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The Foot Musculature of the Rhesus Monkey (*Macaca mulatta*): An Anatomical Study

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Abstract: The rhesus monkey (*Macaca mulatta*) is a non-human primate with a genome that is 93.5% identical to that of humans. Both species, therefore, have numerous phenotypical similarities in common. Consequently, this non-human primate is regularly studied in biomedical research. Not only does the rhesus monkey play an important role as an animal model for studying human disease, but it is also often featured in zoos, and there are substantial feral populations that live in Asia. Since they are exploited as research subjects, their appropriate housing and husbandry and the validation of obtained research data benefit from the comprehension of the rhesus monkey anatomy. Unexpectedly, the number of anatomical documents on the rhesus monkey are largely outnumbered by publications on the anatomy of domestic animals. In addition, the limited number of available anatomical books and atlases are, unfortunately, outdated, e.g., by presenting black-and-white photographs and using archaic nomenclature, or failing to cover the in-depth anatomy of various anatomical systems. Since state-of-the-art data on the rhesus monkey anatomy are requested by biomedical researchers and veterinarians responsible for the daily care of these captive animals, the present study describes the musculature of the foot of the rhesus monkey. It builds on a recently published manuscript on the topographical anatomy of the pelvic limb of this non-human primate. Full-color anatomical (stereomicroscopic) photographs are taken during layer-by-layer dissections of the feet of three rhesus monkeys. All the muscles, from the superficial to the deepest layer, are described using veterinary anatomical nomenclature and annotated on multipaneled figures. Although the foot musculature of the rhesus monkey largely parallels that of its human counterparts, the small number of dissimilarities should be recognized when extrapolating these research data. In addition, a solid understanding of the rhesus monkey anatomy by veterinarians can be valuable during medical interventions, such as surgery for foot injuries.

Keywords: anatomy; musculature; foot; rhesus monkey

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1. Introduction

The close phylogenetic relationship between the rhesus monkey (*Macaca mulatta*) and humans (*Homo sapiens*) is reflected in the high degree of anatomical and physiological similarities between these species [1]. Colonies of feral rhesus monkeys inhabit the southern, southeastern, and central parts of Asia, but this Old World non-human primate (NHP) also lives in research facilities and zoos worldwide [2,3]. As the number one NHP species used in biomedical research, the rhesus monkey functions as an animal model for the unraveling of many human pathologies [4]. The number of biomedical studies in which the rhesus monkey has played a pivotal role is countless [5]. Yet, comprehensive publications on the anatomy of the rhesus monkey are sparse. Sound knowledge of the morphology of the

rhesus monkey is, however, a prerequisite for the correct interpretation of research data and the accuracy of experimental procedures. For example, when the rhesus monkey foot (*pes*) serves as a model for the human foot during the finetuning of surgical procedures, the foot anatomy of both species should be understood [6]. In addition, anatomical expertise is essential for the medical treatment of diseased or wounded animals [7]. The foot is an anatomically complex body part that is frequently exposed to mechanical forces. It is, therefore, often injured during certain physical activities. As a result, medical attention is frequently required. Finally, the appropriate housing and husbandry of the captive rhesus monkey rely on the comprehension of its anatomy [8,9].

With regard to reference works on the rhesus monkey anatomy, Hartman and Straus [10], Szebenyi [11], and Berringer et al. [12] delivered excellent contributions in the years 1933, 1967, and 1974, respectively. However, these works also have their limitations. Since the atlases are at least 50 years old, no modern techniques or color photography (both macroscopic and stereomicroscopic) in casu were applied for the visualization of structures. The work by Hartman and Straus [10] is a textbook with extended textual descriptions of various anatomical structures. Regrettably, the number of supporting illustrations is restricted. Indeed, the foot musculature is only visualized by the means of two illustrations, i.e., a figure of the superficial plantar muscles and one of the deeper plantar muscles. More muscle layers should be presented to allow for the textbook to be used as a dissection guide. Moreover, all illustrations consist of black-and-white line drawings that fail to reveal anatomical details. This sometimes results in doubtful identifications during dissections. On the other hand, the 'idealization' of dissected specimens that is offered by line drawings is preferred over black-and-white photographs.

Black-and-white photographs are displayed in the atlas by Berringer et al. [12]. More specifically, seven images are shown, i.e., a lateral and medial view of the ankle, a superficial and deep dorsal view of the foot, and one superficial and two deeper plantar views of the foot. These images are accompanied by concise textual descriptions of the foot muscles. Although the dissections were meticulously performed by the authors, studying these black-and-white photographs is challenging, since the contrast between adjacent structures is low. In addition, the three-dimensional organization of overlying structures is difficult to interpret.

The Szebenyi atlas presents seven colored line drawings of the musculature of the rhesus monkey foot, i.e., two dorsal views and five plantar views [11]. Therefore, it better fulfils its task in guiding the investigator through the dissection compared to the work by Hartman and Straus [10]. In contrast to the latter work, a textual description of the muscles is absent. In this respect, the atlas by Berringer and colleagues [12] is more valuable, as it finds a fair balance between text and figures. In addition to the lack of color photographs in these three works and the imbalance between the amount of text and the number of figures in the contributions by Hartman and Straus [10] and Szebenyi [11], these works do not consistently use contemporary veterinary nomenclature as officialized in the Nomina Anatomica Veterinaria (N.A.V.) [13].

Another interesting title for researchers working with rhesus monkeys was published in 1975 by Bourne [8,9]. This textbook presents, among other features, numerous data on the allometry of the organs and tissues, histology, management, reproduction, and pathology of the rhesus monkey. Gross anatomists interested in the rhesus monkey anatomy will not find it useful, since an elaboration of the rhesus monkey anatomy by the means of cadaver dissections is not included, despite the suggestion made by the title of the first volume [8]. Also, the latest edition of the title "Primate Anatomy" by Ankel-Simons [14] does not meet expectations when consulting the book in search for data on the rhesus monkey anatomy. It describes the anatomy of the rhesus monkey only fragmentarily. More precisely, the skull, the brain, the teeth, the postcranial skeleton, the viscera, the sense organs, and the reproductive organs are included. The muscular system is, unfortunately, not depicted. In contrast, the muscles of the rhesus monkey are portrayed in a contemporary book chapter by Casteleyn and Bakker [15]. Although it shows many color photographs, the number of photographs of the foot is limited, since the book chapter only offers the essentials for

biomedical researchers. A superficial and deeper dorsal view and a superficial and deeper plantar view are displayed. More details on the foot musculature of the rhesus monkey can be found in the recent manuscript entitled *Topographical anatomy of the rhesus monkey (Macaca mulatta)—Part II: Pelvic limb* [16]. Here, the left lateral, the right lateral, the dorsal, and two plantar views, i.e., the superficial and the deeper layer of the plantar musculature, are shown.

The aim of the present work is to elaborate further on the foot musculature of the rhesus monkey. From a veterinary point of view, it is expected that the foot musculature in the rhesus monkey is more complex compared with that in the common domestic mammals that are included in the N.A.V. [13], i.e., rabbit, cat, dog, pig, ox, sheep, goat, and horse. None of these species contain five functional digits on the hind foot. The small domestic mammals lack the first digit—a regressed hallux or dew claw (sometimes double or even triple) can be present in some dog breeds [17]. The pig sees an additional reduction in the second and fifth digits, which only support the body in loose and muddy soil. These digits are further reduced in ruminants and are dysfunctional. In addition, the metatarsal bones III and IV are fused. Finally, the horse foot contains a single digit, i.e., digit III. Only reduced metatarsal bones remain from digits II and IV [18]. When compared to humans, it is likely that the anatomy of the rhesus monkey foot is more complicated. In particular, the anatomy of the first digit (*digitus primus/I* or *hallux*) is strongly adapted to its role in locomotion and grasping [19]. Adult rhesus monkeys present quadrupedal locomotion, both digitigrade and plantigrade, 70% of the time [20], in contrast to the plantigrade bipedal human [21]. This bipedality resulted in the loss of the grasping function of the human hallux during evolution. Moreover, the morphology of the human foot has undergone alterations that enhance propulsion during walking [22]. Obviously, plantigrade locomotor behaviors require more stability in the foot, with a reduction in flexibility. The responsible anatomic changes show the trade-offs between flexibility and stability in the foot.

To gain insight into the musculature of the rhesus monkey foot, it was dissected layer-by-layer and color photographs of state-of-the-art anatomical dissections were taken as a tool for further investigations. In the discussion, we shed light on our results from a comparative point of view. The rhesus monkey foot was compared with the human foot and the hind foot of small domestic mammals. This will allow for the correct use of the data in translational research. The results can also be valuable in comparative studies among several NHP species. Finally, they may be consulted during the medical care of injured rhesus monkeys. Since this task is primarily delegated to veterinarians, who generally are not trained in primate anatomy during their studies, the present manuscript could play a role in their anatomical education. This manuscript provides an easily accessible source of contemporary anatomical data on the rhesus monkey anatomy, illustrated by the means of numerous color photographs, which can serve as a practical guide during dissections.

2. Materials and Methods

2.1. Animals

The remains of three adult rhesus monkeys, two females and one male, were obtained from the Biobank of the Biomedical Primate Research Centre (BPRC), Rijswijk, The Netherlands (https://www.bprc.nl/en/biobank, last accessed on 28 June 2024). The materials for the Biobank were collected at necropsy from healthy animals that were euthanized for reasons unrelated to this study. After transportation to the Faculty of Veterinary Medicine, Ghent University, Belgium, their remains were stored at −20 °C. They were thawed at room temperature to allow for the anatomical dissections.

2.2. Dissection and Imaging

Each of the six pelvic limbs was amputated and skinned. The foot was dissected layer-by-layer on both its dorsal side (*dorsum pedis*) and its plantar side (*planta pedis*) using the works on the anatomy of the rhesus monkey that were reviewed in the introduction as a guideline [10–12]. Although the results presented below are based on six feet, i.e., three

left and three right feet, photographs were only taken of the left feet, as the musculoskeletal system is traditionally depicted with the left limb in most anatomy books and atlases. A Canon EOS 450D body (Canon Inc., Tokyo, Japan) combined with a Canon EF-S 18–200 mm f/3.5–5.6 IS lens (Canon Inc., Tokyo, Japan) was used for taking macroscopic photographs. Stereomicroscopic images were taken by the means of a stereomicroscope (Olympus SZX7, Olympus Belgium, Aartselaar, Belgium) equipped with a charge-coupled device camera (Olympus DP50, Olympus, Belgium). GIMP 2.10.30 (gimp.org accessed on 17 September 2024) allowed for editing the photographs, which included cropping, equalizing the plain black background, adjusting the contrast and color temperature, and labeling the structures.

2.3. Anatomical Terminology

The anatomical structures that were encountered during the dissections were described using the N.A.V. [13]. Although this reference work is focused on domestic animals, without inclusion of the rhesus monkey, veterinary nomenclature was applied. After all, the rhesus monkey is an NHP whose wellbeing and health status are controlled by veterinarians. It should be noted that the tibial and fibular sides of the rhesus monkey foot are the medial and lateral sides, respectively. The specific terms for structures analogous to human ones present in the rhesus monkey which are absent from any of the domestic animal species included in the N.A.V. were found in Barone [18] or in a human anatomy atlas [21]. The anatomical work by Barone [18] describes both domestic mammals and humans.

When a structure is mentioned in the text for the first time, the Latin term is provided in round brackets next to the English term. Uniquely Latin terms are provided in the figure legends. In contrast, English terminology is used to further detail the structures in the textual descriptions to increase the readability of the text.

3. Results

3.1. Dorsal Side of the Foot–Dorsum Pedis

Figure 1A presents the superficial layer after skinning the dorsal aspect of the foot. The subcutaneous connective tissues, also known as the hypodermis or superficial fascia, were resected. From the deep fascia, specifically denoted here as the *fascia dorsalis pedis*, only the transverse crural ligament (*retinaculum extensorum crurale/retinaculum proximale*) (Figure 1A–D, nr. 1) and the sling-like tarsal ligament (*retinaculum extensorum tarsale/retinaculum distale*) (Figure 1A–D, nr. 2) were retained. These ligaments are reinforcements of the deep fascia at the level of the malleoli and the ankle joint (*articulatio talocruralis*), respectively.

The extensor digitorum longus muscle (*musculus (m.) extensor digitorum longus*) (Figure 1A–C, nr. 3′) was immediately visible. This muscle, which has its origin at the lateral tibial condyle and the fibular head, first passes through the transverse crural ligament and then the sling-like tarsal ligament. The transition from its muscular belly to its common tendon is positioned exactly at the level of the latter ligament, which exclusively encompasses the extensor digitorum longus muscle. The belly of this muscle is flanked by the medially positioned tibialis cranialis muscle (*m. tibialis cranialis*) (Figure 1A–D, nr. 4′) and the laterally positioned fibularis longus muscle (*m. fibularis longus*) (Figure 1A–D, nr. 5′). The origins and insertions, as well as the actions of these two muscles that also travel through the transverse crural ligament, are discussed further. The very short common tendon of the extensor digitorum longus muscle divides into three tendons immediately distal to the sling-like tarsal ligament. More distally, at the level of the heads of the metatarsal bones II and III, the medial-most tendon splits in turn. Consequently, four tendons can be observed that attach to the dorsal sides of the middle and distal phalanges of digits II to V (Figure 1A, nr. 3″). Contraction of the extensor digitorum longus muscle results in the extension of digits II to V, and indirectly in dorsiflexion of the ankle.

Figure 1B was obtained by resecting the extensor digitorum longus muscle. This procedure fully exposed the extensor digitorum et hallucis brevis muscle (*m. extensor digitorum et digiti primi/hallucis brevis*) (Figure 1A,B, nr. 6). Since this muscle finds its origin at the laterodorsal aspect of the calcaneus, it is the only intrinsic extensor muscle of the digits, more

specifically of digits I to IV. Indeed, each of the four muscle bellies sends a tendon towards digits I to IV. The tendon for the first digit attaches to the laterodorsal side of its proximal phalanx, whereas the tendons for digits II to IV insert into their distal phalanges.

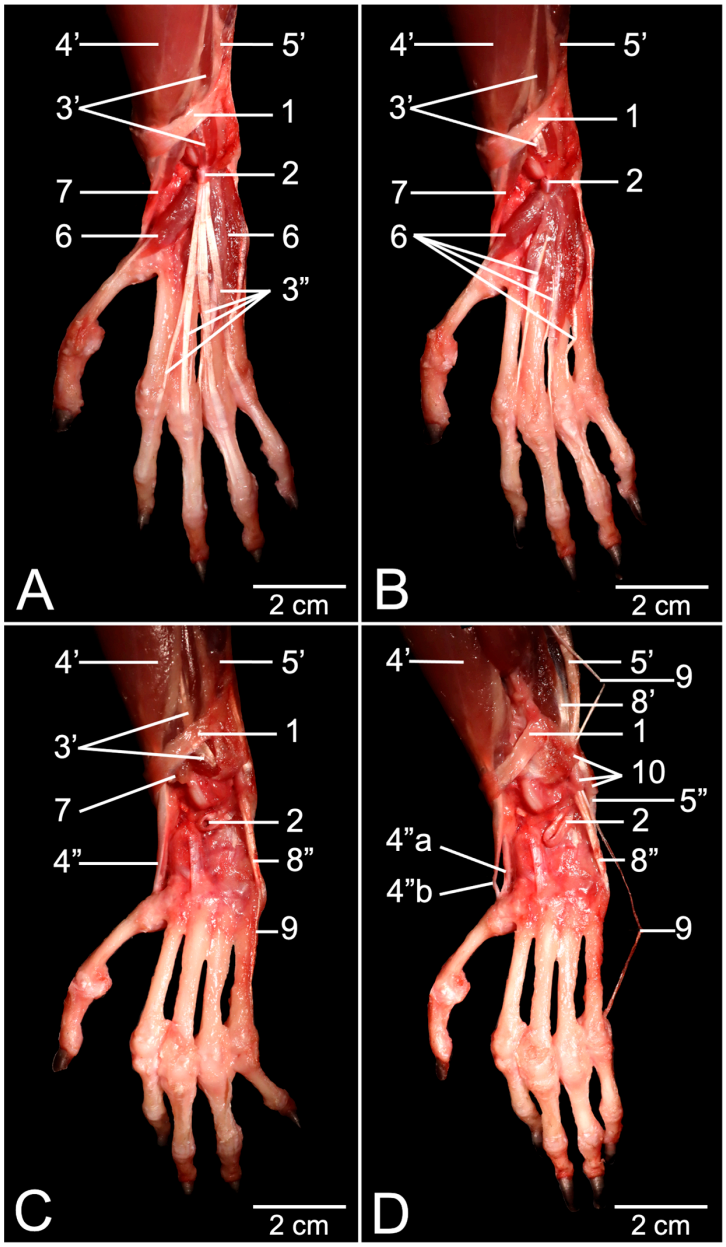

Figure 1. Dorsal aspect of the left foot of a rhesus monkey: (**A**) superficial layer after skinning the dorsal side of the foot and resecting the subcutaneous connective tissues; (**B**) deeper layer after removal of the extensor digitorum longus muscle; (**C**) deeper layer after the extensor digitorum et hallucis brevis muscle had been taken away; and (**D**) deepest layer after partial resection of the transverse crural ligament and dissection of the fibularis muscles. 1: *retinaculum extensorum crurale*, 2: *retinaculum extensorum tarsale*, 3′: muscular belly of the *m. extensor digitorum longus*, 3″: individual tendons of the *m. extensor digitorum longus* to digits II–V, 4′: muscular belly of the *m. tibialis cranialis*, 4″: medial and lateral tendons of the *m. tibialis cranialis*, 4″a: medial tendon of the *m. tibialis cranialis*, 4″b: lateral tendon of the *m. tibialis cranialis*, 5′: muscular belly of the *m. fibularis longus*, 5″: tendon of the *m. fibularis longus*, 6: *m. extensor digitorum et digiti primi/hallucis brevis*, 7: *m. extensor digiti primi/hallucis longus*, 8′: muscular belly of the *m. fibularis brevis*, 8″: tendon of the *m. fibularis brevis*, 9: *m. fibularis digiti quinti*, and 10: *retinacula musculorum fibularium*.

The extensor hallucis longus muscle (*m. extensor digiti primi/hallucis longus*) (Figure 1A,B, nr. 7) can be identified at the medial side of the tarsus, just distal to the transverse crural ligament that secures its position. The origin of this muscle is the medial side of the fibular diaphysis and the interosseous membrane. Its tendon, which originates from the level of the head of the first metatarsal bone, inserts into the dorsal sides of the proximal and distal phalanges of digit I. As a result, its action is the extension of the first digit. This muscle was subsequently transected just distal to the transverse crural ligament, and its tendon was removed, leaving only a short muscle stump (Figure 1C, nr. 7).

Then, the tendons of the tibialis cranialis muscle (Figure 1C, nr. 4″), which originates from the lateral condyle of the tibia and the proximal two-thirds of its shaft, emerged. Both tendons show a transition into a muscular belly as soon as they are covered by the transverse crural ligament. The tendon of the medial belly (Figure 1D, nr. 4″a) is connected to the medioplantar side of the first tarsal bone, while the tendon of the lateral belly (Figure 1D, nr. 4″b) inserts into the abaxioplantar aspect of the base of the first metatarsal bone. Contraction of the tibialis cranialis muscle results in dorsiflexion of the ankle, inversion of the foot, and the abduction of digit I. The latter action is attributed to the lateral belly that could, therefore, also be denoted as the abductor hallucis longus muscle (*m. abductor digiti primi/hallucis longus*).

The transverse crural ligament was transected at the lateral side of the foot in Figure 1D. This enabled the separation of the superficially positioned fibularis longus muscle (Figure 1A–D, nr. 5′), with its origin at the proximal third of the fibular shaft, the fibular head, and the proximal epiphysis of the tibia, from the deeper, more medially located fibularis brevis muscle (*m. fibularis brevis*) (Figure 1D, nr. 8′). The latter muscle arises at the distal two-thirds of the shaft of the fibula. The tendon of the fibularis longus muscle (Figure 1D, nr. 5″) runs lateroplantar to the tendons of both the fibularis brevis muscle (Figure 1D, nr. 8″) and the fibularis digiti quinti muscle (*m. fibularis digiti quinti*) (Figure 1D, 9) (*m. opponens digiti minimi* in human anatomy). The latter muscle is slender and commences at the proximal part of the caudolateral fibular margin. Its tendon runs between the tendons of the short and long fibular muscles.

Three ligaments (*retinacula musculorum fibularium*) (Figure 1D, 10) secure the positions of the fibular muscles at the level of the lateral malleolus. All three fibularis muscles pass through the proximal fibular ligament (*retinaculum musculorum fibularium proximale*). The fibularis brevis muscle and the fibularis digiti quinti muscle additionally run through the middle fibular ligament (*retinaculum musculorum fibularium medius*). In contrast, the fibularis longus muscle also runs through the distal fibular ligament (*retinaculum musculorum fibularium distale*). At the level of the fourth tarsal bone (*os cuboideum*), its tendon subsequently leaves its lateral position to sharply bend towards the plantar side of the foot. Here, a sesamoid bone is present within the tendon. Finally, insertion upon the abaxioplantar aspect of the base of the first metatarsal bone is achieved. Eversion of the foot, extension of the ankle (plantar flexion), and the opposition of digit I are realized by this muscle.

The tendon of the fibularis brevis muscle inserts into the tuberosity of the fifth metatarsal bone (*tuberositas ossis metatarsalis quinti*). It consequently everts the foot and extends the ankle (plantar flexion). Lastly, the tendon of the fibularis digiti quinti muscle attaches to the abaxial side of the distal phalanx of digit V. This muscle extends and slightly abducts the fifth toe.

3.2. Plantar Side of the Foot—Planta Pedis

3.2.1. Long Muscles

Multiple pads (*tori*, singular: *torus*), which are composed of a thick epidermal covering characterized by dermatoglyphics, the dermis, and a subcutaneous fat cushion (*pulvinus*), can be observed at the plantar side of the rhesus monkey foot (Figure 2A). The large pad that is positioned at the base of the hallux on the thenar eminence (*eminentia thenaris*) is the thenar pad (*torus thenaris*) (Figure 2A, nr. 1). Opposite to this pad, at the lateral side of the sole, lies the bifid hypothenar pad (*torus hypothenaris*) on the hypothenar eminence (*eminentia*

hypothenaris) (Figure 2A, nr. 2). Three metatarsophalangeal pads (*tori metatarsophalangei*, singular: *torus metatarsophalangeus*) (Figure 2A, nr. 3) can be recognized at the level of the metatarsophalangeal joints of digits II–V. The middle is a true interdigital pad (*torus interdigitalis*), as it is located at the bases of the third and fourth digits. The medial and the lateral sit at the bases of the second and fifth digits, respectively. Finally, an apical pad (*torus apicalis*) is positioned at the distal phalanx of each of the five toes (Figure 2A, nr. 4).

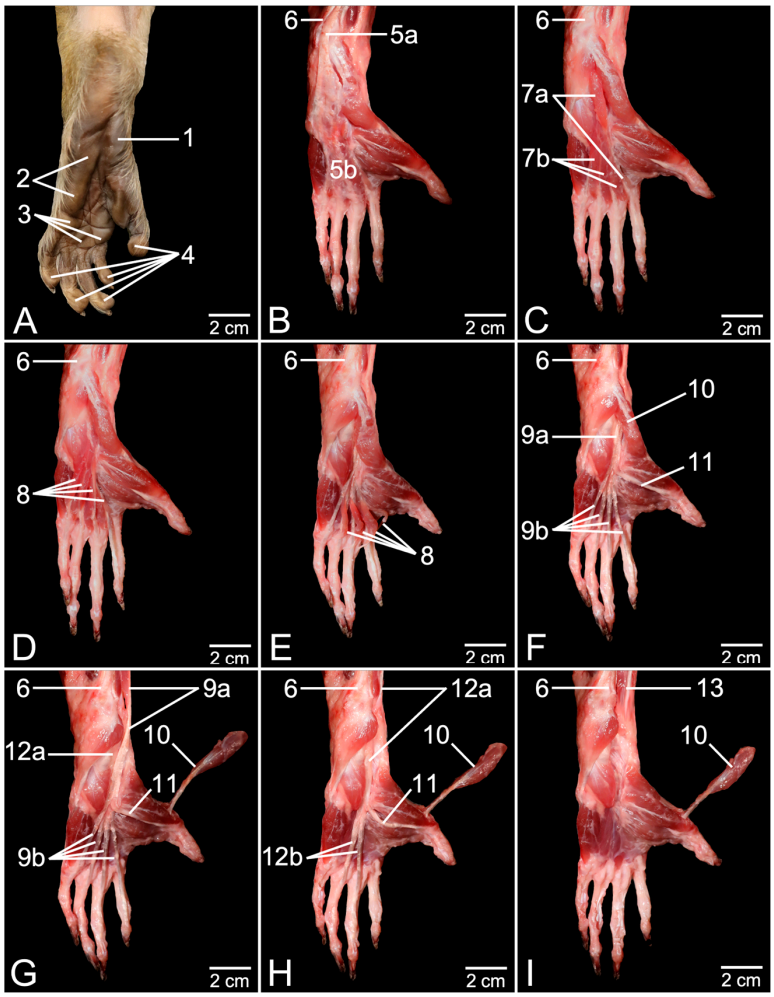

Figure 2. Plantar aspect of the left foot of a rhesus monkey: (**A**) intact sole showing the various pads; (**B**) superficial layer after skinning and resecting the subcutaneous tissues, including the pads; (**C**) deeper layer after the resection of the plantaris muscle and the plantar aponeurosis; (**D**) deeper layer after the removal of the superficial and deep heads of the flexor digitorum brevis muscle; (**E**) deeper layer next to the retraction of the lumbrical muscles of the foot; (**F**) deeper layer following the elimination of the lumbrical muscles of the foot; (**G**) deeper layer after the abductor hallucis muscle is detached from its origin and is retracted; (**H**) deeper layer subsequent to the removal of the flexor digitorum tibialis (medialis)/longus muscle; and (**I**) deepest layer after removal of the flexor digitorum fibularis/lateralis muscle. 1: *torus thenaris*, 2: *torus hypothenaris*, 3: *torus metatarsophalangeus*, 4: *torus apicalis*, 5a: tendon of the *m. plantaris longus*, 5b: *aponeurosis plantaris*, 6: *tendo Achilles*, 7a: *m. flexor digitorum brevis, caput superficiale*, 7b: *m. flexor digitorum brevis, caput profundum*, 8: *mm. lumbricales pedis*, 9a: common tendon of the *m. flexor digitorum tibialis (medialis)/longus*, 9b: individual tendons of the *m. flexor digitorum tibialis (medialis)/longus*, 10: *m. abductor digiti primi/hallucis*, 11: merged tendons of the *m. flexor digitorum tibialis (medialis)/long*us and the *m. flexor digitorum fibularis/lateralis* to digit I, 12a: common tendon of the *m. flexor digitorum fibularis/lateralis*, 12b: individual tendons of the *m. flexor digitorum lateralis*, and 13: *m. tibialis caudalis*.

Subsequently, the sole of the foot was skinned, and the subcutaneous connective tissues and fat cushions of the pads were resected. The thin aponeurotic continuation of the plantaris muscle (*m. plantaris*) (Figure 2B, nr. 5a) that covers the deeper muscles of the sole became visible. This is the plantar aponeurosis (*aponeurosis plantaris*) (Figure 2B, nr. 5b). The plantaris muscle originates from the caudal side of the femur, just proximal to its lateral condyle. Here, the lateral head (*caput laterale*) of the gastrocnemius muscle (*m. gastrocnemius*) also finds its origin, albeit superficial to the origin of the plantaris muscle. In contrast, the medial head (*caput mediale*) begins at a similar region at the opposite side of the femur.

By inserting into the calcanean tuber (*tuber calcanei*), the gastrocnemius muscle promotes the extension of the ankle (plantar flexion). This tuber is also the insertion site of the soleus muscle (*m. soleus*), which aids in the extension of the ankle. Its site of origin is the caudal aspect of the fibular head. Both heads of the gastrocnemius muscle, together with the soleus muscle, form the triceps surae muscle (*m. triceps surae*). The common tendon that emerges just proximal to the calcanean tuber is called the Achilles tendon (*tendo calcaneus* or *tendo Achilles*) (Figure 2B–I, nr. 6).

The plantar aponeurosis has been removed in Figure 2C. This manipulation revealed the flexor digitorum brevis muscle (*m. flexor digitorum brevis*), which is composed of two easily distinguishable heads. The superficial head (*caput superficiale*) (Figure 2C, nr. 7a) originates from the medial sides of the calcanean tuber and the plantar aponeurosis. Its thin tendon, which is initially still bordered by some muscle fibers, attaches to the plantar side of the middle phalanx of digit II. The deep head (*caput profundum*) (Figure 2C, nr. 7b) starts as a single muscle belly at the common tendon of the flexor digitorum tibialis (medialis)/longus muscle (*m. flexor digitorum tibialis (medialis)/longus*) at the level of the medial malleolus. Soon, three muscle bellies arise that each send a thin tendon to the plantar sides of the middle phalanges of digits III, IV, and V. However, these tendons are interdigitally positioned at the level of the metatarsophalangeal joints.

At the distal third of the proximal phalanx, the tendons of the flexor digitorum tibialis (medialis)/longus muscle (digits II to V) and the tendons of the flexor digitorum fibularis/lateralis muscle (digits III and IV) (see further) split the tendons of the flexor digitorum brevis muscle. The four tendons of this flexor digitorum brevis muscle consequently attach bilaterally to the middle phalanges of digits II to V.

The resection of the flexor digitorum brevis muscle, in particular the deep head, exposed the lumbrical muscles of the foot (*mm. lumbricales pedis*), which are four in number, one for each of the digits from II to V (Figure 2D, nr. 8). The lumbrical muscles for digits III, IV, and V arise bilaterally from the respective tendons of the flexor digitorum tibialis (medialis)/longus muscle. In contrast, the tiny lumbrical muscle for digit II begins only at the medial surface of the respective tendon of the aforementioned muscle. Insertion is into the medial sides of the proximal phalanges of digits II to V. This can be noticed in Figure 2E, in which the bellies of the four lumbrical muscles of the foot have been detached from the tendons of the flexor digitorum tibialis (medialis)/longus muscle. Prolongation of the tendons towards the dorsomedial sides of the distal phalanges could be observed by the means of stereomicroscopic examination.

The individual tendons to digits II to V of the flexor digitorum tibialis (medialis)/longus muscle (Figure 2F, nr. 9b), as already mentioned above, were fully visible once the lumbrical muscles were resected. This muscle commences caudally along the middle third of the tibial shaft. It subsequently runs caudal to the medial malleolus, where it is medially flanked by the tibialis caudalis muscle (*m. tibialis caudalis*) and laterally by the flexor hallucis longus muscle (*m. flexor digiti primi/hallucis longus*), preferentially called the flexor digitorum fibularis/lateralis muscle (*m. flexor digitorum fibularis/lateralis*). Here, the abductor hallucis muscle (*m. abductor digiti primi/hallucis*) (Figure 2F, nr. 10) hides these tendons over a short distance, since this muscle runs from the plantar aponeurosis and the medial side of the calcanean tuber towards the abaxial side of the proximal phalanx of digit I. So, it abducts the first digit and aids in its flexion.

When the common tendon of the flexor digitorum tibialis (medialis)/longus muscle (Figure 2F, nr. 9a) reaches the sole of the foot, it lies plantar to the common tendon of the flexor digitorum fibularis/lateralis muscle and, thus, obscures it. The tendon of the flexor digitorum tibialis (medialis)/longus muscle now splits into five individual tendons, one for each digit. The four tendons to digits II to V (Figure 2F, nr. 9b) insert into the plantar surfaces of the distal phalanges of the respective digits. The tendon for the first digit merges with the tendon of the flexor digitorum fibularis/lateralis muscle (Figure 2F, nr. 11). These are difficult to separate from each other. The flexion of digits II to V and the extension of the ankle (plantar flexion) are the actions of the flexor digitorum tibialis (medialis)/longus muscle.

In Figure 2G, the belly of the abductor hallucis muscle has been detached from its origin at the medial aspect of the calcanean tuber (Figure 2G, nr. 10). The common tendon of the flexor digitorum tibialis (medialis)/longus muscle (Figure 2G, nr. 9a) was then fully exposed. The common tendon of the flexor digitorum fibularis/lateralis muscle (Figure 2G, 12a) can be observed along its lateral side as it runs caudal to the talus and plantar to the talal sustentaculum (*sustentaculum tali*) of the calcaneus. This muscle finds it origin at the caudomedial side of the fibula, the interosseous membrane, and the distal part of the tibial shaft.

It is subsequently feasible to resect the flexor digitorum tibialis (medialis)/longus muscle. As a result, the common tendon of the flexor digitorum fibularis/lateralis muscle (Figure 2H, 12a) can be followed in the distal direction. At the base of the hallux, this tendon gives off the individual tendon for the hallux that merges with the one from the flexor digitorum tibialis (medialis)/longus muscle (Figure 2H, nr. 11). The continuation of the tendon soon splits into two tendons, one for digit III and one for digit IV (Figure 2H, nr. 12b). All three tendons insert into the plantar sides of the distal phalanges.

Finally, the flexor digitorum fibularis/lateralis muscle was removed (Figure 2I). Caudal to the medial malleolus, the tendon of the tibialis caudalis muscle, which is bilaterally flanked by muscle fibers (bipennate muscle type), is visualized (Figure 2I, nr. 13). The origins of the tibialis caudalis muscle are the proximal half of the caudal side of the tibia, the interosseous membrane, and the medial side of the fibula. The slender tendon ultimately attaches to the plantar sides of the bases of metatarsal bones II to IV, after tendinous fibers have been given off to various tarsal bones. The short and deep musculature of the foot are described further. Special attention will be paid to the musculature of the hallux.

3.2.2. Anular and Cruciform Ligaments

When the digits are flexed, the tendons of the flexor digitorum tibialis (medialis)/longus muscle (to all five digits) (Figure 3, nr. 1) and the tendons of the flexor digitorum fibularis/lateralis muscle (to digits I, III, and IV) (Figure 3, nr. 2) find their positions against the plantar sides of the digits secured by the means of various fibrous bands (*vaginae fibrosae digitorum pedis*). These bands are three in number in digits II to V. In contrast, only a single fibrous band can be identified in the hallux.

In Figure 3A–C, the three bands that are present in digit III are illustrated. The proximal band is positioned just distal to the metatarsophalangeal joint (Figure 3A), the middle can be observed halfway along the proximal phalanx (Figure 3B), and the distal is located in the middle of the middle phalanx (Figure 3C). All three fibrous bands are composed of transverse fibers (*pars anularis vaginae fibrosae*), abbreviated as the anular ligament (*ligamentum anulare digiti*) (Figure 3, nr. 3), while crossed fibers are called the cruciform ligament (*ligamentum cruciforme digiti*) (Figure 3, nr. 4).

In digits III and IV, the individual tendons of both the flexor digitorum tibialis (medialis)/longus muscle, which is located superficially, and the flexor digitorum fibularis/lateralis muscle, which is located deeper, run jointly towards the plantar side of the distal phalanges of the respective digits. Both tendons are attached to each other by the means of tendon slips and pass through all three fibrous bands.

The tendons of the flexor digitorum brevis muscle (to digits II to V) do not run through the fibrous bands, but run medial to these and become perforated by the tendons of both the flexor digitorum tibialis (medialis)/longus and flexor digitorum fibularis/lateralis muscles

(for digits III and IV), or the flexor digitorum tibialis (medialis)/longus muscle alone (for digit II and V).

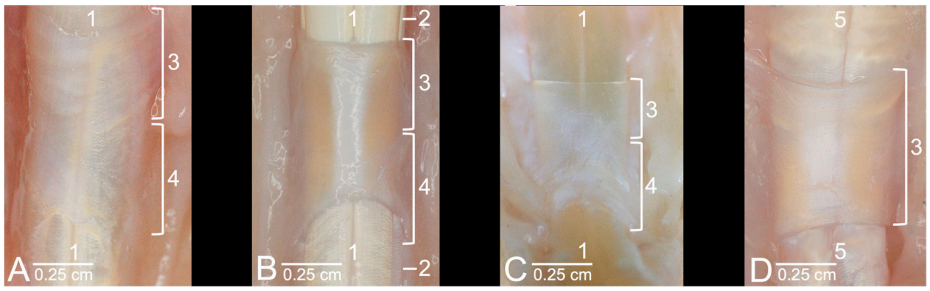

Figure 3. Stereomicroscopic views of the anular and cruciform ligaments of the first and third digits of the left foot of a rhesus monkey: (**A**) anular and cruciform ligaments at the level of the metatarsophalangeal joint of digit III; (**B**) anular and cruciform ligaments located in the middle of the proximal phalanx of digit III; (**C**) anular and cruciform ligaments positioned halfway the middle phalanx of digit III; and (**D**) anular ligament at the metatarsophalangeal joint of the hallux. 1: *m. flexor digitorum tibialis (medialis)/longus*, 2: *m. flexor digitorum fibularis/lateralis*, 3: *ligamentum anulare*, 4: *ligamentum cruciforme*, and 5: merged tendons of the *m. flexor digitorum tibialis (medialis)/longus* and *m. flexor digitorum fibularis/lateralis*.

Only a single fibrous band can be recognized just distal to the metatarsophalangeal joint of the hallux. It is composed of transverse fibers through which the merged tendons of the flexor digitorum tibialis (medialis)/longus and flexor digitorum fibularis/lateralis muscles pass (Figure 3D, nr. 5).

3.2.3. Musculature of the Hallux

The musculature of the hallux can be studied in Figure 4, which shows the plantar side of the foot after the plantar aponeurosis, both heads of the flexor digitorum brevis muscle, and the lumbrical muscles after resection. Medial to the Achilles tendon (Figure 4A–C, nr. 1), the common tendon of the flexor digitorum tibialis (medialis)/longus muscle (Figure 4A, nr. 2), which obscures the common tendon of the flexor digitorum fibularis/lateralis muscle, can be identified. As already mentioned, this tendon splits into four individual tendons for digits II to V (Figure 4A, nr. 2b). Its individual tendon to digit I merges with the respective individual tendon of the flexor digitorum fibularis/lateralis muscle (Figure 4A, nr. 3). The common tendons of both the flexor digitorum tibialis (medialis)/longus and flexor digitorum fibularis/lateralis muscles are obliquely crossed by the abductor hallucis muscle (Figure 4A, nr. 4) that runs from the medial side of the calcanean tuber to the abaxial side of the proximal phalanx of the hallux.

The flexor hallucis brevis muscle (*m. flexor digiti primi/hallucis brevis*) is already partially visible in Figure 4A. However, it can only be investigated properly when the abductor hallucis muscle (Figure 4B, nr. 4) is retracted. The medial head (*caput mediale*) (Figure 4B,C, nr. 5a) seems double, as it has origins at the central tarsal bone (*os tarsi centrale* or *os naviculare*) and the first tarsal bone (*os tarsale primum* or *os cuneiforme mediale*). Surprisingly, a small and deep third part that arises from the first metatarsal bone was uncovered by the retraction of these two parts. The insertion of all three parts occurs together with the tendon of the abductor hallucis muscle into the abaxial side of the proximal phalanx of the hallux.

The lateral head (*caput laterale*) (Figure 4C, nr. 5b) has a single site of origin, which is the first tarsal bone. This head is overlaid by the belly of the medial head that originates from the same tarsal bone. In addition, the merged tendons of the flexor digitorum tibialis (medialis)/longus and flexor digitorum fibularis/lateralis muscles compress the lateral head against the sole of the foot. This inserts into the axial aspect of the proximal phalanx of the hallux together with the oblique head of the adductor hallucis muscle (*m. adductor digiti primi caput obliquum*) (Figure 4C, nr. 6a), thus opposite to the insertion of the medial head.

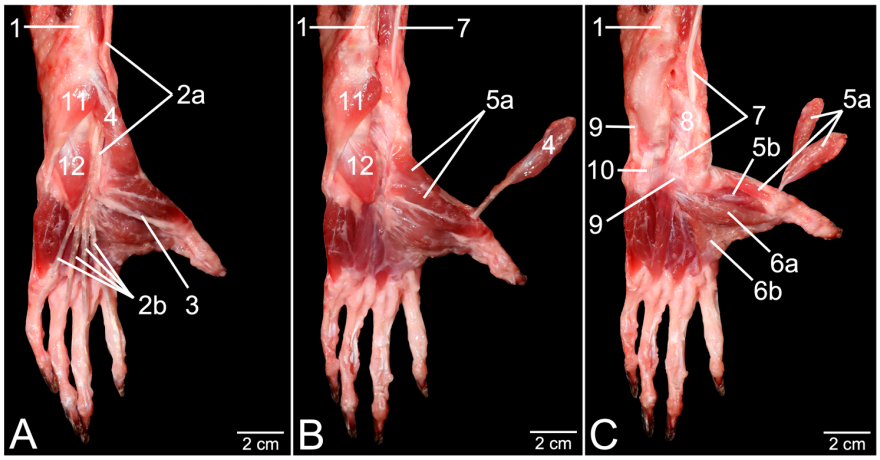

Figure 4. Plantar side of the foot of a rhesus monkey: (**A**) superficial layer after the plantar aponeurosis, both heads of the flexor digitorum brevis muscle, and the lumbrical muscles after resection; (**B**) deeper layer after removal of the flexor digitorum tibialis (medialis)/longus muscle and the flexor digitorum fibularis/lateralis muscle and retraction of the abductor hallucis muscle; and (**C**) deepest layer subsequent to the retraction of the medial head of the flexor hallucis brevis muscle and the additional excision of the abductor digiti quinti muscle and the quadratus plantae muscle. 1: *tendo Achilles*, 2a: common tendon of the *m. flexor digitorum tibialis (medialis)/longus*, 2b: individual tendons of the *m. flexor digitorum tibialis (medialis)/longus*, 3: merged tendons of the *m. flexor digitorum tibialis (medialis)/longus* and the *m. flexor digitorum fibularis/lateralis* to digit I, 4: *m. abductor digiti primi/hallucis*, 5a: *m. flexor digiti primi/hallucis brevis caput mediale*, 5b: *m. flexor digiti primi/hallucis brevis caput laterale*, 6a: *m. adductor digiti primi/hallucis caput obliquum*, 6b: *m. adductor digiti primi/hallucis caput transversum*, 7: tendon of the *m. tibialis caudalis*, 8: *ligamentum centroquartale plantare*, 9: tendon of the *m. fibularis longus*, 10: *ligamentum calcaneoquartale plantare*, 11: *m. abductor digiti quinti*, and 12: *m. quadratus plantae*.

The oblique head of the adductor hallucis muscle finds origins at the bases of the second and third metatarsal bones and at the common aponeurosis of the contrahentes muscles (see further). The transverse head (*caput transversum*) is initiated at the heads of the second and third metatarsal bones and at the contrahentes muscles II and IV (see further). They insert together into the axial aspect of the head of the first metatarsal bone and the proximal phalanx of the first digit. The adductor hallucis muscle is responsible for the adduction and opposition of the hallux.

To obtain more insight into the insertions of the fibularis longus and tibialis caudalis muscles, the abductor digiti quinti muscle (*m. abductor digiti quinti*) (Figure 4A,B, nr. 11) and the quadratus plantae muscle (*m. quadratus plantae*) (Figure 4A,B, nr. 12) were removed. The latter muscle arises from the lateral side of the calcaneus, plantar to the tendon of the fibularis longus muscle. The muscle fibers run obliquely towards the individual tendon for digit V from the flexor digitorum tibialis (medialis)/longus muscle. Smaller tendinous slips also attach to the individual tendons for digits IV, III, and II. As a result, this muscle assists the flexor digitorum tibialis (medialis)/longus muscle in the flexion of digits II to V.

The abductor digiti quinti muscle is discussed in the next chapter, together with two other intrinsic muscles that act upon the fifth digit. The tendon of the tibialis caudalis muscle (Figure 4B,C, nr. 7) can be followed in the distal direction from behind the medial malleolus. In the sole of the foot, it is shortly covered by the plantar centroquartal ligament (*ligamentum centroquartale plantare*) (Figure 4C, nr. 8). Finally, its insertions into the bases of the second to fifth metatarsal bones can be appreciated. The tendon of the fibularis longus muscle (Figure 4C, nr. 9) curves laterally around the cuboid bone, where a sesamoid bone can be observed. Subsequently, the tendon crosses the sole of the foot, where it is covered by the plantar calcaneoquartal ligament (*ligamentum calcaneoquartale plantare*) (Figure 4C, nr. 10) and the insertions of the tibialis caudalis muscle. It finally inserts into the abaxioplantar aspect of the base of the first metatarsal bone.

3.2.4. Musculature of the Fifth Digit

Three muscles intrinsically affect the fifth digit. These include the abductor digiti quinti muscle, the abductor ossis metatarsi quinti muscle (*m. abductor ossis metatarsi quinti*), and the flexor digiti quinti brevis muscle (*m. flexor digiti quinti brevis*).

The abductor digiti quinti muscle (Figure 5A–C, nr. 1) arises from the calcanean tuber, just lateral to the origin of the abductor hallucis muscle (Figure 5A, nr. 2), and from the lateral side of the plantar aponeurosis. The transition from the piriform muscle belly to the tendon covers the origin of the quadratus plantae muscle (Figure 5A–C, nr. 3). The abaxial side of the head of the proximal phalanx of the fifth digit is where the long, slender tendon inserts. As a result, abduction of the fifth digit is the action of this muscle.

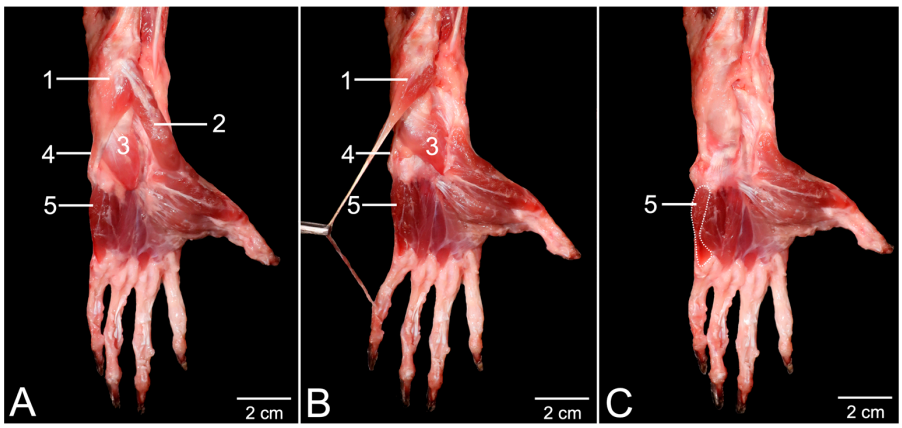

Figure 5. Plantar side of the foot of a rhesus monkey: (**A**) superficial layer after the plantar aponeurosis, both heads of the flexor digitorum brevis muscle, the flexor digitorum tibialis (medialis)/longus muscle, the flexor digitorum fibularis/lateralis muscle, and the lumbrical muscles were resected; (**B**) deeper layer after resection of the abductor hallucis muscle of the hallux and retraction of the abductor digiti quinti muscle; and (**C**) deepest layer subsequent to the removal of the abductor digiti quinti muscle and the quadratus plantae muscle. 1: *m. abductor digiti quinti*, 2: *m. abductor digiti primi/hallucis*, 3: *m. quadratus plantae*, 4: *m. abductor ossis metatarsi quinti*, and 5: *m. flexor digiti quinti brevis*.

Lateral to the tendon of the abductor digiti quinti muscle, just proximal to the tuberosity of the fifth metatarsal bone, some muscle fibers can be noticed. These also originate from the calcanean tuber and form a thin tendon, in a unipennate manner, that inserts into the tuberosity of the fifth metatarsal bone. The abductor ossis metatarsi quinti muscle (Figure 5A–C, nr. 4) aids in the abduction of the fifth digit.

The flexor digiti quinti brevis muscle (Figure 5A–C, nr. 5) commences at the base of the fifth metatarsal bone and at the distal aspect of the tendon of the fibularis longus muscle. This hourglass-shaped muscle inserts, with muscle fibers, into the lateral side of the base of the proximal phalanx of the fifth digit.

3.3. Deep Musculature of the Foot

The deep musculature of the sole of the foot consists of the contrahentes muscles of the foot (*mm. contrahentes digitorum pedis*) and the interosseous muscles of the foot (*mm. interossei pedis*). There are three contrahentes muscles that lie in the middle of the foot, plantar to the interosseous muscles. They have an aponeurosis in common that attaches to the tendon of the long fibular muscle. However, this aponeurosis, as well as the medial-most contrahens muscle, was only visible after the resection of the adductor hallucis muscle (Figure 6A, nr. 2). The medial-most or second contrahens muscle (*m. contrahens digiti II/secundi pedis*) inserts into the axial aspect of the base of the proximal phalanx of the second digit (Figure 6B, nr. 5^{II}). It should be noted that the axis of the foot passes in between the third and the fourth digit in mammals with four or five digits. The fourth contrahens muscle (*m. contrahens digiti IV/quarti pedis*) inserts into the axial aspect of the base of the

proximal phalanx of the fourth digit (Figure 6B, nr. 5^{IV}). Finally, the fifth contrahens muscle (*m. contrahens digiti V/quinti pedis*) inserts into the axial aspect of the base of the proximal phalanx of the fifth digit (Figure 6B, nr. 5^{V}). The adduction of digits II, IV, and V towards the axis of the foot, together with some degree of flexion, is the action that can be attributed to the contrahentes muscles.

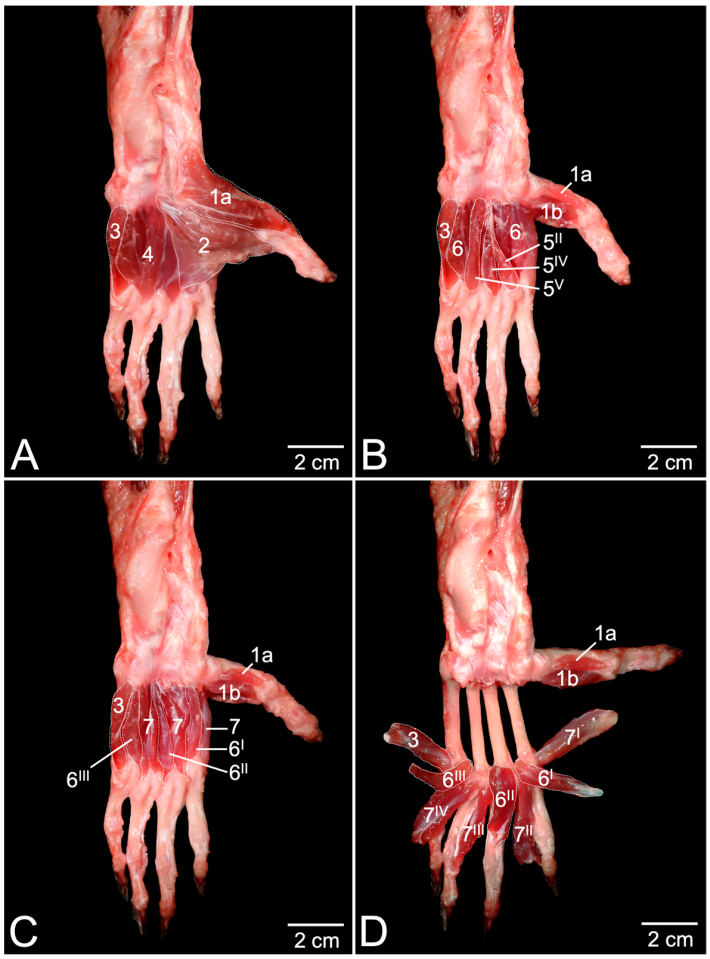

Figure 6. Deep plantar view of the left foot of a rhesus monkey demonstrating the deep musculature of the sole: (**A**) this figure recapitulates Figure 5C in which the flexor hallucis brevis muscle, the adductor hallucis muscle, the flexor digiti quinti brevis muscle, and the deep muscles of the sole are present; (**B**) the superficial part of the medial head of the flexor hallucis brevis muscle was removed, as well as the adductor hallucis muscle. The contrahentes muscles, which lie more superficially, have been isolated from the deeper interosseous muscles; (**C**) the contrahentes muscles were subsequently resected, rendering a full view on the interosseous muscles; and (**D**) both the plantar and the dorsal interosseous muscles and the flexor digiti quinti brevis muscle were detached from their origins and retracted in distal direction. 1a: *m. flexor digiti primi/hallucis brevis caput mediale*, superficial part outlined in A, deep part in B–D; 1b: *m. flexor digiti primi/hallucis brevis caput laterale*; 2: *m. adductor digiti primi/hallucis*; 3: *m. flexor digiti quinti brevis*; 4: deep musculature of the sole representing the unseparated contrahentes and interosseous muscles; 5^{II}: *m. contrahens digiti II/secundi pedis*; 5^{IV}: *m. contrahens digiti IV/quarti pedis*; 5^{V}: *m. contrahens digiti V/quinti pedis*; 6: unseparated interosseous muscles; 6^{I}: *m. interosseus pedis plantaris primus*; 6^{II}: *m. interosseus pedis plantaris secundus*; 6^{III}: *m. interosseus pedis plantaris tertius*; 7: unseparated dorsal interosseous muscles; 7^{I}: *m. interosseus pedis dorsalis primus*; 7^{II}: *m. interosseus pedis dorsalis secundus*; 7^{III}: m. *interosseus pedis dorsalis tertius*; and 7^{IV}: *m. interosseus pedis dorsalis quartus*.

The interosseous muscles of the foot are composed of three plantar interosseous muscles (*mm. interossei pedis plantares*) and four dorsal interosseous muscles (*mm. interossei pedis dorsales*). Nevertheless, all seven interosseous muscles have their origins at the plantar side of the foot, but the dorsal interosseous muscle can be seen from the dorsal side in between the metatarsal bones. The first plantar interosseous muscle (*m. interosseus pedis plantaris primus*) (Figure 6C,D, nr. 6^{I}) inserts into the axial side of the base of the proximal phalanx of the second digit. The second plantar interosseous muscle (*m. interosseus pedis plantaris secundus*) (Figure 6C,D, nr. 6^{II}) attaches to the axial side of the base of the proximal phalanx of the fourth digit. The third plantar interosseous muscle (*m. interosseus pedis plantaris tertius*) (Figure 6C,D, nr. 6^{III}) inserts into the axial side of the base of the proximal phalanx of the fifth digit. The first dorsal interosseous muscle (*m. interosseus pedis dorsalis primus*) (Figure 6D, nr. 7^{I}) runs towards the abaxial side of the proximal phalanx of the second digit. The second dorsal interosseous muscle (*m. interosseus pedis dorsalis secundus*) (Figure 6D, nr. 7^{II}) inserts into the abaxial side of the proximal phalanx of the third digit. The third dorsal interosseous muscle (*m. interosseus pedis dorsalis tertius*) (Figure 6D, nr. 7^{III}) attaches to the axial side of the proximal phalanx of the third digit. Finally, the fourth dorsal interosseous muscle (*m. interosseus pedis dorsalis quintus*) (Figure 6D, nr. 7^{IV}) runs towards the abaxial side of the proximal phalanx of the fourth digit.

In regard to the origins of the interosseous muscles, the following two groups can be recognized: the medial group and the lateral group. The medial group comprises the first plantar and the first and second dorsal interosseous muscles. They have a common origin situated at the plantar side of the base of the second metatarsal bone. The lateral group is composed of the second and third plantar and the third and fourth dorsal interosseous muscles. They arise from the plantar surfaces of the bases of the fourth and fifth metatarsal bones.

The action of the interosseous muscles can be deduced from carefully interpreting their origins and insertions. The plantar interosseous muscles perform the adduction of digits II, IV, and V towards the axis of the foot that passes in between digits III and IV. In contrast, the dorsal interosseous muscles abduct digits II, III, and IV from this axis. Furthermore, all the interosseous muscles aid in the flexion of the digits, except the hallux.

An overview of the described muscles is given in Table 1, in the order in which they appear in the text. Their origins, insertion sites, and actions are provided.

Table 1. List of the muscles of the rhesus monkey foot, including their origins, insertions, and actions, in order of appearance in the text.

Muscle	Origin	Insertion	Action
m. extensor digitorum longus	Lateral tibial condyle and fibular head	Middle and distal phalanges of digits II to V	Extension of digits II to V and dorsiflexion of the ankle
m. tibialis cranialis	Lateral condyle of the tibia and proximal two-thirds of its shaft	Medial belly: medioplantar side of the first tarsal bone Lateral belly: abaxioplantar aspect of the base of the first metatarsal bone	Dorsiflexion of the ankle, inversion of the foot, and abduction of digit I
m. fibularis longus	Proximal third of the fibular shaft, fibular head, and proximal epiphysis of the tibia	Abaxioplantar aspect of the base of the first metatarsal bone	Eversion of the foot, extension of the ankle (plantar flexion), and opposition of digit I
m. extensor digitorum et digiti primi/hallucis brevis	Laterodorsal aspect of the calcaneus	Laterodorsal, proximal phalanx of digit I, and distal phalanges of digits II to IV	Extension of digits I to IV
m. extensor digiti primi/ hallucis longus	Medial side of the fibular diaphysis	Dorsal, proximal, and distal phalanges of digit I	Extension of digit I

Table 1. *Cont.*

Muscle	Origin	Insertion	Action
m. fibularis brevis	Distal two-thirds of the shaft of the fibula	Tuberosity of the fifth metatarsal bone	Eversion of the foot and extension of the ankle (plantar flexion)
m. fibularis digiti quinti	Proximal part of the laterocaudal fibular margin	Abaxial and distal phalanx of digit V	Extension (and abduction) of digit V
m. plantaris	Caudal, proximal to the lateral femoral condyle	Plantar aponeurosis	Extension of the ankle (plantar flexion) (and flexion of the knee) through tension on the plantar aponeurosis
m. gastrocnemius	Caudal, proximal to the lateral and medial femoral condyle (*caput laterale* and *caput mediale*, respectively)	Calcanean tuber	Extension of the ankle (plantar flexion) (and flexion of the knee)
m. soleus	Caudal aspect of fibular head	Calcanean tuber	Extension of the ankle (plantar flexion)
m. flexor digitorum brevis	*Caput superficiale*: medial sides calcanean tuber and plantar aponeurosis *Caput profundum*: tendon of *m. flexor digitorum tibialis/longus*	*Caput superficiale*: plantar-side middle phalanx of digit II *Caput profundum*: plantar-side middle phalanges of digits III to V	Flexion of digits II to V
mm. lumbricales pedis	Tendons of the tibial (medial)/long digital flexor muscle	Medial sides of the proximal phalanges of digits II to V	Extension of the digits
m. flexor digitorum tibialis (medialis)/longus	Caudal, middle third of the tibial shaft	Plantar and distal phalanges of digits II to V	Flexion of digits II to V and extension of the ankle (plantar flexion)
m. flexor digiti primi/hallucis longus (m. flexor digitorum fibularis/lateralis)	Mediocaudal side of the fibula, interosseous membrane, and distal part of the tibial shaft	Plantar and distal phalanges of digits I, III, and IV	Flexion of digits I, III, and IV
m. abductor digiti primi/hallucis	Plantar aponeurosis and medial side calcanean tuber	Abaxial and proximal phalanx of digit I	Abduction (and flexion) of digit I
m. tibialis caudalis	Proximal half of caudal side tibia, interosseous membrane, and medial-side fibula	Plantar bases of metatarsal bones II to IV	Extension of the ankle (plantar flexion) and inversion of the foot
m. flexor digiti primi/ hallucis brevis	*Caput mediale*: central and first tarsal bone *Caput laterale*: first tarsal bone	*Caput mediale*: abaxial, proximal phalanx digit I *Caput laterale*: axial and proximal phalanx of digit I	Flexion of digit I
m. adductor digiti primi/hallucis	*Caput obliquum*: bases of second and third metatarsal bones and common aponeurosis of the contrahentes muscles *Caput transversum*: heads of second and third metatarsal bones and contrahentes muscles II and IV	Axial, head of metatarsal bone I, and proximal phalanx of digit I	Adduction and opposition of digit I
m. quadratus plantae	Lateral side of the calcaneus	Tendons of m. flexor digitorum tibialis (medialis)/longus to digits II to V	Flexion of digits II to V

Table 1. *Cont.*

Muscle	Origin	Insertion	Action
m. abductor digiti quinti	Calcanean tuber and plantar aponeurosis	Abaxial and proximal phalanx of digit V	Abduction of digit V
m. abductor ossis metatarsi quinti	Calcanean tuber	Tuberosity of fifth metatarsal bone	Abduction of digit V
m. flexor digiti quinti brevis	fifth metatarsal bone, and the tendon of the *m. fibularis longus* at this level	Abaxial side, proximal phalanx of digit V	Flexion of digit V
mm. contrahentes digitorum pedis	Common aponeurosis at the tendon of the long fibular muscle	Axial side, proximal phalanx of digit II, IV and V	Adduction (with flexion) of digits II, IV, and V towards the axis in between digits III and IV
mm. interossei pedis plantares	Plantar surfaces of the bases of the second, fourth, and fifth metatarsal bones	Axial side, proximal phalanx of digit II, IV, and V	Adduction (with flexion) of digits II, IV, and V towards the axis in between digits III and IV
mm. interossei pedis dorsales	Plantar surfaces of the bases of the second, fourth, and fifth metatarsal bones	Proximal phalanges of digit II (abaxial), III (axial and abaxial), and digit IV (abaxial)	Abduction (with flexion) of digits II, III, and IV from the axis in between digits III and IV

4. Discussion

Researchers and veterinarians who work with rhesus monkeys often request detailed anatomical data on this species. They are, unfortunately, confronted with the fact that there is currently no comprehensive atlas of rhesus monkey anatomy that is up-to-date both in terms of descriptions of musculoskeletal features and in terms of high-definition images. As a result, researchers with a background in human anatomy consult typical human resources such as the Sobotta Atlas of Human Anatomy [21], whereas veterinarians largely rely on their knowledge of veterinary gross anatomy. However, because neither the typical human nor typical veterinary anatomy resources are fully transferable to the anatomy of the rhesus macaque, the present manuscript makes reference to both. Veterinary anatomical nomenclature was primarily used, with the N.A.V. utilized as a reference work. In addition, the typical human terminology that is frequently encountered in research articles with the rhesus monkey as a study subject is provided where appropriate. The present manuscript consequently enhances comparative anatomic study between domestic animals, humans, and rhesus monkeys. As such, it also bridges the gaps in both anatomic and surgical guides, which might alternatively be consulted for various aspects of clinical and surgical practice.

Using veterinary nomenclature to describe the anatomy of the rhesus monkey is challenging, since the N.A.V. does not apply to this species. The following underlined terms can be found in the publications on the anatomy of the rhesus monkey that were cited in the introduction, but not in the N.A.V. [13]: *m. extensor digitorum et digiti primi/hallucis brevis*, *m. plantaris*, *m. fibularis digiti quinti*, *m. abductor ossis metatarsi quinti*, *m. flexor digiti quinti brevis*, *mm. interossei pedis dorsales* and *plantares*, and finally, *mm. contrahentes digitorum pedis*. It can be concluded from this enumeration that only a small number of muscles that are present in the rhesus monkey foot are not existent in any of the species included in the N.A.V. [13]. These muscles are, thus, specific for the rhesus monkey. Since the N.A.V. only covers typical domestic animals and not the rhesus monkey, the number of muscles that they have in common is a prediction of the degree of the similarity of their foot musculature. In other words, it is likely that the musculature of the rhesus monkey foot largely resembles that of one of the species included in the N.A.V. It is evident that the rabbit and domestic carnivores, i.e., the dog and cat, with their four-digit hind feet, lean more directly towards the rhesus monkey. The largest distinction lies in the presence of the hallux in the rhesus monkey. Although domestic carnivores apparently lack the hallux,

they present a reduced first metatarsal bone. In the dog, this rudimentary bone can be followed by phalanges [23]. It is then called a dew claw, which exists in a few variations [17]. On the other hand, the very reduced first metatarsal bone of the cat is never followed by phalanges [23]. Moreover, the first metatarsal bone is completely absent in the rabbit [23]. As a consequence, some of the muscles with action on the hallux of the rhesus monkey have analogues in the hind foot of the dog, and to a lesser extent in the cat. This allows for veterinarians to transfer their knowledge of the canine hind foot musculature with minimum effort to the rhesus monkey foot. This could be required when wounds need medical attention or surgery must be performed on the rhesus monkey foot. The present detailed anatomical study on the rhesus monkey foot will prove valuable, for small differences can lead to insecurity.

Discrepancies between the nomenclature used in the anatomical works on the rhesus monkey anatomy that were cited in the introduction are discussed. For example, the muscle designated by Hartman and Straus [10] with the term *m. flexor digitorum tibialis* is called the *m. flexor digitorum longus* by Berringer et al. [12]. None of these terms are listed in the N.A.V. [13]. However, since the tibial side of the lower leg corresponds with the medial side, the term *m. flexor digitorum medialis*, which is in the N.A.V. [13], seems to be a valuable alternative. A comparable example includes the muscle that is named the *m. flexor digitorum fibularis* by Hartman and Straus [10]. Berringer et al. [12] use the term *m. flexor hallucis longus*. Again, these terms are not listed in the N.A.V. [13], but since the fibular side of the lower leg corresponds with the lateral side, the term *m. flexor digitorum lateralis*, which is in the N.A.V. [13], could be preferred to avoid any misinterpretation. We included the various terms used in the descriptions of these muscles so that it is clear to any reader which specific muscle is being portrayed. To further complicate this matter, it could be mentioned here that the *m. flexor digitorum medialis* and the *m. flexor digitorum lateralis* form, together with the *m. tibialis caudalis*, the deep digital flexor (*m. flexor digitorum profundus*) in domestic mammals. In the rhesus monkey, however, the *m. flexor digitorum lateralis* not only lies lateral to the *m. flexor digitorum medialis*, as their names suggest, but also deeper to it. As a result, the medial and lateral digital flexor muscles could erroneously be labeled as the superficial digital flexor muscle (*m. flexor digitorum superficialis*) and the deep digital flexor muscle, respectively.

In regard to the flexor digitorum fibularis/lateralis muscle, it could be questioned how accurate the term *m. flexor digiti primi/hallucis longus*, used by Berringer et al. [12], is. According to its name, this muscle flexes the first digit or hallux. Likewise, it is expected that a single tendon inserts into the hallux. In the rhesus monkey, however, this muscle initially shows a transition to a common tendon, from which a tendon to the hallux first branches off. The continuation of the common tendon more distally splits into two tendons that insert into the third and fourth digits. Therefore, this muscle is not uniquely responsible for the flexion of the hallux, but also for the flexion of the third and fourth digits. Since the term *m. flexor hallucis longus* is misleading, the term *m. flexor digitorum lateralis* should be preferred. The former term obviously derives from human anatomy. Indeed, in the human foot, the flexor hallucis longus muscle sends a single tendon to the hallux, rendering its name appropriate [21].

A dissimilarity between the human and rhesus monkey foot was also noticed in the insertions of the flexor digitorum tibialis (medialis)/longus muscle. In the three specimens that were dissected during the present study, the common tendon of this muscle sent individual tendons to each of the five digits. However, according to Hartman and Straus [10], a high degree of variability is present in the number and heaviness of individual tendons. In particular, the tendon to the third digit can be weak. Nevertheless, the human hallux is not provided by any tendon from the flexor digitorum tibialis (medialis)/longus muscle [21]. This may not be surprising, since the human hallux is flexed by the flexor hallucis longus muscle, whose force uniquely acts upon the hallux. In the rhesus monkey, the analogous muscle (the flexor digitorum fibularis/lateralis muscle) is also activated to flex the third and fourth digits.

With respect to the foot, the following long muscles present diverse insertions when comparing the rhesus monkey with humans. The tibialis anterior muscle in humans usually has a single tendon that inserts into the medial cuneiform bone and the first metatarsal bone [18,21]. According to Hartman and Straus, the splitting of the tendon, or even the muscle belly, may occur [10]. The tibial cranialis muscle of the rhesus monkey is always composed of a lateral and a medial belly, with the former inserting with a tendon into the medial cuneiform bone and the latter into the first metatarsal bone [10]. The tendon of the human fibular longus muscle always terminates at the first metatarsal bone and generally has additional attachments to the medial cuneiform bone and the second metatarsal bone [18]. In the rhesus monkey, the main insertion site is also the first metatarsal bone, but anatomists can incidentally be confronted with an additional tendinous attachment to the fifth metatarsal bone and perhaps also to the cuboid bone [10]. The fibularis tertius muscle (*m. fibularis tertius*) is, in contrast to humans, absent in the rhesus monkey [10,15,16]. However, the fibularis tertius muscle in humans is very weak or can be absent. The muscle belly that finds its origin at the distal half of the fibula sends a tendon towards the head of the fifth metatarsal bone [18,21]. In domestic mammals, the fibularis tertius muscle presents a large degree of variation. It is absent in domestic carnivores and the rabbit. In contrast, this muscle is well developed and constant in ungulates [18].

In regard to the intrinsic muscles of the foot, the quadratus plantae muscle is first discussed. The quadratus plantae muscle is double in humans. Here, this muscle, which is alternatively named the accessory part of the flexor digitorum longus muscle (*m. flexor accessorius*), is composed of two parts [18]. After the tendons of both parts have united, the common tendon inserts into the common and individual tendons of the flexor digitorum longus muscle to digits II to V [18,21]. This condition is slightly different in the foot of the rhesus monkey, in which the muscle fibers from the single muscle belly primarily attach to the individual tendon for digit V from the flexor digitorum tibialis (medialis)/longus muscle. Only smaller tendinous slips also attach to the individual tendons for digits II to V. In contrast to the well-developed quadratus plantae muscle in humans and the rhesus monkey, the dog merely presents with a very weak analogue. The diminutive muscle bundle lies between the common tendons of the superficial and deep digital flexor muscles and terminates at the latter by the means of a tiny tendon [18].

The flexor digitorum brevis muscle is composed of only the superficial head in the human foot. It sends tendons to the middle phalanges of digits II to V [21]. In the rhesus monkey, the second digit is provided by the single tendon of the superficial head of this muscle, while the deep head sends tendons to digits III to V. Interestingly, this muscle is vestigial or even absent in domestic mammals. Only in the dog can some muscle fibers representing the flexor digitorum brevis muscle be observed at the plantar aspect of the tendon of the superficial digital flexor muscle, more specifically at the level of the tarsometatarsal joint, where its common tendon splits into the four individual tendons for digits II to V [18]. As already discussed, a true superficial digital flexor muscle is absent in the rhesus monkey.

The opposite situation, in which a muscle is embodied by two parts in the human foot and only one part in the rhesus monkey foot, is seen when studying the extensor digitorum et hallucis brevis muscle of the rhesus monkey. Although the term used to designate this muscle in this species signifies that a single muscle is responsible for the extension of all five digits, this assumption is not fully accurate. The three specimens that were dissected in the present study did not possess a muscle belly with a tendon for the fifth digit. According to Hartman and Straus [10], such a condition is only occasionally encountered. In humans, the function of the extensor digitorum et hallucis brevis muscle is performed by the extensor digitorum brevis muscle (*m. extensor digitorum brevis*) and the extensor hallucis brevis muscle (*m. extensor hallucis brevis*). The former extends digits II, III, and IV, while the latter is responsible for the extension of the hallux [21]. Like in humans, the extensor digitorum brevis muscle of domestic carnivores also extends digits

II, III, and IV. Given the reduced nature of the hallux in these species, no extensor hallucis brevis muscle exists [18].

In humans, no specific muscle for the second toe is present [18]. The same is true for the rhesus monkey [10–12]. In contrast, the terms *m. adductor digiti II* and *m. abductor digiti II* are listed in the N.A.V., meaning that these muscles can be observed in one or more domestic animal species [13]. Indeed, the adductor digiti secundi muscle can be observed in the hind limbs of domestic carnivores, the rabbit, and the pig, in which it attaches to the head of the proximal phalanx of digit II. Due to its origin at the plantar tarsal ligament, this muscle is suited to adduct the second digit towards the midline of the foot. The abductor digiti secundi muscle is only present in the porcine hind limb. In fact, the adductor and abductor muscles of the second digit in the pig are portions of the interosseous muscle of that digit, but they can be identified as independent muscles. In humans and rhesus monkeys, they are completely included in the interosseous muscles.

In the human and rhesus monkey foot, both dorsal and plantar interosseous muscles are present. This contrasts with the situation in domestic mammals, in which only plantar interosseous muscles can be identified [18]. Small differences can be observed when comparing the organization of the interosseous muscles between the human and rhesus monkey foot. The second dorsal interosseous muscle attaches to the second digit in humans, whereas this is the third digit in the rhesus monkey. The first plantar interosseous muscle inserts into the human third toe. In the rhesus monkey, however, the insertion site is the second digit. Based on the organization of the interosseous muscles, the axis of the rhesus monkey foot passes through the third digit. In humans, this axis shifts medially and, hence, passes through the second digit [10]. Nevertheless, the axial and abaxial directions were used in the present study as terms to designate the sides of the digits, with reference to the functional longitudinal axis of the rhesus monkey foot passing between the third and fourth digits, as custom in domestic mammals other than the horse [10].

Further elaborating the deep musculature of the rhesus monkey foot, it was demonstrated that four contrahentes muscles are present. Three are specified by the terms *m. contrahens digitorum pedis*, i.e., *m. contrahens digiti II/secundi pedis*, *m. contrahens digiti IV/quarti pedis*, and *m. contrahens digiti V/quinti pedis*. The remaining is the adductor hallucis muscle, that is, the *m. contrahens digiti I/primi/hallucis*. This original arrangement, which is also present in the rhesus monkey hand [24], is gradually reduced from monkeys to human primates, with a complete disappearance in humans [10].

The anatomic similarities of the rhesus monkey with domestic animals include the shared conservative traits of mammals. They reflect the preservation of synapomorphies despite the development of unique locomotor adaptations in these different species, as follows: digitigrade locomotion in domestic mammals compared to plantigrade weight-bearing and locomotor behaviors in primates [20]. This degree of similarity is a manifestation of concurrent phylogeny and externalizes a comparable functional morphology. Human, canine, and rhesus monkey feet show a few remarkable differences. Some muscles are absent or present in one species and not another, or are differently arranged. The plantaris muscle is a prime example here. It is lacking in dogs, but shows a similar organization in rhesus monkey and human feet. In contrast, the contrahentes muscles are unique to the rhesus monkey and cannot be identified in canine and human feet. The fibularis tertius muscle is usually present in humans, but is absent in dogs and rhesus monkeys. The adductor digiti secundi muscle can be observed in the canine foot, while no specific muscles for the second digit develop in humans and rhesus monkeys. Fortunately, the observation that the musculature of the rhesus monkey foot shows much resemblance with both the hind foot of domestic carnivores and the human foot allows the veterinarian responsible for the daily care of captive rhesus monkeys to easily transfer their knowledge of the anatomy of domestic mammals, in particular the dog. A biomedical researcher holding an M.D., on the other hand, will effortlessly apply human anatomy when performing examinations on rhesus monkeys. It is confusing, however, that certain muscles have diverse names in different species. For example, the human flexor hallucis longus muscle is more accurately

termed the flexor digitorum fibularis/lateralis muscle in the rhesus monkey, since this muscle also flexes the third and fourth digits in this species. This example demonstrates that not only the names, but also the functions of muscles, can vary between species.

5. Conclusions

To provide descriptions of the musculature of the rhesus monkey foot, the left and right feet of three specimens were dissected. These dissections followed the same pattern from the superficial to the deepest muscle layer. Every step was documented by the means of color photographs. Together with the accompanying text, they will prove valuable as a dissection guide. While identifying and labeling the different muscles and associated structures, the scarce literature on the anatomy of the rhesus monkey foot was consulted. As an NHP, veterinary anatomical terminology was applied for the descriptions of the foot musculature of the rhesus monkey. The unequivocal naming of all structures was, however, challenging, since the N.A.V. only includes the rabbit, cat, dog, pig, ox, sheep, goat, and horse [13]. Furthermore, the available anatomical works on the rhesus monkey do not use contemporary veterinary anatomical terminology. Consequently, not all muscles previously described in the rhesus monkey foot and encountered during the dissections hold an official name listed in the N.A.V. [13].

The dissections of the rhesus monkey foot revealed many similarities with human and canine feet. The observation that some muscles are typical for the rhesus monkey, or inversely, cannot be identified in this species, warrants attention when modeling the rhesus monkey foot in biomedical research. Nevertheless, anatomical knowledge of the human foot may be very useful for this matter. Similarly, a veterinarian studying or taking care of rhesus monkey feet is facilitated by their expertise in veterinary anatomy. The present manuscript could be instrumental in identifying ambiguities that arise from differently named muscles, the altered presence of muscles, or different muscle functionalities.

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