biomedical Sciences, IPB University.

Morphological Observations of Lower Hindlimb and Foot

The lower hindlimb muscles were prepared by performing skin incision from the caudal side of the knee joint to the tarsus joint. The skin on the foot was incised on the dorsal side to the metatarsophalangeal

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joint. The skin is carefully prepared and the fat and connective tissue under the skin are removed from the muscle surface. After the skin is exposed, the deep fascia is incised and reflected dorsally.

Observations of the lower hindlimb and foot muscles were carried out from the medial, lateral, caudal, plantar, and dorsal planes. The parameters that were observed are distinctive anatomical shape and the size of the lower hindlimb and foot muscles in adult male Bornean orangutans. Several muscles were cut midway between their origin and insertion to allow for more profundal muscle groups to be seen. Determination of the origin and insertion of the muscles were done by preparing some superficial muscles and examining the ends of muscle attachments in bones or other parts and assisted by the guidance of the atlas of orangutans *Photographic and Descriptive Musculoskeletal Atlas of Orangutans* (Diogo *et al*. 2013). The morphological observations of the lower hindlimb and foot muscles were taken using a Canon® EOS 700D. The photos are schematically drawn and processed using Adobe® Photoshop CC 2020.

The name of the lower hindlimb and foot muscles was based on the Nomina Anatomica Veterinaria (WAVA, 2017). The lower hindlimb and foot muscles were listed in the order in which they were used by Diogo *et al*. (2013). The muscles were analyzed descriptively and comparatively with that in other great apes, such as gorillas and chimpanzees from anatomical characteristics associated with adaptation and daily behavior.

Behavioral Observation

Behavioral observations were carried out through video observations from Youtube media (Fred 2014; Sharon 2017; National Geographic 2018). Parameters observed were arboreal activity, the use of hindlimb, and terrestrial activity. The results of the observations are presented in the form of schematic drawings of body postures in various activities associated with the morphology of the lower hindlimb and foot muscles.

RESULTS AND DISCUSSION

The leg of the Bornean orangutan observed in the present study has brown skin in the lower hindlimb area and is covered with reddish-brown hair, while the foot is not covered by hair and has black skin. The leg has five digits, with digit I shorter than the other digits and doesn't have nails. Tuttle and Rogers (1966) noted that 60% of the sample of orangutans lacked nails and the distal *os phalanx* in digit I. The orangutan's forelimb locomotor acts as a primary mover during brachiation, while the orangutan's hindlimb locomotor helps in its movement (Glinka 2008), especially when moving between tree branches and when walking bipedally.

The extensor muscles of the tarsus joint, as well as the plantar flexors (*m. gastrocnemius*, *m. soleus*, and *m. tibialis caudalis*) in orangutans, are relatively smaller than the digital flexor muscles, with relatively short calcaneus/Achilles tendons (Figure 1). According to Myatt *et al*. (2011), the plantar flexor muscles of orangutans are relatively less developed than those in chimpanzees. Terrestrial quadrupedal is dominated by the hindlimb locomotor as the main mover and retaining body weight. It is characterized by the chimpanzee's more developed plantar flexor muscles, exhibiting strong propulsive abilities that would be advantageous in pursuing prey (Nowak *et al*. 2010), and can be related to their feeding activity, such as hunting other non-human primates for their meat (Mitani and Watts 1999). On the other hand, the orangutan's plantar flexor muscles are relatively small in size with the *m. tibialis caudalis* have a long and relatively slender figure (Figure 1), but has higher mobility, even though it doesn't have great strength (Thorpe *et al.* 2007).

Orangutans have coxofemoral and femorotibial joints that are in an extended state (Figure 5) during arboreal bipedal activities, similar to the position seen in human bipedalism. This type of extended bipedal locomotion requires balance and a firm grip of the foot. This condition is aided by the pronator (*m. fibularis longus* and *m. fibularis brevis*) and supinator (*m. tibialis cranialis*) muscles of orangutans which are longer (Figure 2) than in chimpanzees (Thorpe *et al.* 2007). According to Lewis (1980) the size of *m. fibularis longus* and *m. fibularis brevis* provides greater control and reach for foot placement when gripping tree branches.

There is a thin and small tendon slip that was found in the insertion tendon at the tuberosity of the fifth metatarsal bone of *m. fibularis brevis*, it's expanded to attach along a line on the dorsolateral side of the fifth digit. It was the tendon of *m. peroneus digiti quinti* (Figure 3). Schwartz (1988) stated that *m. peroneus digiti quinti* is relatively common in some monkeys but rare in hominoids. Some anatomists (cited in Straus 1930) have never identified a complete *m. peroneus digiti quinti* in orangutans. The form of *m. peroneus digiti quinti* as a vestigial tendon was found in hominoids, such as in gorillas (Raven 1950), orangutans (Sonntag 1924), and chimpanzees (Sonntag 1923). The *peroneus digiti quinti* muscle has generally been lost in hominoidea and only the distal part of the tendon is left which fuses with the tendon of *m. fibularis brevis*. In orangutans, this tendon functions as a very weak pronator of the foot (Schwartz 1988).

The digital extensor muscles (*m. extensor digitorum longus*, *m. extensor digitorum brevis*, *m. extensor hallucis brevis*, and *m. extensor hallucis longus*) (Figure 3) are relatively underdeveloped in orangutans than their digital flexor muscles. In their arboreal locomotion, the orangutan digital flexor muscles play a more important role than the digital extensor muscles, especially in gripping tree branches (Payne *et al*. 2006). On the other hand, the digital extensor muscles in gorillas and chimpanzees are more developed. It is thought to be related to quadrupedal terrestrial behavior that requires strong digital extensor muscles to perform hyperextension digit movements when walking on the

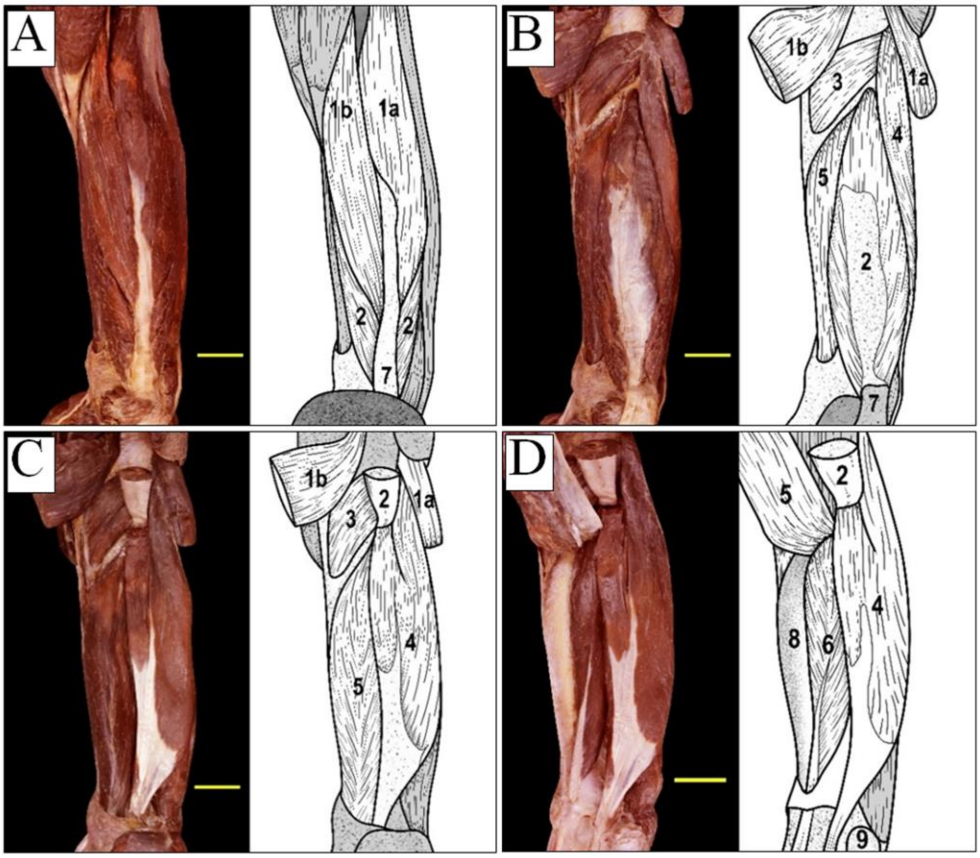

Figure 1. The caudal view of superficial and profundal layers of the lower hindlimb muscles of Bornean orangutan. A= Superficial layer, B= Profundal layer after *m. gastrocnemius* removed, C= Profundal layer after *m. soleus* removed, D= Profundal layer after *m. flexor digitorum longus* removed. 1a= *m. gastrocnemius caput laterale*, 1b= *m. gastrocnemius caput mediale*, 2= *m. soleus*, 3= *m. popliteus*, 4= *m. flexor hallucis longus*, 5= *m. flexor digitorum longus*, 6= *m. tibialis caudalis*, 7= tendo *calcaneus*, 8= *os tibia*, 9=*os calcaneus.* Bar= 5cm

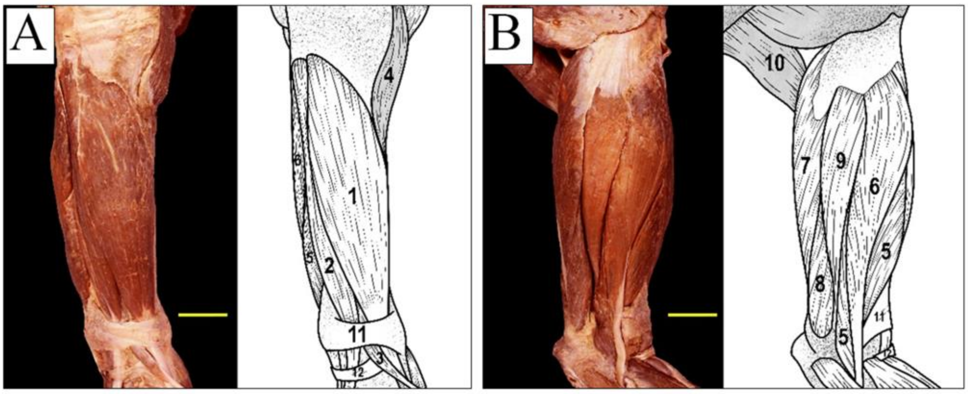

Figure 2. The cranial and lateral view of superficial layer of the lower hindlimb muscles of Bornean orangutan. A= Cranial view, B= Lateral view. 1= *m. tibialis cranialis*, 2= *m. extensor digitorum longus*, 3= *m. extensor hallucis longus*, 4= *m. gracilis*, 5= *m. fibularis brevis*, 6= *m. fibularis longus*, 7= *m. gastrocnemius*, 8= *m. soleus*, 9= *m. flexor hallucis longus*, 10= *m. semitendinosus*, 11= *retinaculum extensorum tarsale proximalis*, 12= *retinaculum extensorum tarsale distalis*. Bar= 5cm

ground (Tuttle 1970). The relationship between the terrestrial quadrupedal and the development of the digital extensor muscles is also seen in the digital extensor muscles of young orangutans which are less developed compared to adult male orangutans that are more terrestrial (Payne *et al*. 2006).

The digital flexors (*m. flexor digitorum longus*, *m. flexor hallucis longus*, and *m. flexor digitorum brevis*) muscles are large and have a relatively long and thick insertion tendon (Figure 4). Orangutan digital flexor muscles are more developed than in chimpanzees (Oishi *et al*. 2012), and serves as a flexor of the metatarsophalangeal and interphalangeal joints of digits II-V to grip tree branches in arboreal activities. The *flexor hallucis longus* muscle in orangutans, which is located at the most profundal layer of the other digital flexor muscles, is larger than in gorillas and chimpanzees (Oishi *et al*. 2012), and has an important role in generating strength to grip tree branches that are needed during hanging, swinging, and walking on tree branches (Hunt *et al*. 1996).

Variations in the structure and location of the insertion of the digital flexor muscles are relatively common in primates. In the research of Oishi *et al.*

(2012), chimpanzees have tendons of *m. flexor hallucis longus* which inserts on digits I, III, and IV, while the tendons of *m. flexor digitorum longus* in digits II-IV. The *m. flexor hallucis longus* in gorillas has only one tendon that inserts at digit I similar to that found in humans (Zihlman *et al*. 2011), and the tendon of *m. flexor digitorum longus* inserts to digits II-V. In contrast to the two African great apes, in orangutans only *m. flexor hallucis brevis* that plays a role in digit I flexor movement. The *m. flexor hallucis longus* in orangutans only has insertions to digits III and IV, while *m. flexor digitorum longus* inserts to digits II, IV, and V (Figure 4).

Digit I of orangutans hindlimb are relatively short with a tendon of *m. flexor hallucis longus* does not insert on digit I. According to Oishi *et al.* (2012), the force produced by the flexor muscle of digit I in orangutans is smaller than in chimpanzees. This is shown in the mass and size of the intrinsic muscles of digit I (*m. abductor hallucis, m. adductor hallucis, m. flexor hallucis brevis, m. extensor hallucis brevis*) (Figure 4) of orangutans which are relatively smaller than other great apes (Patel *et al*. 2020). On the other hand, the digit I of the chimpanzee is relatively long and can be moved, with the insertion tendon of *m. flexor hallucis longus* (Oishi *et al*. 2012). Morphofunctionally, this structure is advantageous for digit I-assisted gripping movements during arboreal locomotion (Figsure 5) because digits II-V in chimpanzees are relatively shorter and less curved than in orangutans (Marchi 2005).

The foot of the orangutan is very specialized as a supporting organ during arboreal locomotion, with rudimentary digit I and relatively long and curved II-V digits (Kanamoto *et al*. 2011), so orangutans are more dominant using digits II-V with hook-like gripping while hanging and gripping tree branches (Figure 5), therefore a greater force is required on digits II-V which is indicated by the development of the intrinsic muscles of the foot (*mm. lumbricales* and *mm. interossea plantaris*) (Figure 4). *Musculi lumbricales* in orangutans are relatively developed as flexors and adductors of digits II-V, but in gibbons, *m. lumbricalis* leading to digit V is often not found (Lemelin and Diogo 2016). The *mm. interossea plantaris* of orangutans has a relatively larger muscle mass than that

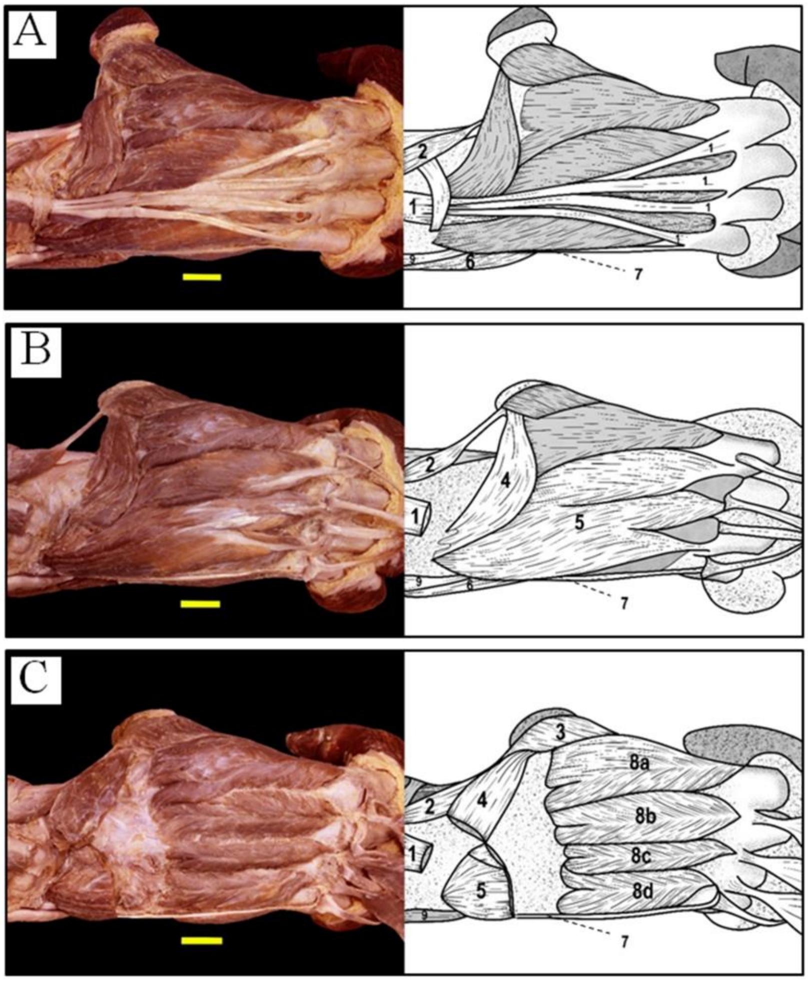

Figure 3. The dorsal view of superficial and profundal layers of foot muscles of Bornean orangutan. A= Superficial layer, B= Profundal layer after tendon *m. extensor digitorum longus* removed, C= Profundal layer after *m. extensor digitorum brevis* and *m. extensor hallucis brevis* removed. 1= *m. extensor digitorum longus*, 2= *m. extensor hallucis longus*, 3= *m. adductor hallucis*, 4= *m. extensor hallucis brevis*, 5= *m. extensor digitorum brevis*, 6= *m. abductor digiti minimi*, 7= tendo *m. peroneus digiti quinti*, 8a= *m. interosseus dorsalis I*, 8b= *m. interosseus dorsalis II*, 8c= *m. interosseous dorsalis III*, 8d= *m. interosseus dorsalis IV*, 9= tendo *m. fibularis longus*. Bar= 2.5cm

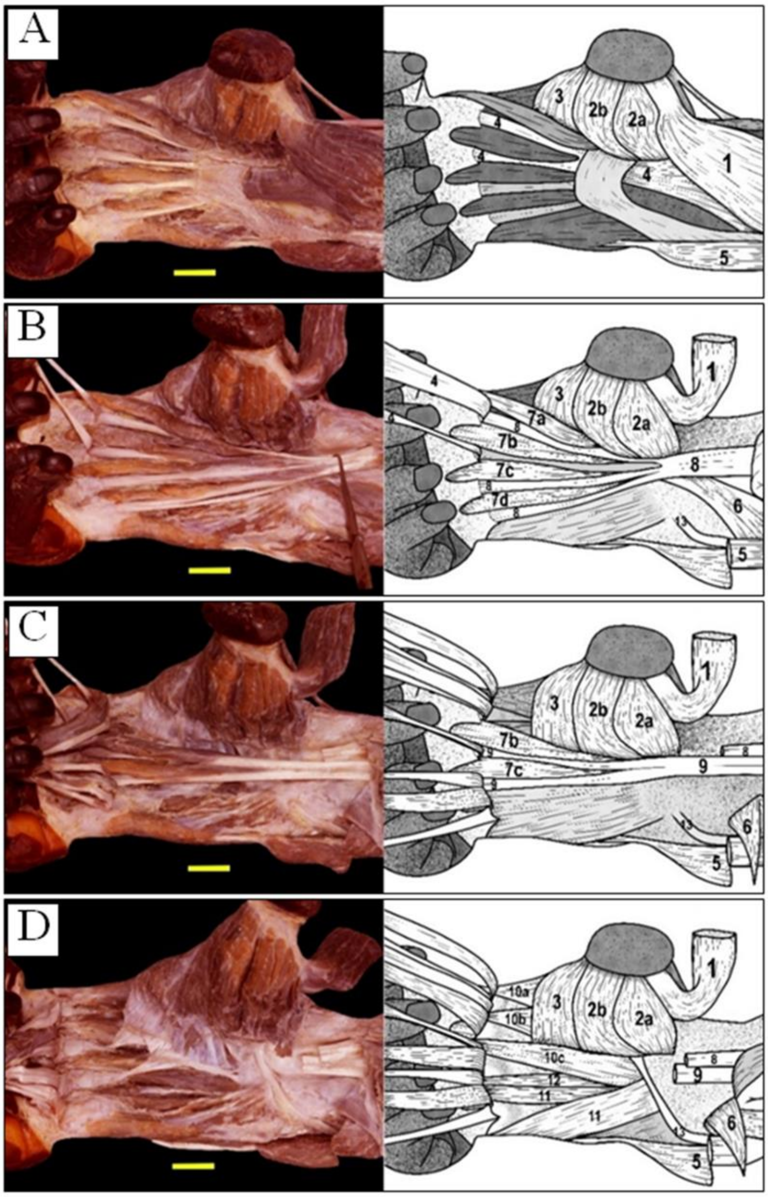

Figure 4. The plantar view of the superficial and profundal layers of foot muscles of Bornean orangutan. A= Superficial layer, B= Profundal layer after *m. flexor digitorum brevis* and *m. abductor hallucis* removed, C= Profundal layer after tendon *m. flexor digitorum longus* opened, D= Profundal layer after tendon of *m. flexor hallucis longus* opened. 1= *m. abductor hallucis,* 2a= *m. flexor hallucis brevis caput mediale*, 2b= *m. flexor hallucis brevis caput laterale*, 3= *m. adductor hallucis caput transversum*, 4= *m. flexor digitorum brevis*, 5= *m. abductor digiti minimi*, 6= *m. quadratus plantae*, 7a= *m. lumbricales I,* 7b= *m. lumbricales II,* 7c= *m. lumbricales III,* 7d= *m. lumbricales IV,* 8= tendo *m. flexor digitorum longus*, 9= tendo *m. flexor hallucis longus*, 10a= *m. interosseus plantaris I*, 10b= *m. interosseus plantaris II*, 10c= *m. interosseus plantaris III*, 11= *m. flexor digiti minimi brevis*, 12= *m. opponens digiti minimi*, 13= tendon of *m. fibularis longus*. Bar= 2.5cm

of gorillas and chimpanzees (Oishi *et al*. 2018), and this muscle has the most potential to generate the greatest force among the intrinsic muscles of the foot (Oishi *et al*. 2012). Morphological differences in the intrinsic muscles of the foot indicate specific locomotor functions that differ between orangutans and other great apes in their arboreal locomotion.

Adult male Bornean orangutans has higher percentage of terrestrial activities than other species of orangutans (Prayogo *et al*. 2014), but it didn't mean that they are more terrestrial than gorillas and chimpanzees. This is shown by the adaptation of the orangutan's hindlimb locomotor structure which is more adapted to swinging, hanging, and gripping tree branches with hook-like gripping, which predominantly uses flexor digits II-V movements. In contrast, the more terrestrial primates such as gorillas and chimpanzees have hindlimb locomotor structures that are more adapted for propulsion and weight-bearing movements, predominantly using plantar flexor movements and the hyperextension of the digit (Figure 6).

CONCLUSION

The Bornean orangutan is a primate that behaves more arboreal with the hindlimb locomotor doing a lot of flexor digit movements to grip tree branches. Most of the plantar flexor muscles insert on the calcaneus tuber, whereas the digital flexor muscles insert on the proximal and distal phalangeal bones of each digit. The flexor digits of the foot of orangutans are highly

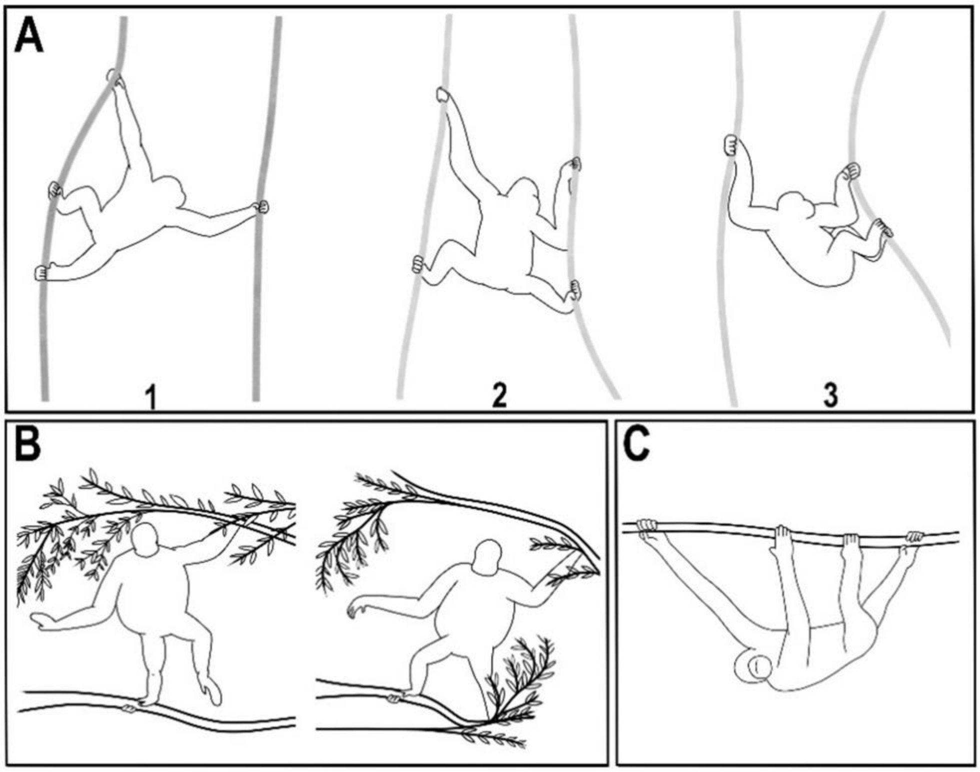

Figure 5. Schematic drawing of some of the arboreal behavior of the Bornean orangutan. A= The process of moving in trees, B= Extended bipedal locomotion type, C= Pronograde posture in arboreal behavior. 1= Pulling a new tree branch with one of the forelimb locomotors 2= One leg pulling a new tree branch 3= The other leg moving to a new tree branch

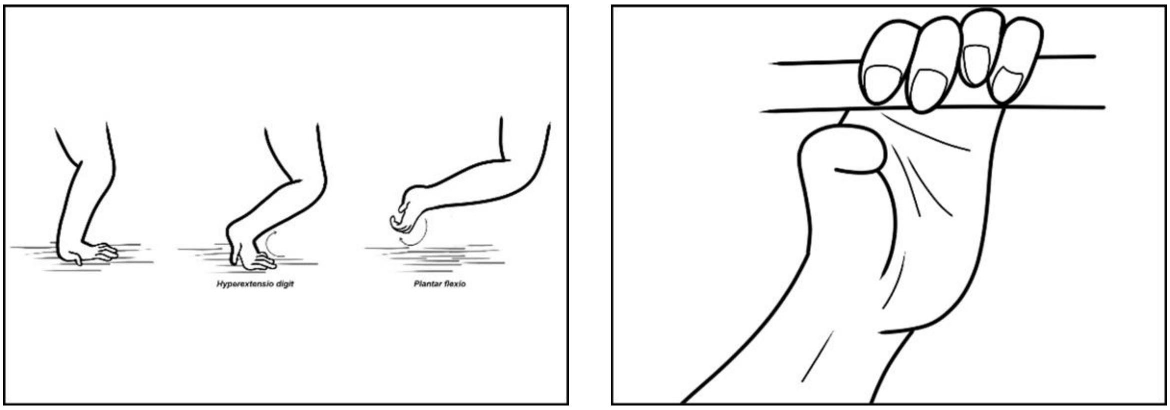

Figure 6. Schematic drawing of the use of the hindlimb locomotor of the Bornean orangutan. A= Terrestrial walking process, B= Hook-like gripping

developed compared to that in other great apes with terrestrial behavior. Orangutan has a rudimentary of the first digit so that they use digits II-V more dominantly when performing arboreal activities. Adult male Bornean orangutans perform terrestrial activities for a certain time so that the size of the extensor digit muscles of adult male Bornean orangutans is relatively more developed than in young orangutan.

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