

Morphofunctional Characteristics of the Pelvic and Thigh Muscles Bornean Orangutan (*Pongo pygmaeus*)

YASMIN N. NARINDRIA, SUPRATIKNO, SAVITRI NOVELINA, DANANG D. CAHYADI,
CHAIRUN NISA', SRIHADI AGUNGPRIYONO, NURHIDAYAT*

Laboratory of Anatomy, Division of Anatomy, Histology, and Embryology, School of Veterinary Medicine and Biomedical Sciences,
IPB University, Bogor

Received: 10 January 2025 – Accepted: 1 August 2025
© 2025 Department of Biology, Cenderawasih University

ABSTRACT

Primates have various type of locomotion according to adaptation to their habitat. Orangutans, gorillas, and chimpanzees are primates belong to the same family, Hominidae. Despite their anatomical and physiological similarities, there are differences in adaptation and life behavior that cause differences in the distinctive anatomical structures of all three hominids. This research aims to study the anatomical characteristics of Bornean orangutans' pelvic and thigh muscles associated with the function and daily behavior. This research was conducted by observing the morphology of the orangutan's pelvic and thigh muscles, also observing the orangutans' arboreal and terrestrial behavior through video observations. The results showed that the pelvic muscles and extensor muscles of the hind limb of the orangutans were less developed than in gorillas and chimpanzees. Orangutans have well-developed *m. scansorius* to compensate the absence of *m. tensor fasciae latae*. *Musculus ischiofemoralis* in orangutans has a unique structure because it is separated into a distinctive muscle. The absence of *m. adductor minimus* is associated with the orangutans' standing posture that more open than in gorillas. The differences in the development of these muscles are due to the adaptation of the orangutans' arboreal behavior to its habitat.

Key words: arboreal; locomotion; orangutan; pelvic and thigh muscles; terrestrial.

INTRODUCTION

Primates have various types of locomotion depending on their adaptation to their environment. Generally, primates have quadrupedal locomotion, although some other primates use different types of locomotion. These types of locomotion include bipedal, brachiation, knuckle walking, and vertical clinging and leaping (Schmitt, 2010). Orangutans are large apes that have predominantly arboreal behavior with a

semi-bipedal type of locomotion (Oishi *et al.*, 2009). Several types of orangutan locomotion have been observed, including quadrupedal, bipedal, and brachiation. Orangutans perform quadrupedal locomotion using all four of their legs, and this type of locomotion is usually used when walking on the ground. Bipedal locomotion in orangutans is performed using both hind legs to walk. Generally, bipedal locomotion is performed when orangutans are carrying something with their front legs/hands. Brachiation using both front legs is performed to swing from one branch to others. This movement utilizes the strength of the upper arm muscles of both arms. Brachiation is generally performed when foraging, playing, or defecating (Muslimah *et al.*, 2020).

The locomotor structure influences the locomotion patterns, habits, and behavior of

* Corresponding Author:

Laboratory of Anatomy, Division of Anatomy, Histology, and Embryology, School of Veterinary Medicine and Biomedical Sciences, IPB University. Jalan Agathis, IPB Dramaga Campus, Bogor 16680, Indonesia. Tel: +62-8128959620. E-mail: nhdayat@apps.ipb.ac.id

primates. Orangutans undergo specific adaptations in both their front and hind legs, resulting in the characteristic locomotion and behavior of orangutans. The muscles in the forelegs of orangutans are more developed than those in the hind legs (Ankel-Simons, 2007). This supports orangutans' movement in trees as predominantly arboreal primates (Oishi *et al.*, 2009). Meanwhile, orangutans' hind legs are used

for bipedal walking and are relatively flexible with strong muscles for gripping tree branches. Orangutans rarely stand bipedally without the aid of hand contact with a nearby surface or object (Tuttle *et al.*, 1979). This is because the hind legs are used more to propel the body forward than to support it. These significant differences in the structure and function of the front and rear locomotor systems are an interesting topic for

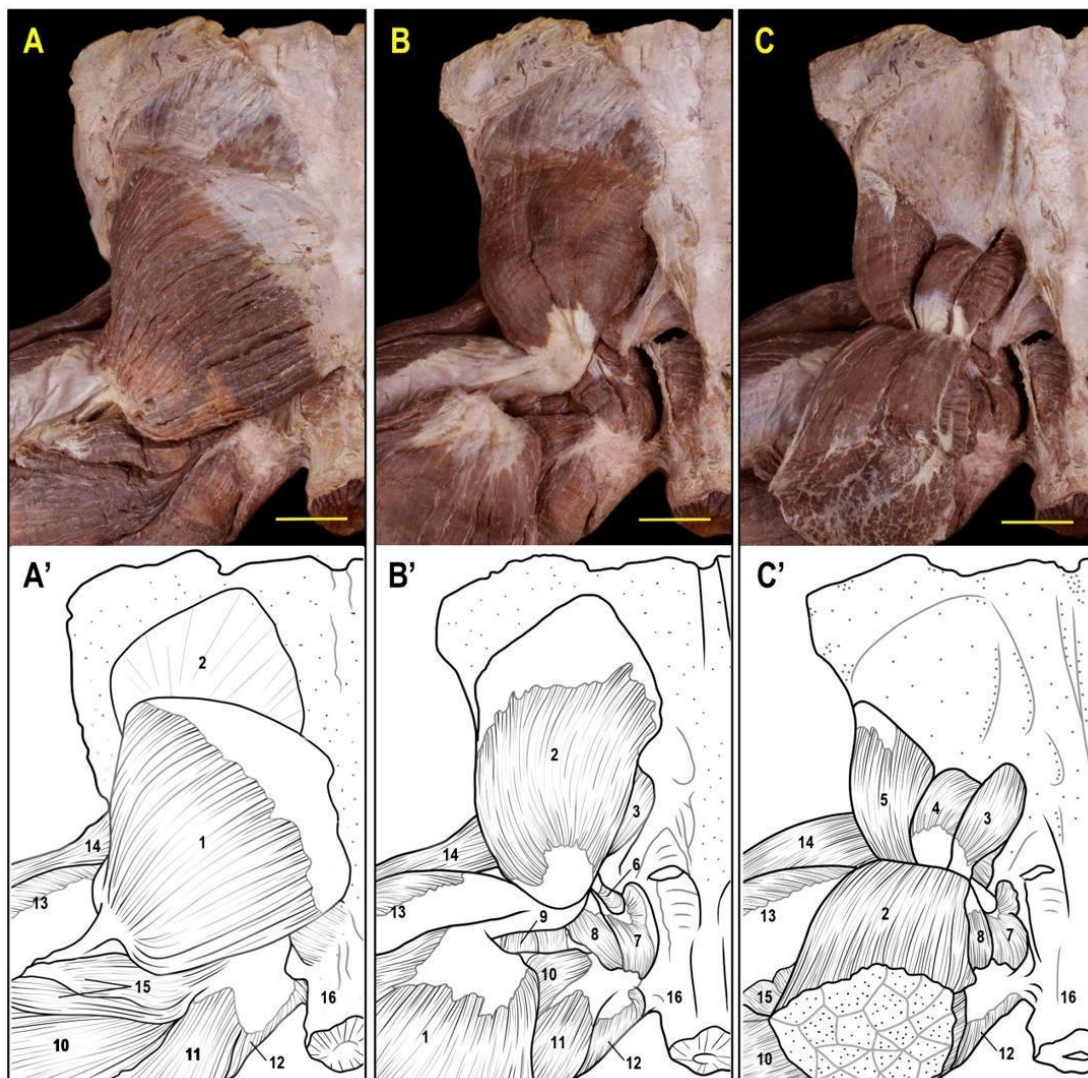


Figure 1. Superficial and deep layers of the pelvic muscles of the Bornean orangutan, viewed dorsally, along with a schematic diagram. A. Superficial layer; B. Deep layer after the *m. gluteus maximus* has been retracted; C. Deep layer after the *m. gluteus medius* has been retracted; Scale bar = 5 cm. Legend: 1. *M. gluteus maximus**, 2. *M. gluteus medius* *, 3. *M. piriformis*, 4. *M. gluteus minimus* *, 5. *M. scansorius***, 6. *M. gemellus superior**, 7. *M. obturatorius internus*, 8. *M. gemellus inferior**, 9. *M. quadratus femoris*, 10. *M. biceps femoris*, 11. *M. semitendinosus*, 12. *M. adductor magnus*, 13. *M. vastus lateralis*, 14. *M. rectus femoris*, 15. *M. ischiofemoralis***, 16. anus. Naming based on: *FIPAT (2019), **Diogo *et al.* (2013a).

further study. Therefore, research on the structure of the pelvic and thigh muscles of Bornean orangutans (*Pongo pygmaeus*) is important to determine the relationship between the rear locomotor structure of orangutans and their behavior and type of locomotion. In addition, this research 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

Place and Time of Research

This research was conducted at the Anatomy Laboratory, Division of Anatomy, Histology, and Embryology, School of Veterinary Medicine and Biomedical Sciences, IPB University from January–May 2023.

Research Procedure

Muscle morphology observation

This study used a set of pelvic and thigh specimens from adult male Bornean orangutans preserved in 10% formalin. The specimens were obtained from the Pathology Division of SKHB IPB. The specimens were opened by incising the skin on the dorsomedial side to the caudal part of the pelvic. The incision was continued to the distal knee joint, then a circular incision was made around the distal knee area. The skin was reflected and the fatty tissue and loose connective tissue located in the profundal skin were removed. The pelvic and thigh muscles were observed from the dorsal, cranial, lateral, and medial views in the superficial and deep layers. The parameters observed were the characteristic structures of the pelvic and thigh muscles in adult Bornean orangutans. Photographs of the morphological observations of the pelvic and thigh muscles were taken using a Canon® EOS 700D camera.

Observation of hind leg function

The observation of orangutan hind leg function was conducted exploratively through video observation of the behavior and daily activities of orangutans and other great apes, accessed on the YouTube platform as follows: Orangutan – Man of the Forest HD (Heiman, 2014),

A Rare Look at the Secret Life of Orangutans (National Geographic, 2018), and Orangutan: King of the Treetops (Animalogic, 2018). The parameters observed were the main arboreal and terrestrial activities related to the use of the pelvic and thigh muscles.

Data analysis

The results of muscle morphology photographs and video observations of orangutan behavior were schematically drawn and processed using Adobe® Photoshop 2021 software. The pelvic and thigh muscles were named based on Nomina Anatomica Veterinaria (ICVGAN, 2017) and other literature. These muscles were analyzed descriptively and comparatively with other great ape species, such as gorillas and chimpanzees.

RESULTS AND DISCUSSION

Orangutans are arboreal primates that use their forelegs more as their primary means of locomotion than their hind legs, although Bornean orangutans have a higher frequency of terrestrial locomotion than Sumatran orangutans (Kralick *et al.*, 2024). Based on research, there are several differences in the characteristics of the limb muscles in orangutans compared to other great apes (Oishi *et al.*, 2018; Kartjito *et al.*, 2022; Pietrobelli *et al.*, 2024), including the abundance of the iliopubic eminence associated with the *musculus adductor longus* (Shearer *et al.*, 2019). The most developed muscles in the dorsal pelvis consist of the gluteal muscle group, especially the *m. gluteus maximus* (Figure 1). This muscle is thin and wide, covering almost the entire dorsal pelvic region. The proximal part of this muscle is thinner than the distal part. The *m. gluteus maximus* has an insertion at the cranial third of the lateral side of the femur, so this muscle works to perform thigh extension by pulling the femur until it is parallel to the body. The *m. gluteus medius* is located just deep to the *m. gluteus maximus* (Figure 1).

This muscle is relatively thinner in the cranial region, while the caudal region of this muscle is relatively thicker, and inserts laterally from the

greater trochanter (*trochanter major*). So that when this muscle contracts, it works synergistically with the *m. gluteus maximus* as a thigh extensor. In addition, the *m. gluteus medius*, together with the *m. gluteus minimus*, plays a role in supporting the stability of the pelvis and body when lifting the leg during walking (Warwick & Williams, 1973; Gottschalk *et al.*, 1989). The *m. gluteus minimus* is fan-shaped and inserts into the *trochanter major* (Figure 1). This muscle, together with the *m. gluteus medius*, abducts the hind leg. The pelvic muscles of orangutans are relatively less

developed than those of gorillas and chimpanzees, which are more terrestrial. This is because these muscles play a lesser role in supporting the arboreal behavior of orangutans. Larger primates require larger and stronger leg muscle structures than those needed for fast movement, especially the hind legs, which have relatively short muscle fascicles to generate greater force (Marchi *et al.*, 2018).

Generally, the balance of primates when walking is supported by the presence of the *m. tensor fasciae latae*, but in this study, this muscle

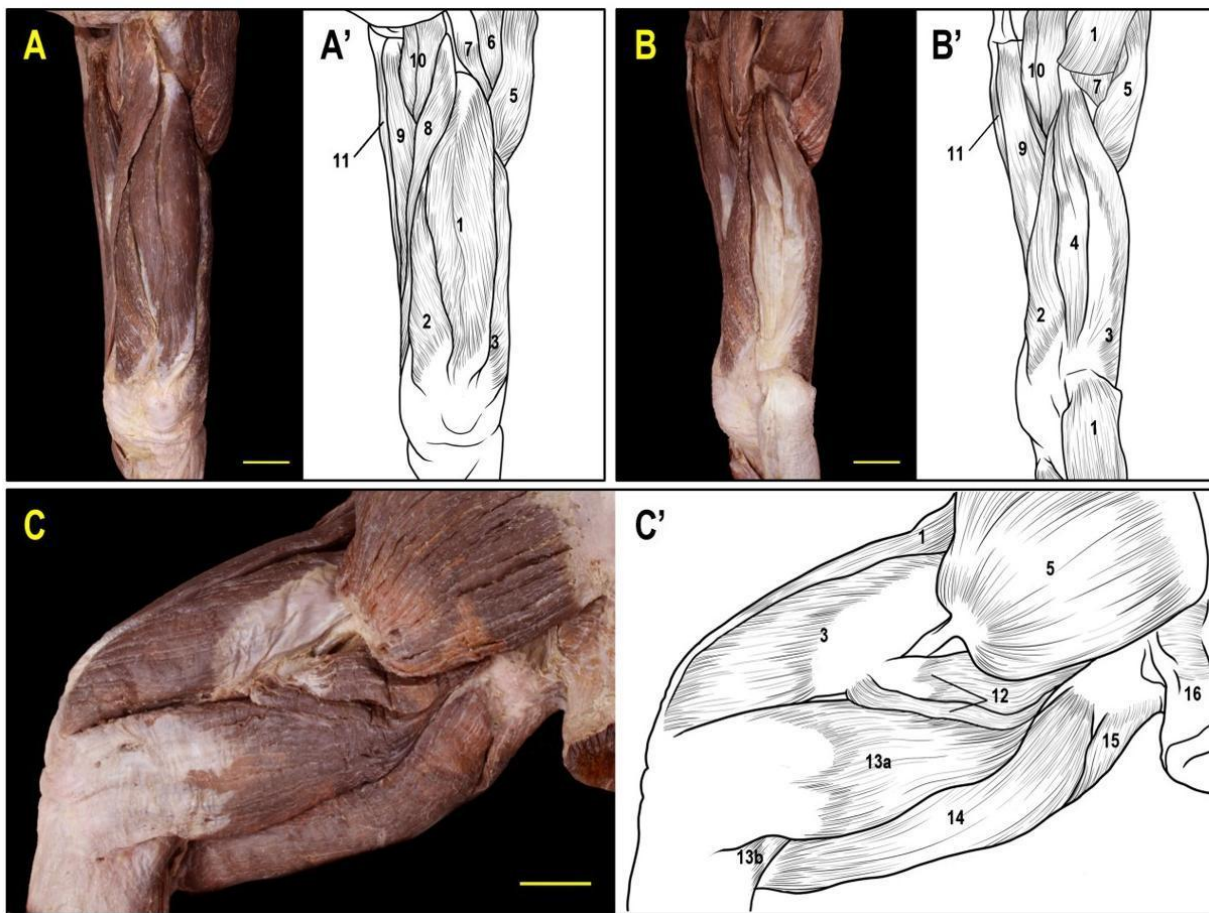


Figure 2. The superficial and deep layers of the thigh muscles of the Bornean orangutan, viewed cranially and laterally, along with a schematic diagram. A. Cranial view of the superficial layer; B. Cranial view of the deep layer after the *m. rectus femoris* has been retracted; C. Lateral view; Scale bar = 5 cm. Legend: 1. *M. rectus femoris*, 2. *M. vastus medialis*, 3. *M. vastus lateralis*, 4. *M. vastus intermedius*, 5. *M. gluteus maximus**, 6. *M. gluteus medius**, 7. *M. scansorius***, 8. *M. sartorius*, 9. *M. adductor longus*, 10. *M. iliacus*, 11. *M. gracilis*, 12. *M. ischiofemoralis***, 13a. *M. biceps femoris caput longum*, 13b. *M. biceps femoris caput brevis*, 14. *M. semitendinosus*, 15. *M. adductor magnus*, 16. Anus. Naming based on: *FIPAT (2019), **Diogo *et al.* (2013a).

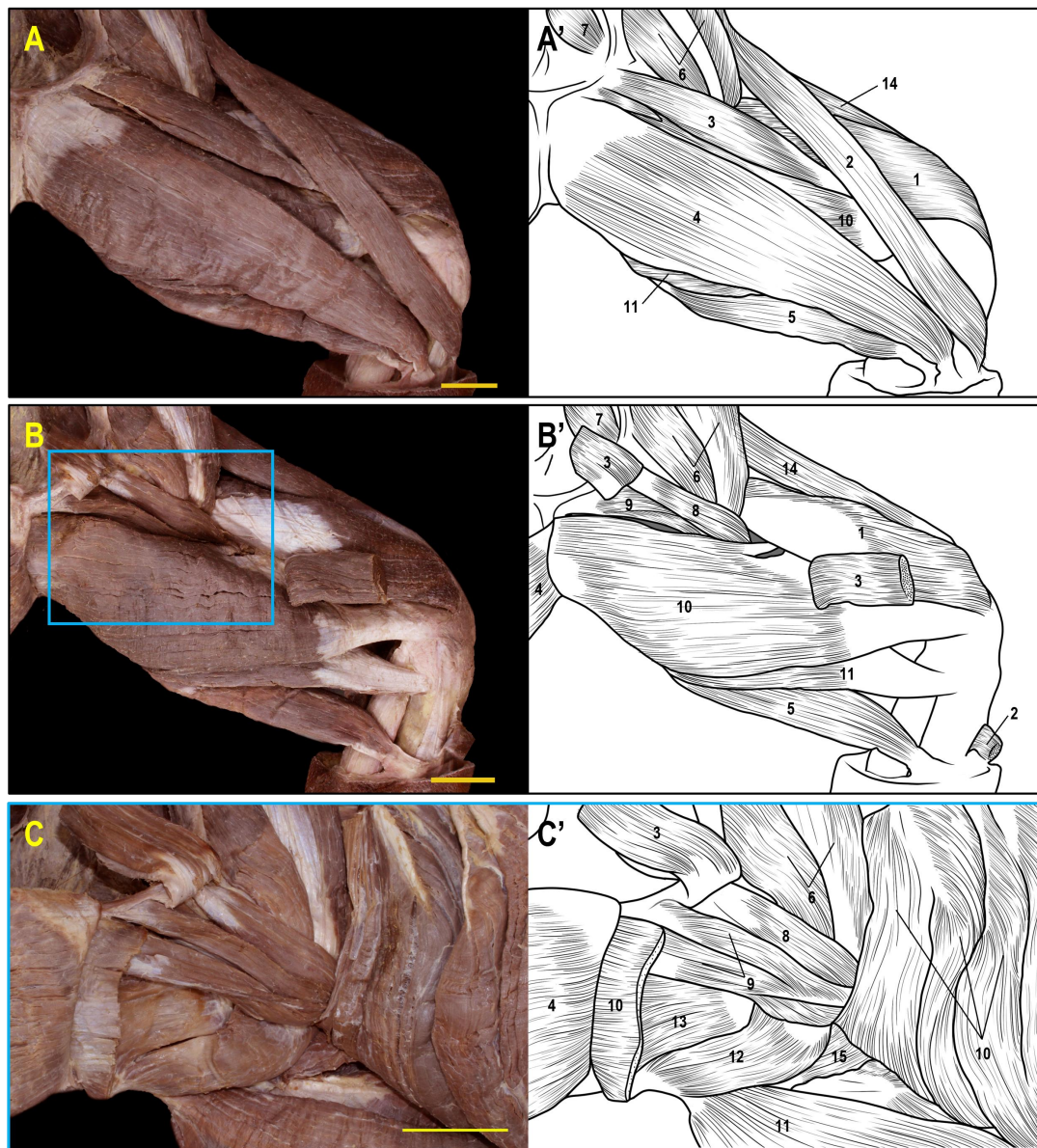


Figure 3. The superficial and deep layers of the thigh muscles of the Bornean orangutan are shown medially, along with a schematic diagram. A. Medial view of the superficial layer; B. Medial view of the deep layer after the *m. sartorius*, *m. adductor longus*, and *m. gracilis* have been retracted; C. Medial view of the deep layer after the *m. adductor magnus* has been retracted; Scale bar = 5 cm. Legend: 1. *M. vastus medialis*, 2. *M. sartorius*, 3. *M. adductor longus*, 4. *M. gracilis*, 5. *M. semitendinosus*, 6. *M. iliacus*, 7. *M. piriformis*, 8. *M. pectineus*, 9. *M. adductor brevis*, 10. *M. adductor magnus*, 11. *M. semimembranosus*, 12. *M. quadratus femoris*, 13. *M. obturatorius externus*, 14. *M. rectus femoris*, 15. *M. ischiofemoralis***. Naming based on: **Diogo *et al.* (2013a).

was not found. According to Diogo *et al.* (2013a), the *m. tensor fasciae latae* in orangutans is underdeveloped and rarely found. With the absence of the *m. tensor fasciae latae*, when walking

bipedally, orangutans rarely stand stably, so that their front legs or arms usually hold on to surrounding objects (Tuttle *et al.*, 1979). Although the *m. tensor fasciae latae* was not found, the

function of this muscle is thought to be replaced by the *m. scansorius*, which is more developed than in gorillas and chimpanzees. This is thought to be a compensation for the absence of the *m. tensor fasciae latae*, which plays a role in thigh flexion (Sigmon, 1969) and balancing body weight when standing and walking (Gottschalk *et al.*, 1989). The *m. scansorius* is a triangular-shaped muscle with a relatively flat surface. This muscle is located deep within the *m. gluteus medius* and runs along the lateral edge of the ilium (Figure 1). In gorillas and chimpanzees, the *m. scansorius* is rarely found as a separate muscle (Diogo *et al.*, 2010; Diogo *et al.*, 2013b). This is because both species have a relatively well-developed *m. tensor fasciae latae*, so the *m. scansorius* is not significant in replacing the function of the *m. tensor fasciae latae*.

The abduction function of the hind leg is supported by the role of the *m. piriformis*. This muscle is located on the dorsal ilium, which is more medial than the *m. gluteus minimus* and *m. scansorius* (Figure 1). The abduction movement of the femur is very important for shifting the body's weight to the opposite side and preventing falls. In addition to supporting abduction, the *m. piriformis* also plays a role in rotating the hind leg laterally together with the *m. gemellus superior et inferior*, the *m. obturatorius internus et externus*, and the *m. quadratus femoris* (Chang *et al.*, 2023). The lateral rotation of the hind leg plays a role in the flexibility of orangutans when moving and swinging in trees. These muscles rotate the orangutan's hind legs laterally so that the hind legs open and extend the reach of the feet to grasp the surrounding tree branches. With these muscles, the orangutan's hind legs become very flexible for grasping and moving from one tree branch to another.

The posterior leg flexor muscles are composed of the *m. ischiofemoralis*, *m. biceps femoris*, and *m. semitendinosus* on the lateral side (Figure 2), and the *m. semimembranosus*, *m. sartorius*, and *m. gracilis* on the medial side (Figure 3). In general, these flexor muscles act as extensors of the hip joint and flexors of the knee joint. The *m. ischiofemoralis* in orangutans is unique because it appears as a separate muscle from the *m. gluteus maximus*. This

muscle in orangutans is thought to help strengthen the flexor muscle group to reach tree branches during arboreal movement. In chimpanzees, this muscle is still found to be fused and is considered part of the posterior portion of the *m. gluteus maximus* (Kaseda *et al.*, 2008), while in gorillas this muscle is not found.

The *m. biceps femoris* in orangutans has two heads, namely the long head (*caput longum*) and the short head (*caput brevis*) (Figure 2). The *caput longum* inserts into the *caput tibia*, while the *caput brevis* inserts into the *caput fibula* and the *fascia cruris*. The insertion location of the *m. biceps femoris* indicates the role of this muscle in lateral knee flexion, while medial knee flexion is performed by the *m. sartorius*, *m. gracilis*, *m. semitendinosus*, and *m. semimembranosus*. The role of the posterior leg flexor muscles is essential for orangutans during arboreal activities. These muscles in orangutans serve to bring closer the tree branches they reach for. This is consistent with the research by Tuttle *et al.* (1979) that the *m. biceps femoris* plays a role in helping orangutans climb and move from one tree to another as well as during bipedal walking. In addition, the developed hamstring muscles in orangutans are related to this animal's standing activity. When standing, orangutans' knees appear bent due to several flexor muscles that insert distally at the knee joint.

The extensor muscles of the hind leg are composed of the *m. quadriceps femoris*, which consists of the *m. rectus femoris*, *m. vastus lateralis*, *m. vastus intermedius*, and *m. vastus medialis* (Figure 2). These muscles are well developed, but relatively smaller than the flexor muscles of the hind leg. These muscles work synergistically to extend the knee joint and protract the hind leg. The hind limb protraction movement is performed by lifting the leg and directing it forward during bipedal walking and climbing. The *m. rectus femoris* assists the terrestrial movement of this animal during bipedal walking. During the bipedal walking process, the *m. rectus femoris* works antagonistically with the *m. biceps femoris* (Tuttle *et al.*, 1979).

The antagonistic action of the *m. rectus femoris* and *m. biceps femoris* also plays a role in the

arboreal activities of orangutans when reaching for branches to move. The orangutan's hind legs extend when reaching for tree branches, and then flex when the branches are brought closer (Figure 4). The extension and protraction of the hind legs are reinforced by the *m. vastus lateralis et medialis* and *m. vastus intermedius*. The *m. vastus lateralis* plays a role when orangutans straighten their legs

while climbing. Orangutans rarely use their thighs to grip tree trunks while climbing, so the *m. vastus medialis* is relatively less developed than the *m. vastus lateralis*. According to Zihlman *et al.* (2011), the extensor muscles play a role in generating strong propulsive force on the ground. Therefore, in gorillas, the extensor muscles of the hind legs are relatively more developed than in orangutans,

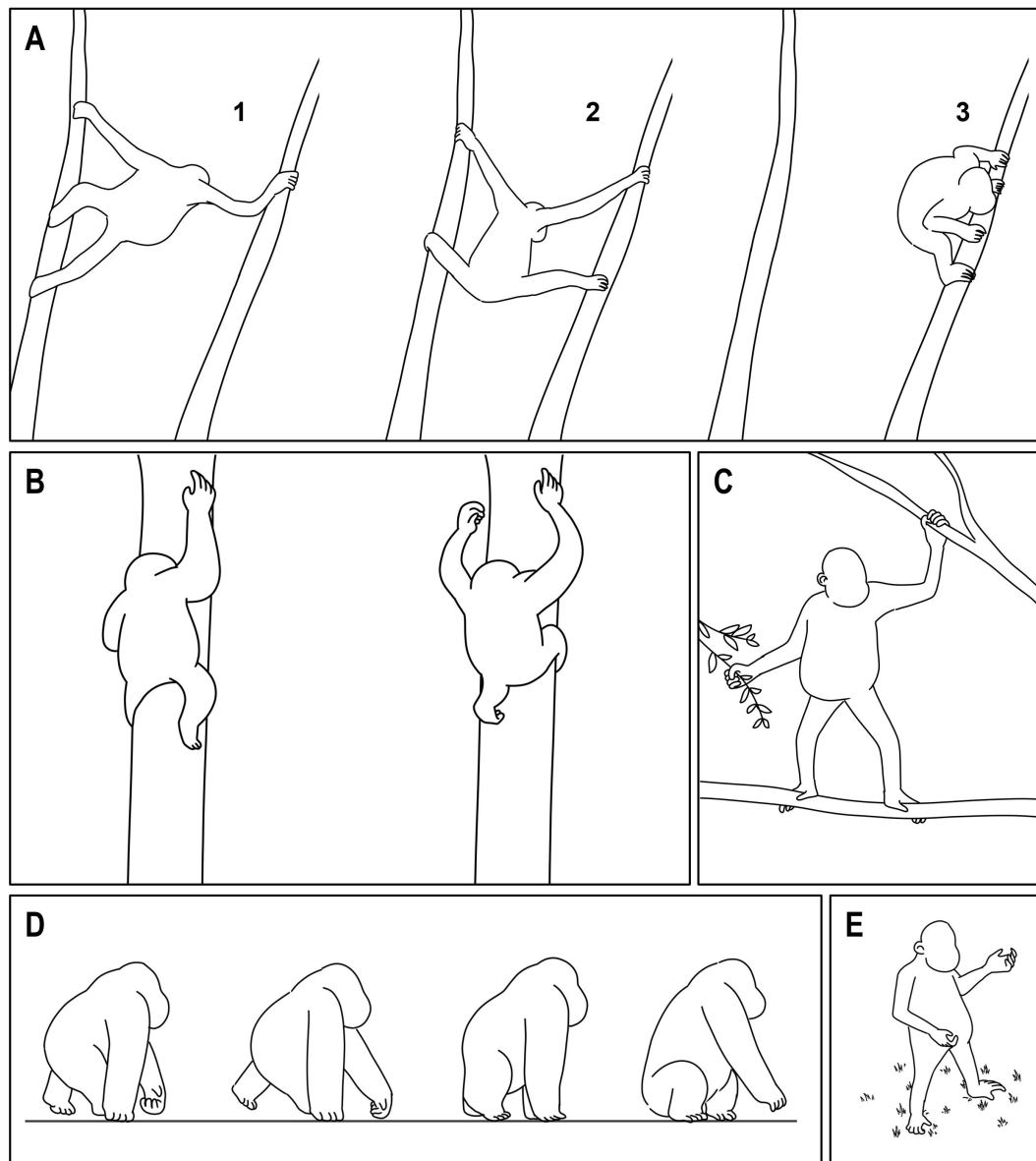


Figure 4. Arboreal and terrestrial behavior of Bornean orangutans. A. Brachiation movement (Heiman, 2014). B. Climbing process (Heiman, 2014). C. Bipedal position on a tree (National Geographic, 2018). D. Quadrupedal position when walking (Heiman, 2014). E. Bipedal position on the ground (Animalogic, 2018). Description: 1. Body leaning forward and one arm reaching for a tree branch, 2. Front and rear limbs grasping the tree branch, 3. Orangutan moving to the next tree branch.

which live arboreally. The adductor muscles of orangutans are composed of the *m. adductor longus*, *m. adductor magnus*, *m. adductor brevis*, and *m. pectineus* (Figure 3). In this study, no *m. adductor minimus* was found, whereas in gorillas, a more developed *m. adductor minimus* was found (Raven *et al.*, 1950). The *m. adductor minimus* in orangutans and chimpanzees is generally not found and is often referred to as part of the *m. adductor magnus* (Diogo *et al.*, 2013a; Diogo *et al.*, 2013b). The absence of the *m. adductor minimus* in orangutans is thought to cause the hind legs to be more open and farther apart (Figure 4). In addition, the wide stance of orangutans serves to distribute body weight across both hind legs due to the bent knee position. This differs from gorillas, which have a well-developed *m. adductor minimus*. The hind legs of gorillas appear relatively more closed and closer to each other.

CONCLUSION

In general, the structure of orangutan pelvic and thigh muscles is similar to that of gorillas and chimpanzees. Orangutan pelvic muscles are relatively less developed than those of gorillas and chimpanzees, which are more terrestrial. The *m. tensor fasciae latae* is not found, and the function of this muscle is thought to be replaced by the *m. scansorius*, which is more developed than in gorillas and chimpanzees. The flexibility of orangutans during arboreal activities is supported by the rotator, extensor, and abductor muscles of the hind legs. The *m. ischiofemoralis* is unique to orangutans and appears as a separate muscle from the *m. gluteus maximus*. The hind leg extensor muscles of orangutans are relatively less developed than those of gorillas and chimpanzees because extensor muscles are more active during terrestrial movement. The *m. adductor minimus* is not found in orangutans, which is related to the more open standing posture of orangutans compared to gorillas.

REFERENCES

- [FIPAT] Federative International Programme for Anatomical Terminology. 2019. *Terminologia anatomica*. 2nd ed. Dalhousie University Libraries. Halifax.
- [ICVGAN] International Committee on Veterinary Gross Anatomical Nomenclature. 2017. *Nomina anatomica veterinaria*. 6th ed. Editorial Commite of WAVA. Hannover.
- Animalogic. 2018. Orangutan: King of the Treetops [Internet]. [Accessed: Jun 9, 2023]. Available from: <https://www.youtube.com/watch?v=1Y4uCrG6Bo8&t=300s>.
- Ankel-Simons, F. 2007. *Primate anatomy an introduction* 3rd Edition. Academic Press. London.
- Chang C, Jen SH, Varacallo MA. 2023. Anatomy, Bony Pelvis and Lower Limb: Piriformis Muscle. [Updated 2023 Nov 13]. In: StatPearls [Internet]. Treasure Island (FL): StatPearls Publishing; 2025 Jan-. Available from: <https://www.ncbi.nlm.nih.gov/books/NBK519497/>
- Diogo, R., J.M. Potau, J.F. Pastor, F.J. de Paz, E.M. Ferrero, G. Bello, M. Barbosa, and B.A. Wood. 2010. *Photographic and descriptive musculoskeletal atlas of gorilla*. CRC Press. New York.
- Diogo, R., J.M. Potau, J.F. Pastor, F.J. de Paz, E.M. Ferrero, G. Bello, M. Barbosa, M.A. Aziz, J. Arias-Martorell, and B.A. Wood. 2013a. *Photographic and descriptive musculoskeletal atlas of orangutans*. CRC Press. New York.
- Diogo, R., J.M. Potau, J.F. Pastor, F.J. de Paz, E.M. Ferrero, G. Bello, M. Barbosa, M.A. Aziz, J. Arias-Martorell, A.M. Burrows, et al. 2013b. *Photographic and descriptive musculoskeletal atlas of chimpanzees*. CRC Press. New York.
- Gottschalk F., S. Kourosh, and B. Leveau. 1989. The functional anatomy of tensor fasciae latae and gluteus medius and minimus. *Journal of Anatomy*. 166: 179-189.
- Heiman, F. 2014. Orangutan-Man of the Forest HD [Internet]. [Accessed: Jun 9, 2023]. Available from: <https://www.youtube.com/watch?v=lZYWfoQ3tjg&t=729s>.
- Kartjito, N. E. C., I. Kadarusman, S. Novelina, C. Nisa', S. R. Laila, D.D. Cahyadi, and Nurhidayat. 2022. Morphofunctional characteristics of the lower hindlimb and foot muscles of Bornean orangutan (*Pongo pygmaeus*). *Indonesian Journal of Veterinary Science/Jurnal Kedokteran Hewan*. 16(4): 132-138. DOI:10.21157/j.ked.hewan.v16i4.28199.
- Kaseda, M., M. Nakamura, N. Ichihara, T. Hayakawa, and M. Asari. 2008. A macroscopic examination of m. biceps femoris and m. gluteus maximus in the orangutan.

- Journal of Veterinary Medical Science*. 70(3): 217-222. DOI:10.1292/jvms.70.217.
- Kralick, A.E., B.S. Zemel, C. Nolan, P. Lin, and M. W. Tocheri. 2024. Relative leg-to-arm skeletal strength proportions in orangutans by species and sex. *Journal of Human Evolution*. 188: 103496. DOI:10.1016/j.jhevol.2024.103496.
- Marchi, D., C. L. Leischner, F. Pastor, dan A. Hartstone-Rose. 2018. Leg muscle architecture in primates and its correlation with locomotion patterns. *The Anatomical Record*. 301(3): 515-527. DOI:10.1002/ar.23745.
- Muslimah, N.U., T. Widiyanti, and A. Budiharjo. 2020. Studi perilaku harian dan tingkat kesejahteraan orangutan kalimantan (*Pongo pygmaeus* Linnaeus, 1760) di Taman Satwa Taru Jurug (TSTJ), Kota Surakarta. *Zoo Indonesia*. 29(1): 1-18. DOI:10.52508/zi.v29i1.3975.
- National Geographic. 2018. A rare look at the secret life of orangutans [Internet]. [Accesed: Feb 16, 2023]. Available from: https://www.youtube.com/watch?v=0fts6x_EE_E&t=606s.
- Oishi, M., N. Ogihara, D. Shimizu, Y. Kikuchi, H. Endo, Y. Une, S. Soeta, H. Amasaki, and N. Ichihara. 2018. Multivariate analysis of variations in intrinsic foot musculature among hominoids. *Journal of Anatomy*. 232(5): 812-823. DOI:10.1111/joa.12780.
- Oishi, M., N. Ogihara, H. Endo, N. Ichihara, and M. Asari. 2009. Dimensions of forelimb muscles in orangutans and chimpanzees. *Journal of Anatomy*. 215(4): 373-382. DOI:10.1111/j.1469-7580.2009.01125.x.
- Pietrobelli, A., R. Sorrentino, S. Benazzi, M.G. Belcastro, and D. Marchi. 2024. Linking the proximal tibiofibular joint to hominid locomotion: A morphometric study of extant species. *American Journal of Biological Anthropology*. 184(2): e24696. DOI:10.1002/ajpa.24696.
- Raven, H.C., W.B. Atkinson, H. Elftman, J.E. Hill, A.H. Schultz, W.L. Straus Jr., and S.L. Washburn. 1950. *The Henry Cushier Raven memorial volume: the anatomy of the gorilla*. W.K. Gregory, editor. Columbia University Press. New York.
- Schmitt, D. 2010. Primate locomotor evolution: biomechanical studies of primate locomotion and their implication for understanding. In: Platt, M.L., dan A.A. Ghazanfar (Editor). *Primate neuroethology*. Oxford University Press. Oxford.
- Shearer, B. M., M. Muchlinski, and A.S. Hammond. 2019. Large pelvic tubercle in orangutans relates to the adductor longus muscle. *PeerJ*. 7: e7273. DOI:10.7717/peerj.7273.
- Sigmon, B.A. 1969. The scansorius muscle in pongids. *Primates*. 10: 247-261. DOI:10.1007/BF01730346.
- Tuttle, R.H., J.V. Basmajian, H. Ishida. 1979. Activities of pongid thigh muscles during bipedal behavior. *American Journal of Physical Anthropology*. 50: 123-136. DOI:10.1002/ajpa.1330500113.
- Warwick, R., and P.L. Williams. 1973. *Gray's anatomy*. 35th edition. Saunders Company. Philadelphia.
- Zihlman, A.L., R.K. McFarland, and C.E. Underwood. 2011. Functional anatomy and adaptation of male gorillas (*Gorilla gorilla gorilla*) with comparison to male orangutans (*Pongo pygmaeus*). *Anatomical Record*. 294: 1842-1855. DOI:10.1002/ar.21449.