ABSTRACT

GENUS VARECIA: ANATOMY, MORPHOLOGY, AND PATHOLOGY

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An anatomical normal was established for the forelimb and hindlimb of the Genus Varecia through observation of skeletal remains and a detailed dissection of the musculature of a black and white ruffed lemur, Varecia variegata. This was used as a healthy state for comparison with a red ruffed lemur, Varecia rubra, displaying a periosteal disease affecting the long bones. This disease presented as large lesions growing along the diaphyses and epiphyses of the ulna, radius, tibia and fibula as well as on the carpals, metacarpals, tarsals, metatarsals, and phalanges. Dissection showed that these lesions avoided the points of origin and insertion of the limb musculature. Instead, the calcified lesions grew over the tendons and some muscle in the wrist and ankles reducing dexterity and range of motion in climbing and walking activities. This study determined the initial diagnosis of primary hypertrophic osteoarthropathy to be a misdiagnosis based on the absence of the three main symptoms of the disease: finger clubbing, pachydermia, and periostitis. Instead the location, size, and progression of the bony lesions make Nora’s lesions (bizarre parosteal osteochondromatous proliferation) are more appropriate diagnosis. The skeletomuscular data provided in this work allow for Varecia to be used as a model for morphological studies, in disease recognition and diagnosis, and answered questions regarding the effects of the periosteal disease described.
GENUS VARECIA: ANATOMY, MORPHOLOGY, AND PATHOLOGY

BY

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VIRGINIA L. NAPLES
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CHAPTER 1

INTRODUCTION

Strepsirrhines have often played an important role as research models for a variety of primate based studies and the lemur genus, *Varecia*, continues to contribute in this regard. Lemurs have frequently been used as models in a number of ways to better understand primate morphology and evolution (e.g., Napier and Walker 1967, Sigmon and Farslow 1986, Leliveld, Scheumann and Zimmerman 2008, Schmidt, Voges and Fischer 2002, Makungu, et al. 2013). *Varecia* in particular has played a role in understanding the systematic biology of primates (see Roberts 1974, Roberts and Davidson 1975, Jungers 1979, D. L. Gebo 1986, Forsythe, et al. 1988, Meldrum, Dagosto and White 1997).

Unfortunately, the anatomical data currently available for the gross anatomy of *Varecia* can be considered scattered and incomplete. Studies such as that of Jouffroy (1975) explore specific parts of the anatomical body of *Varecia* in comparison to other lemur species but a comprehensive look at the muscle anatomy of this genus has yet to be compiled. Chapter two of this project provides a detailed description of the skeletal and muscular anatomy of the black and white ruffed lemur, *Varecia variegata*.

This project has the opportunity to explore a bone pathology found in a captive female red ruffed lemur, *Varecia rubra*. This individual presented initially with lethargic behavioral symptoms. Radiographs showed abnormal growth of the periosteum, resulting in the diagnosis of hypertrophic osteoarthropathy, a disease resulting in periosteal reactions of the
long bones. This thesis project seeks to document the normal muscle and bone anatomy for *Varecia* as an anatomical model to compare with the diseased individual. After completing this work, this study has been able to show that the original diagnosis of osteoarthropathy to be incorrect and the correct diagnosis of Nora’s lesions better accounts for the bone pathologies present in this individual.

**Veterinary Records**

The following information was taken from veterinary records provided by Don Neiffer, a veterinarian at the Walt Disney World Animal Kingdom. The original records were written by Steve Marks at the Pittsburgh Zoo. In June of 1990, the individual was observed by keepers to have a stiff gait. A year later the subject refused to leave her enclosure and had to be hand fed. Testing showed high alkaline phosphatase (ALP) levels, which had been steadily increasing since her arrival in 1990. Over the next three years, stiffness in gait and lethargic behavior was noted regularly. A variety of medications were used, such as meclofenamic acid, which are typically used as anti-inflammatory drugs for arthritic discomfort. This seemed to help the individual but never fully relieved the stiffness in gait and lethargy. In 1994 the ALP levels peaked and the diagnosis of hypertrophic osteoarthropathy was first noted in the veterinary notes from observation of radiographs. The individual began to exhibit hindlimb weakness and tremors. Similar symptoms (stiffness in gait and lethargy) also began presenting themselves in a black and white ruffed lemur at the St. Louis Zoo and a red ruffed lemur at the Miami Zoo. Radiographs in 1996 showed no pulmonary lesions or abdominal masses but did show worsening condition of bone lesions. In 1997, one of the affected
individual’s daughters is showing signs of stiffness. In 1998, the individual was euthanized due to worsening condition.

The subject was initially diagnosed with a condition called primary hypertrophic osteoarthropathy. This diagnosis was based on several criteria: observation of pachydermia in the affected individual, a genetic link, due to similar symptoms presenting in the individuals’ offspring, and no other underlying pathology (Rothschild, Neiffer and Marks 2011).

It was hypothesized that perhaps the periosteal reactions, observed by the original caretakers, had affected the sites of origin and insertion of the musculature. If this was the case, then the reduced mobility and difficulty moving and climbing would be explained. The first goal of this study would require the establishment of a normal condition for both the skeletal and muscular anatomy of Varecia. This has been presented in Chapter 2. Second, removal of the overlying skin allowed direct observation of the disease’s effect on the skeleton and look for possible disruption of musculature.

Rothschild and Martin (2006) discuss what is necessary for the establishment of criteria for disease recognition. One of these criteria is being able to recognize changes that are not part of the normal condition. Detailed gross anatomical descriptions of Varecia will permit its use as a research model, and will allow for an anatomical normal to be established for the species. Having established a healthy condition for Varecia, will allow the question behind this study to be answered: were the origins and insertions of the diseased individual disrupted?

Genus Varecia
Varecia variegata was first illustrated and named in the late 1700’s, although it was initially called L. macacus variegatus (Tattersall, Buettner-Janusch and Sussman 1975). There has been some speculation as to the line separating full species from subspecies. Buettner-Janusch (1975) affirmed that consideration of specimens, both skeletal and preserved (with muscle still intact) is needed. The two species studied here include the black and white ruffed lemur and the red ruffed lemur. These animals were once considered subspecies of Varecia variegata (Varecia variegata variegata and Varecia variegata rubra respectively), but are currently listed as two separate species, Varecia variegata and Varecia rubra (Mittermeier, et al. 2010). This is how they will be treated for the remainder of this study.

Varecia are the largest and most frugivorous members of the Family Lemuridae. The red ruffed lemur, Varecia rubra, inhabits the rainforest of the Masoala Peninsula in Eastern Madagascar (Mittermeier, et al. 2010). The black and white ruffed lemur, Varecia variegata, has a more extensive range in the eastern rainforests of Madagascar. This species ranges from the northernmost limit of the Antainambalana River and Nosy Mangabe island to the southernmost Manombo Reserve (Garbutt 2007). The behavioral study conducted by Pereira et al. (1988) gave detailed descriptions of the strategies used by Varecia variegata for both climbing and leaping. They found that when ascending trees without branches, Varecia grasped the trunk and used hind legs to propel their body upward releasing the hands and regripping the target substrate, in a lumber jack like motion (Pereira, Seeligson and Macedonia 1988). When leaping, strepsirrhine primates typically use upward leaping, while anthropoids use downward leaping (D. L. Gebo 2014). However Varecia differs from other strepsirrhines in this behavior. Varecia will propel itself from a branch by leading with the
forelimbs and leaping with the tail and hind limbs, and in this manner can descend from five
to fifteen meters in a single jump (Pereira, Seeligson and Macedonia 1988). *Varecia variegata*
and *Varecia rubra* are listed as critically endangered by the IUCN Red List of Threatened
Species. Not to have the basic anatomy of such a species well documented is taking a chance
on losing an important component of primate history.

**Materials and Methods**

Skeletal elements used for the following descriptions and photographs were obtained
from the Smithsonian Institution, United States National Museum of Natural History (USNM)
and the Los Angeles County Museum of Natural History (LACMNH). For this study, I sought
out only adult specimens of *Varecia variegata* or *Varecia rubra*. Only two specimens, one
from each museum, met these standards and are outlined in Table 1.

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<tr>
<td>90811</td>
<td><em>Varecia variegata</em></td>
<td>Los Angeles County Museum (LACMNH)</td>
<td>San Diego Zoo</td>
<td>Adult Female Captive</td>
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The specimens dissected were acquired from Don Neiffer, a veterinarian at Walt
Disney World Animal Kingdom. The healthy specimen is an adult male black and white
ruffed lemur, *Varecia variegata*. The majority of the dissection was performed with two
forceps and detailed descriptions were written. Individual variation can cause differences in
muscular attachment sites and bone shape among all species. The most common variations
can only be identified through multiple dissections. While the sample size of this study is a single individual, it is appropriate for the general descriptive purposes of this paper.

The specimen displaying the bone pathology is an adult female red ruffed lemur, *Varecia rubra*. While the pelage of *Varecia rubra* differs from that of *Varecia variegata*, their similar lifestyle, locomotor habits, and close genetic relation allows for their muscular and skeletal anatomy to be nearly, if not completely, identical. Therefore, due to limited availability of specimens this study uses the healthy form of *Varecia variegata* as an anatomical normal for the genus *Varecia* as a whole.

**A note on Anatomical Position**

Anatomical textbooks often describe mammals in a specific anatomical position. For humans, this position is standing vertically with the upper limbs supinated at the sides of the body with the hands facing forward. For primates, such as the lemur described below, a human body position is inappropriate given their more generalized horizontal or pronograde body position. In contrast to humans, lemurs stand quadrupedally on a branch with the palms of their hands facing one another. This hand position is called a palmigrade, and in this forelimb position the ulna and radius do not cross over one another. This type of hand position is also true for their grasping feet. These limb positions make up the normal body position held by *Varecia* when traveling arboreally on top of and along horizontal branches.
CHAPTER 2

THE ANATOMY OF VARECIA VARIEGATA, THE BLACK AND WHITE RUFFED LEMUR

Forelimb Skeleton

Scapula (Figures 1, 2)

The scapula of Varecia is elongated and rectangular (in comparison with the triangular human scapula). The caudal and superior borders are relatively flat while the cranial border curves outward slightly. In the posterior view, the proximal portion of the cranial border curves over the infraspinous fossa. This results in a concave infraspinous fossa. The supraspinous fossa remains relatively flat. The scapular spine runs from the cranial portion of the superior border and thickens and widens to form the acromion. This feature extends past the glenoid cavity proximally. In anterior view, the cranial half of the subscapular fossa is slightly convex. The coracoid process is a thick protrusion from the cranial border of the glenoid fossa. It curves caudally. The glenoid fossa is a small, shallow, oval, articular area.
Humerus (Figures 3, 4, 5)

The humerus of *Varecia* is straight to the distal end of the deltoid tuberosity. At this point, the proximal half exhibits a posterior bend, when seen in lateral or medial view (Fig. 2c). Anteriorly, the humerus displays a greater and lesser tuberosity, with the greater only
slightly more pronounced than the lesser. The humerus tapers into the humeral surgical neck just distal to the head. The deltoid tuberosity is well defined, elevated and curved slightly medially, extending from the head to about mid shaft (this gives the deltoid tuberosity a concave appearance when inspected from a medial view, Fig. 2c). At the distal end, the diaphysis flares out into the relatively flat supinator crest, with an end that curves slightly anteriorly, to appear concave. The small rounded articulation of the capitulum is immediately distal. The trochlea is medial to the capitulum, but shorter and wider. The small protuberance of the medial condyle is the most medial aspect of the distal end of the humerus. From the posterior aspect of the humerus, the proximal head and greater tuberosity can be seen (Fig. 2b). The lateral epicondyle can be seen distally, opposite the medial epicondyle, separated by the articulating trochlea and the olecranon fossa just above.
Figure 3. Left humerus, anterior view.
Figure 4. Left humerus, posterior view.
Figure 5. Right humerus, medial view.
Ulna (Figures 6, 7)

The ulna in *Varecia* is a long bone that is rounded proximally. The diaphysis tapers and gradually thins distally. The olecranon process is pronounced proximally. The trochlear notch is just distal to it, for articulation with the trochlea of the humerus. The coronoid process is an anterior protrusion of the distal edge of the trochlear notch. The radial notch is visible in medial view at the distal edge of the trochlear notch, for articulation with the radius. The styloid process at the distalmost end of the ulna is thick. Just above this the rounded and small ulnar head extends anteriorly.
Figure 6. Left ulna, lateral view
Figure 7. Right ulna, medial view
Radius (Figures 8, 9)

The radius is thin and rounded proximally. It widens gradually and becomes less rounded toward the distal end. The head of the radius on the proximal end is smooth and rounded for articulation with the capitulum of the ulna. Below the neck of the ulna, the radial tuberosity protrudes from the posterior edge of the bone to articulate with the ulna. The styloid process extends from the very distal end of the bone on the anterior side. The medial aspect of radius further displays the radial tuberosity protruding posteromedially from the arm. The distal end of the bone can be seen to flatten and becomes slightly concave in this view.
Figure 8. Right radius, posterior view
Figure 9. Left radius, anterior view

Forelimb Musculature
**Panniculus carnosus** (Figure 10)

Panniculus carnosus is a cutaneous muscle that begins as a thin flat sheet in the fascia that wraps around the forelimb on the caudal side of the humerus two and a half to three centimeters from the ulnar olecranon. It ascends the length of the humerus, thickening slightly through the axillary fascia, caudal to the latissimus dorsi. It joins another sheet of thin muscle in the fascia surrounding the thorax around the level of the fourth rib. This aspect of the muscle begins at the terminus of the axilla as a small triangle of muscle invested in the axillary fascia just inferior to the latissimus dorsi. Caudally, this muscle gradually fans out superiorly and inferiorly, partially covering the latissimus dorsi. Superiorly, the fibers stop before the vertebral column (however the fascia in which those fibers are invested has a strong attachment to the spinous processes of the vertebrae). Inferiorly, the muscle forms a line just above the curve of the ribs, in a thin but wide sheet over the lateral side of the body as far as the pelvic cavity. Here, it begins to narrow until the level of the iliac crest. It continues as a thin strip of muscle past and lateral to the pelvic cavity, with a thin strip of fascia connecting the lower abdominal wall to the hindlimb. Panniculus carnosus inserts within the fascia surrounding the rectus femoris musculature. It can be distinguished as muscle fibers until two-thirds of the distance along the femur. The surrounding fascia continues to insert on the patella.
Pectoralis major (Figure 11)

Pectoralis major originates along the midline of the body from the clavicle to rib seven. It then inserts on the lateral portion of the humerus, distal to the humeral head, along the border of the lateral head of deltoid to the deltoid tuberosity. Pectoralis major medially rotates the arm.

Pectoralis abdominus (Figure 11, 12)

Pectoralis abdominus is a thin sheet like muscle that originates between ribs eight and rib nine. It fans out laterally and caudally along the rib cage. Pectoralis abdominus converges to insert by a tendon on the deltoid tuberosity, deep to the pectoralis major insertion.
Pectoralis Minor (Figure 12)

Pectoralis minor originates deep to pectoralis major along the sternum from ribs two to five. The muscle converges to insert tendinously to the head of the humerus, medial to the pectoralis abdominus insertion. Pectoralis minor medially rotates the arm.
Extensor carpi radialis brevis (Figure 13)

This muscle originates from the lateral epicondyle of the humerus. Its belly fuses proximally with the belly of extensor digitorum communis (that also originates from the lateral epicondyle of the humerus). It travels parallel to extensor carpi radialis longus and deep to the tendon of extensor pollicis longus. Proximally, extensor carpi radialis brevis sends a small extension of muscle fibers to attach to the belly of extensor carpi radialis longus, just before the start of the extensor carpi radialis longus tendon. Extensor carpi radialis brevis inserts on the anterolateral aspect of the proximal end of metacarpal III. Extensor carpi radialis brevis abducts the hand at the wrist (in human anatomical position this would be wrist extension).
**Biceps brachii** (Figure 13)

Biceps brachii is divided into two heads, long and short.

**Long head**: This head has a tendinous origin from the supraglenoid tubercle of the scapula. Its tendon lies deep to the tough fibrous sheath surrounding the head of the humerus. Proximally the muscle is deep to the insertion of pectoralis major and minor.

**Short head**: This head originates from the coracoid process of the scapula in combination with the tendon of coracobrachialis medius. These form a very thick tendon that does not separate until the separation of the short head of biceps brachii and continues, eventually thickening into the muscle belly.

The two heads of biceps brachii join at the last third of the humerus before inserting as a tendon on the tuberosity of the radius. Biceps brachii flexes the forearm, with the palmar surface facing medial.

**Palmaris longus** (Figure 13)

This muscle originates from the medial epicondyle of the humerus. It shares its origin with several flexor muscles which are covered by a thick fascia. The muscles are tightly adhered to this fascia, each other, and the bone. Palmaris longus is a relatively small, thin muscle that becomes tendinous midway along the forearm and inserts on the flexor retinaculum. The tendon also sends fibers to a cartilaginous attachment to the trapezium, superficial to the muscles along the 1st digit. Palmaris longus flexes the hand.
Flexor carpi radialis (Figures 13, 14)

This muscle originates from the medial epicondyle of the humerus and interdigitates with fibers of the pronator teres. It becomes a thin tendon that passes deep to the tendons of flexor digitorum superficialis, flexor digitorum profundus, and flexor pollicis longus at the wrist. Flexor carpi radialis continues over the trapezium to insert at the base of metacarpal II. This muscle flexes the hand at the wrist joint.

Flexor carpi ulnaris (Figure 13)

This muscle has a fleshy origin from the medial epicondyle of the humerus and along the medial side of the shaft of the ulna by a tendinous sheath superficial to the muscle body. It inserts by a thick well-defined tendon to the pisiform. Flexor carpi ulnaris flexes the hand medially at the wrist joint (with palmar surface medial) and slightly supinates the hand.

Figure 13. Superficial musculature of left forelimb, medial view.
**Coracobrachialis (Figure 14)**

This muscle originates from the coracoid process of the scapula, blending with the origin of the short head of biceps brachii, to create a thick attachment for both muscles. It extends distally along the medial aspect of the humerus until the midpoint of the shaft and has a muscular attachment to the medial shaft of the humerus. The insertion is on the medial supracondylar ridge of the humerus. Coracobrachialis adducts the arm.

**Flexor digitorum superficialis (Figure 14)**

This muscle has a fleshy origin from the medial epicondyle of the humerus. It extends along the length of the forearm and divides into four separate tendons, just proximal to the wrist. Held together by a sheath of fascia, these tendons run below the flexor retinaculum. A tendinous connection is sent to the flexor digitorum profundus/flexor pollicis longus tendon bundle at the wrist. Each tendon, I, II, III, and IV, inserts the distal metacarpals of digits II, III, IV, and V respectively.

- **Tendon 1**: inserts at the distal metacarpal of digit II
- **Tendon 2**: inserts at the distal metacarpal of digit III
- **Tendon 3**: inserts at the distal metacarpal of digit IV
- **Tendon 4**: inserts at the distal metacarpal of digit V

The four tendons flex digits II through V respectively.
Figure 14. Deep musculature of left forelimb, medial view.

**Pronator teres** (Figure 15)

This muscle originates from the medial epicondyle of the humerus, crosses over the anterior aspect of the arm to attach by muscle and fascia along the anterior border of the radius from the distal two thirds of the radius to its insertion. Pronator teres inserts on the
anterior, distal end of the radius, just deep to the insertion of the brachioradialis. It is a pronator of the forearm and hand.

**Flexor digitorum profundus/ Flexor pollicis longus** (Figure 15)

This muscle is two separate muscles in humans, but is combined in *Varecia*. This composite muscle has three origins: superficial, ulnar, and radial.

- **Superficial origin:** The most superficial origin is from the medial epicondyle
- **Ulnar origin:** The ulnar origin arises from the proximal portion of the medial aspect of the ulna, distal to the olecranon process. The belly attaches along the shaft of the ulna, until the distal third of the bone.
- **Radial origin:** The radial origin arises from the proximal portion of the medial aspect of the radius, distal to the neck. The muscle belly adheres along the shaft of the radius, deep to the attachment of pronator teres.

All three muscle bellies become bound tightly to one another at the wrist and then separate again into three large tendons: ulnar, middle, and radial.

- **Ulnar tendon:** The ulnar tendon is less tightly bound than the other two and receives a small tendon from flexor digitorum superficialis at the wrist. The ulnar tendon continues to insert on the distal phalange of digit V.
Middle tendon and radial tendon: At the wrist these tendons are tightly bound and a thin tendon leaves this bundle to insert on digit I. The bundle then separates into three tendons that insert on digits II through IV respectively.

The ulnar tendon flexes digit V and the middle and radial tendons flex digits II through IV.

Figure 15. Deep musculature of right forelimb, medial view.

Dorsoepitrochlearis (Figure 16)
This muscle originates from the deep surface of the latissimus dorsi tendon. The insertion is by a tendinous sheath covering the olecranon of the ulna and the head of the radius.

**Deltoideus complex (Figures 13, 16)**

The deltoideus complex has three portions of muscle (clavicular, acromial, and spinal), which originate separately but join at a single insertion.

**Clavicular:** The clavicular portion originates by a thick attachment on the inferior portion of the most distal third of the clavicle (before the acromial end). This is connected to the acromial portion by a thin fascia. The clavicular portion of the deltoid moves the arm anteriorly.

**Acromial:** The acromial portion originates from the acromial end of the clavicle and joins the clavicular potion. The acromial deltoid is superficial to the spinal portion of the deltoid. The acromial portion abducts the arm.

**Spinal:** The spinal portion originates as fascia anchored to the ventral spine of the scapula. It is completely muscular by the acromion. The dorsal portion extends along the dorsal side of the body above the infraspinous fossa of the scapula. It stretches laterally toward the humerus, and attaches on the underside of the lateral portion of the deltoid. The spinal deltoid laterally rotates the arm.

The deltoideus complex has a single fleshy insertion on the ventral portion of the shaft of the humerus, covering the deltoid tuberosity.
**Triceps brachii** (Figures 14, 16)

Triceps brachii is composed of three heads with separate origins: long, lateral, and medial.

**Long head**: The long head originates from a flat tendinous sheath that attaches along the caudal border of the scapula.

**Lateral head**: The lateral head originates from a tendinous sheath that extends distally from the lateral aspect of the neck of the humerus.

**Medial head**: The medial head originates by tendinous fibers on the posterior part of the humeral neck. These fibers continue to originate distally along the humeral shaft.

The three heads of triceps brachii join around the midhumeral shaft and insert as a single tendinous sheath to the olecranon process. Triceps brachii acts to extend the arm.

**Anconeus** (Figure 16)

Anconeus is a small, thin muscle originating around the posterior edge of the trochlea. It inserts along the lateral edge of the olecranon and along a few centimeters of the ulnar shaft.

**Brachioradialis** (Figures 13, 16)

Brachioradialis lies on the lateral side of the body throughout its length. It originates halfway down the length of the humerus along the supinator crest. The proximal portion of its body sends fibers to the superficial and lateral bellies of brachialis anticus. Brachioradialis has
a tendinous insertion on the distal portion of the ventral side of radius, just before the extensor retinaculum. Brachioradialis flexes the arm with the palmar surface of the hand facing medially.

**Extensor carpi radialis longus** (Figure 16)

This muscle originates on the lateral edge of the humerus just distal to brachioradialis, along the supinator crest. The insertion ends just above the lateral epicondyle of the humerus. Proximally, it receives muscle fibers from the belly of the extensor carpi radialis brevis. Extensor carpi radialis longus becomes tendinous toward the first third of the radius and runs beneath the insertion tendon of extensor carpi pollicis longus to insert on the anterior side of the proximal portion of metacarpal II. Extensor carpi radialis flexes the wrist anteriorly, with the palmar surface of the hand facing medially.

**Extensor digitorum** (Figure 16)

The muscle originates from the lateral epicondyle of the humerus just distal to the origin of extensor carpi radialis brevis. Its fibers fuse with extensor digiti minimi for almost its entirety but they become indistinguishable at its origin. Extensor digitorum becomes tendinous at the distal third of the radius and then divides into four separate tendons at the radio-carpal joint. Tendons are hereafter numbered one through four, with the first tendon the most lateral and the fourth and last tendon most medial.

**Tendon 1**: The most cranial tendon inserts on the lateral aspect of the extensor expansion of phalange II
Tendon 2: The second tendon inserts on the lateral aspect of the extensor expansion of phalange III.

Tendon 3: The third tendon inserts on the lateral aspect of the extensor expansion of phalange IV.

Tendon 4: The fourth tendon inserts on the lateral aspect of the extensor expansion of distal phalange.

The four tendons of extensor digitorum abducts digit two through five respectively.

Extensor digiti minimi (Figure 16)

This muscle originates on the lateral epicondyle of the humerus with the origin of extensor digitorum. Its tendon separates from those of extensor digitorum around the mid-humeral shaft. This tendon divides into two at the metacarpals. The first tendon inserts on the dorsal aspects of the extensor expansions of phalange IV. The second tendon inserts on the posterior aspect of the extensor expansion of phalange V. Extensor digiti minimi abducts digits four and five.

Extensor carpi ulnaris (Figure 16)

This muscle originates from the lateral epicondyle of the humerus, distal to the extensor digitorum. This muscle is contained within a fascia that includes the supinator. Flexor carpi ulnaris is completely tendinous by the distal third of the ulna and inserts on the lateral aspect of the hamate. Extensor carpi ulnaris is an extensor of the hand at the wrist joint.
Abductor pollicis longus (Figure 17)

This muscle originates deep to the anconeus on the radial tuberosity of the ulna by a thin muscular attachment. The muscle attaches fibrously to the radius. The muscular body ends in a tendon. The tendon of abductor pollicis longus wraps towards the medial, distal end of the radius and inserts on the proximal portion of metacarpal I. Abductor pollicis longus abducts and extends the thumb.

Extensor pollicis longus (Figure 17)

Extensor pollicis longus originates distal to the origin of the abductor pollicis longus on the neck of the ulna. The muscle is very thin and becomes tendinous in the distal portion of the ulna. Extensor pollicis longus runs deep to a bony process of the lateral portion of the trapezium to insert on the distal portion of the first carpal. Extensor pollicis longus extends the thumb.
Extensor indicus (Figure 17)

The muscle originates as fibers about halfway distally along the humerus. It is attached to the humerus until the last third where it continues mostly tendinously as far as the radio-ulnar joint. Here it separates into radial and ulnar tendons.

Radial tendon: This tendon inserts on the posterior side of the metacarpal II.

Ulnar tendon: This tendon splits once again into two tendons that insert on the posterior side of metacarpals III and IV.

The radial tendon of extensor indicus flexes digit II and the ulnar tendon extends digits III and IV.

Supinator (Figure 17)

This muscle originates by a tendinous sheath attached to the lateral epicondyle of the humerus and covers the head of the radius laterally. This muscle thins and remains covered superficially by its tendinous sheath, until inserting muscularly on the first third of the anterior portion of the radius. Supinator supinates the forearm.
**Hindlimb Skeleton**

**Pelvis** (Figures 18, 19)

The pelvis of *Varecia variegata* is long, narrow, and appears rather straight in the lateral view. It is composed of three distinct but fused bones, the ilium, ischium, and pubis. The acetabulum is spherical and deep for articulation with the head of the femur.

**Ilium**: The ilium of *Varecia variegata* is a rectangular structure elongated cranially. The cranial half of the ilium curves laterally as the level of the first sacral vertebrae and is flat dorsolaterally. In the ventral view, the medially facing iliac fossae appears
more as a flat, lateral incline than a depression of the bone. The iliac crest is has a slight cranial curvature. The anterior superior iliac spine is oriented ventrally and curves laterally. The posterior superior iliac spine is oriented dorsally. The anterior inferior iliac spine is well developed and protrudes laterally and ventrally. There is no posterior inferior iliac spine or greater sciatic notch. Overall, the ilium creates more of a fossa on its lateral face than medial.

**Ischium:** The ischial spine is a small dorso-caudally pointing structure. Its projection defines the lesser sciatic notch just caudal to it. The ischial tuberosity is an oblong structure at the very caudal end of the ischium that protrudes slightly dorsally.

**Pubis:** The inferior pubic ramus has no curvature but runs straight in the dorso-lateral direction. The pubic tubercle is a small process protruding from the superior ramus of the pubis.
Figure 18. Left pelvis, lateral view.
Femur (Figures 20, 21)

At the proximal diaphysis the head of the femur is rounded, with the fovea located slightly off center in the ventral direction. The anatomical neck is short but thick. The greater trochanter is very well developed and curves cranio-dorsally, with its most cranial portion being just slightly more cranial than the head. In the posterior view, the trochanteric fossa is especially deep and elongated cranio-caudally. The lesser trochanter is a small, medial protrusion caudal to the anatomical neck. The third trochanter is a rounded protrusion on the lateral side of the femur inferior to the greater trochanter and the intertrochanteric fossa. The medial and lateral epicondyles are small on their respective sides. The smooth lateral and
medial condyles can be seen in the ventral view, with the medial condyle being larger of the two.

Figure 20. Right femur, dorsal view.
Figure 21. Right femur, ventral view.

Tibia (Figure 22)

The medial and lateral condyles are well developed in the *Varecia* tibia. In the anterior view, the tibial tuberosity is well defined in the proximal part of the shaft as a raised
semicircular ridge. The medial malleolus is well developed and has a pronounced medial curvature, resulting in a concave, hooked appearance.

Figure 22. Right tibia, anterior view.

Fibula (Figure 23)
The fibulae of *Varecia* are characteristically thin with the head a thickened proximal epiphysis. At the distal epiphysis the lateral malleolus is a small projection from the lateral side of the bone.

![Figure 23. Right fibula, lateral view.](image)

**Hindlimb Musculature**

*Gluteus maximus* (Figure 24)
Gluteus maximus originates cranially by a tough fibrous fascia that connects to the iliac crest. This fascia is tightly invested to gluteus medius for the cranial half of gluteus medius. The ventral portion originates directly by muscle on the anterior portion of the iliac crest. Dorsocranially, gluteus maximus originates by a fascia from the iliac crest. Dorsocaudally, gluteus maximus originates by the thoracolumbar fascia at the level of the sacral vertebrae. The muscle is very wide at the origin and gradually tapers as it reaches the end of its insertion. This muscle inserts directly on the entire length of the diaphysis of the femur. Gluteus maximus acts to extend the hip and abduct the hip.

**Gluteus medius**

Gluteus medius originates from the ventrolateral aspect of the sacrum. Its origin is deep to the gluteus maximus but far less broad. This muscle tapers toward its insertion on the posterior side of the greater trochanter. Gluteus medius acts to abduct the hip.

**Gluteus minimus**

Gluteus minimus has a muscular origin from the caudal portion of the ilium, broader than that of gluteus medius. This muscle runs deep to gluteus medius. The body of gluteus minimus tapers toward its insertion on the head of the greater trochanter of the femur. It acts to abduct the hip.

**Vastus lateralis** (Figure 24)

Vastus lateralis is highly developed in *Varecia*. Originating from the greater trochanter of the femur, it travels along the entire lateral side of the femur to insert on the lateral side of the patella. Vastus lateralis acts to extend the knee.

**Biceps femoris** (Figure 24)
Biceps femoris originates as two thin sheets of muscle off the proximal portion of the muscle belly of the semitendinosus. This muscle runs along the lateral side of the semitendinosus. This muscle is not bicipital but it does have two distinct and almost entirely separable portions. The more dorsal portion has a thicker muscle belly proximally, before flattening in its distal half. The more ventral portion receives a thin contributing muscle about halfway down the semitendinosus muscle belly. Biceps femoris inserts as a broad, flat fascial sheet investing itself along the lateral shaft of the tibia from the tibial tuberosity to the last third of the shaft, where muscle fibers are still visible. Biceps femoris acts to flex the knee.

Figure 24. Superficial musculature of the right hindlimb, lateral view.

**Rectus femoris** (Figure 25)

Rectus femoris originates by muscle from the anterior inferior iliac spine. It travels linearly in the dorsal compartment, as a thick muscle body, to insert on the patella by thick tendon. Acts to flex the leg at hip joint and extend the knee joint.
**Vastus medialis** (Figure 25)

Vastus medialis originates from the intertrochanteric line on the dorsal side of the femur. This muscle travels down the medial side of the thigh to insert by fascia on the medial side of the patella. Vastus medialis acts to extend the knee.

**Sartorius** (Figure 25)

Sartorius originates by fascia from the anterior portion of the iliac crest. It is a thin muscle passes obliquely in the medial compartment of the thigh. It attaches as a flat sheet of muscle to its point of insertion on the medio-anterior aspect of the tibia. Sartorius acts to flex the hip and flex the knee.

**Gracilis** (Figure 25)

Gracilis originates along the entire length of the pubic symphysis. Gracilis remains medial throughout its length until its insertion on the medio-anterior aspect of the tibia with the other two members of the pes anserinus (gracilis, sartorius, and semitendinosus). As gracilis joins with the pes anserinus it becomes completely tendinous and relatively flat. Gracilis adducts the thigh and flexes the knee.

**Semitendinosus** (Figure 25)

Semitendinosus originates from the ischial tuberosity by muscular attachments lateral to the semimembranosus. This muscle remains robust as it travels in the posterior compartment of the thigh until its insertion on the medio-anteior aspect of the proximal third of the tibia. Semitendinosus acts to extend the hip and flex the knee.

**Semimembranosus** (Figure 25)
Semimembranosus originates from the ischial tuberosity medial to the semitendinosus. It is a robust muscle and remains so throughout its length. This muscle begins to taper in the last third of the femur. It inserts by a thick tendon to the medial condyle of the tibia. Semimembranosus acts to flex the knee and flex the hip.

![Figure 25. Superficial musculature of the right hindlimb, medial view.](image)

**Vastus intermedius** (Figure 26)

Vastus intermedius originates from the diaphysis of the dorsal side of the femur. The muscle body begins at the proximal portion of the diaphysis and remains attached to the bone as it widens along the dorsal face, until the distal end of the femur. Vastus intermedius inserts laterally and medially on the fascia surrounding the patellar joint. Vastus intermedius acts to extend the knee.

**Pectineus** (Figure 26)
Pectineus originates by muscle from the superior ramus of the pubis, lateral to the origin of adductor longus. It is flat and thick at its origin but tapers and becomes tendinous just before its insertion on the medial aspect of the proximal femoral shaft. Just below the surgical neck. This muscle inserts superficial to the insertion of adductor brevis. Pectineus acts to adduct the hindlimb.

**Adductor longus** (Figure 26)

This muscle has a fleshy origin from the pubic tubercle, just cranial to pubic symphysis. It is a thin muscle that tapers and becomes a flat tendon just before its insertion on the dorsomedial aspect of the femur midway down but more medial to the cranial portion of the adductor magnus insertion. Adductor longus acts to adduct the hindlimb.

**Adductor brevis** (Figure 26)

This muscle has a thick muscular origin, deep to adductor longus, from the cranial portion of the pubic symphysis and caudal to the pubic tubercle. It originates as a relatively thick muscle but tapers towards its flat, brief muscular insertion. This insertion is deep but slightly distal to the insertion of pectineus, on the proximomedial aspect of the femoral shaft.

**Adductor magnus** (Figure 26)

In *Varecia variegata* adductor magnus is comprised of two muscles that are separable except at an overlapping portion of its insertion, caudal portion of adductor magnus and the cranial portion.

**Caudal portion**: The caudal portion of adductor magnus originates from the caudalalmost portion of the pubic symphysis by flat musculature. The muscle remains flat throughout its length but broadens as it elongates in the medial compartment of the thigh. Its
insertion begins in the first third of the ventral aspect of the femur. This muscular insertion extends down the midline of the dorsal aspect of the femur, medial to the insertion of gluteus maximus, along the entirety of the shaft.

**Cranial portion:** The cranial portion of adductor magnus originates along the pubic symphysis just cranial to the origin of the caudal portion of adductor magnus. It is slightly thicker and overlaps the caudal portion for most of its muscle belly. However its insertion is more proximal and slightly medial to it. Its insertion is partially by muscular slips and partially tendinous beginning in the first third of the femoral shaft and terminating almost midway down. Both the cranial and caudal portions of adductor magnus act to adduct the hindlimb.

![Deep musculature of the left thigh, medial view.](image)

**Tibialis anterior** (Figure 27)

This muscle originates from the lateral side of the shaft of the tibia as a thick muscle. The muscle body separated from the bone in the distal third of the tibia. At this point, the
muscle belly also becomes drastically thinner and more tendinous. Tibialis anterior breaks into two major insertions. The larger insertion is on the plantar side of the first cuneiform and the smaller insertion travels dorsally and inserts on the dorsal side of the distal phalange of digit I. Tibialis anterior acts to dorsiflex the foot.

**Extensor digitorum longus (Figure 27)**

This muscle originates from below the lateral condyle of the tibia, as a thin muscle. In the distal third of the tibia, the muscle belly becomes completely tendinous. After the level of the carpals, it breaks into four separate tendons.

**Tendon 1:** This tendon inserts on the proximal phalange of digit II.

**Tendon 2:** This tendon inserts on the proximal phalange of digit III.

**Tendon 3:** This tendon inserts on the proximal phalange of digit IV.

**Tendon 4:** This tendon inserts on the proximal phalange of digit V.

Extensor digitorum longus acts to extend digits II through V.

**Peroneus longus (Figure 27)**

Peroneus longus originates as muscle from the lateral condyle of the tibia and the head of the fibula. The muscle belly is thick and becomes completely tendinous in the distal third of the shaft. It travels behind the lateral malleolus of the fibula to reach the plantar aspect of the foot. It inserts on the base of metatarsal I. Peroneus longus acts to plantarflex digit I.

**Peroneus brevis (Figure 27)**

This muscle originates from the anterior portion of the fibula. The muscle belly remains invested to the shaft of the fibula until its distal end. Here, it becomes a thin tendon that inserts on the base of metatarsal V. Peroneus brevis acts to plantarflex digit V.
Gastrocnemius (Figure 28)

Gastrocnemius has two heads in the dorsal compartment of the leg, the lateral and medial heads.
Medial head: The medial head originates from the medial condyle of the femur.

Lateral head: The lateral head originates from the lateral condyle of the femur.

The two heads converge to insert on the calcaneus via the calcaneal tendon. Gastrocnemius acts to plantarflex the foot.

Soleus

Soleus travels on the underside of gastrocnemius. It originates as a tendinous attachment to the head of the fibula. The muscle belly is first seen in the first third of the fibula. Soleus inserts on the calcaneus via the calcaneal tendon. Soleus acts to plantarflex the foot.
Flexor digitorum fibularis (Figure 29)

This muscle originates as a thick muscle from the head of the fibula and remains invested on the shaft of the fibula until almost its distal end. The muscle belly tapers into a thick tendon and travels to the plantar side of the foot. At the level of the metacarpals, it becomes highly invested with the tendon of flexor digitorum tibialis. It then separates into five distinct tendons. These tendons run deep to those of flexor digitorum tibialis but appear much thicker.
Tendon 1: This is a large tendon that inserts on the distal phalanx of digit I. Before its insertion this tendon receives a contributing fiber from flexor digitorum tibialis.

Tendon 2: This tendon inserts on the distal phalanx of digit II.

Tendon 3: This tendon inserts on the distal phalanx of digit III.

Tendon 4: This tendon inserts on the distal phalanx of digit IV.

Tendon 5: This tendon inserts on the distal phalanx of digit V.

Flexor digitorum fibularis acts to flex digits I through V.

Flexor digitorum tibialis (Figures 28, 29)

This muscle originates from the posterior shaft of the tibia. In the first third of the tibia this muscle begins to thin and become tendinous. Slips of muscle still invest along the shaft until the distal third of the tibia. Here, flexor digitorum tibialis is a well developed tendon. It passes behind the medial malleolus and breaks into four tendons which insert independently.

Tendon 1: This tendon inserts on the plantar aspect of distal phalanx II.

Tendon 2: This tendon inserts on the plantar aspect of distal phalanx III.

Tendon 3: This tendon inserts on the plantar aspect distal phalanx IV.

Tendon 4: This tendon inserts on the plantar aspect of distal phalanx V.

This muscle also contributes a thin tendon to the tendon of flexor digitorum fibularis. Flexor digitorum tibialis acts to flex digits I through V in the foot (digit I being flexed by the contributing fiber to flexor digitorum fibularis).

Tibialis posterior (Figure 29)

This muscle originates from proximal underside of the muscle belly of flexor digitorum fibularis. It begins to separate and become an individual muscle about midway
down the tibia and is completely tendinous by the distal third of the shaft. This muscle runs between the flexor digitorum fibularis and flexor digitorum tibialis. It travels posterior to the medial malleolus to the plantar aspect of the foot where it expands to insert on the plantar aspect of the navicular and cuneiform I. Tibialis posterior acts to plantarflex the foot.

![Deep musculature of left leg, posterior view.](image)

**Figure 29.** Deep musculature of left leg, posterior view.

**Discussion Skeleton**

This section will discuss the skeletal elements that stood out as unique or important to the locomotor behaviors previously documented for this species.

The primate scapula has been studied in great detail by morphologists and determined to be capable of a wide range of locomotor behaviors. The anatomy of a species’ shoulder provides strong anatomical evidence for locomotor habits (Kikuchi, Takemoto and Kuraoka 2012). In particular, the scapular morphology of lemurids is uniquely adapted to permit a wide range of behaviors from clinging and leaping to arboreal quadrupedalism (Roberts and Davidson 1975). These differences in locomotor patterns in such closely related species correlate with their different locomotor strategies. *Varecia variegata* is has been placed in
many different locomotor categories but is mostly considered to be an arboreal quadruped, spending much of its time on all fours in the forest canopy. *Varecia variegata* poses an interesting case, in that this species’ scapula has relatively broad fossae in comparison to other quadrupeds, but these are more narrow than in arboreal climbing species.

The size of the scapular fossae correspond directly to the musculature which arises from them. In this case those muscles are part of a complex known as the rotator cuff musculature. The rotator cuff muscles are the supraspinatus, infraspinatus, subscapularis, and teres minor. The supraspinatus originates from the lateral side of the scapula within the supraspinous fossa, while the infraspinatus and teres minor originate from the infraspinous fossa. The subscapularis originates from the medial side of the scapula in the large subscapular fossa. The larger and more robust these muscles become in life the broader these fossae will ultimately become. The robustness of muscle also correlates to the frequency of use. The supraspinatus abducts the forelimb. The infraspinatus and teres minor rotate the forelimb laterally. The subscapularis rotates the forelimb medially. The exact origins, insertions, and actions are summarized in Table 2. Used together these muscles allow the forelimb to be lifted cranially away from body while also maintaining the ability to rotate around its axis.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Origin</th>
<th>Insertion</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Supraspinatus</td>
<td>Supraspinous fossa</td>
<td>Greater tubercle</td>
<td>Abduction of forelimb</td>
</tr>
<tr>
<td>Infraspinatus</td>
<td>Infraspinous fossa</td>
<td>Greater tubercle</td>
<td>Lateral rotation at the shoulder</td>
</tr>
<tr>
<td>Teres Minor</td>
<td>Infraspinous fossa</td>
<td>Greater tubercle</td>
<td>Lateral rotation at the shoulder</td>
</tr>
<tr>
<td>Muscle</td>
<td>Origin</td>
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</tr>
<tr>
<td>Subscapularis</td>
<td>Subscapular fossa</td>
<td>Lesser tubercle</td>
<td>Medial rotation at the shoulder</td>
</tr>
</tbody>
</table>

Given this information, broad fossae in such a species is necessary for climbing activities. They must regularly stretch their arms above their heads to grasp branches above themselves. The individual’s orientation relative to the target branch may also require a medial or lateral rotation of the arms. Quadrapeds do not have broader fossae because they do not require strong rotator cuff musculature (Roberts and Davidson 1975). For example, the scapular fossae of *Lemur catta* (ring-tailed lemur), another quadrapedal lemurid, are notably more narrow than that of *Varecia variegata*. *Lemur catta* primarily moves quadrapedally along the forest floor. This species spends thirty percent of its overall time and sixty five percent of its travel time on the ground (Ward and Sussman 1979). If most of its travel is spent moving on all fours along the forest floor, the rotator cuff musculature is being used far less than in an individual which is consistently climbing up trees to jump to the next.

Although *Varecia* tend to move quadrapedally along tree limbs, they would still need to reach upward to climb to the higher levels that they tend to inhabit. Climbing would also be important in regard to leaping activities during travel, especially given *Varecia’s* penchant for long descent leaps. A certain height would need to be reached for these leaps to be successful.

*Varecia* is the largest species of lemurid and larger body size might play a role in similarities or differences compared to other species. If body size were to affect scapular fossa size, then it could complicate morphological interpretation. However, Roberts (1974) determined that scapular shape shares a much stronger connection to locomotor habits than
does individual body size. Scapular shape is more closely related to function than to body size, suggesting that *Varecia’s* greater size is a minimal contributor to overall scapular shape. It can then be deduced that because *Varecia* spends longer time in the higher canopy, that its wider scapular fossa demonstrates a locomotor need, and that need perhaps being stronger rotator cuff musculature.

The humerus of *Varecia variegata* has a distinct dorsal curvature on the proximal end of the diaphysis. Richmond and Whalen (2001) determined that humeral curvature can be indicative of locomotor habits in primates. They found that species with relatively straight humeri tend to be suspensory, while curved humeri belong to quadrupedal groups. More specifically, species with proximal curvature, such as the macaque and howler monkeys, were likely to be arboreal quadrupeds. The specific curvature of *Varecia variegata* confirms that dorsal curvature at the proximal end of the humeral shaft is unique to arboreal quadrupeds.

Another notable skeletal structure in the *Varecia* humerus is the highly developed deltoid tuberosity. It presents as a pronounced elevated structure on the lateral face of the shaft. It shows a slight medial curvature that extends from the head to midshaft. The same concept applies here that was used earlier. This pronounced deltoid tuberosity is due to the repeated use of the muscles inserting there. In this case, those muscles are the pectoralis major, pectoralis abdminus, and deltoideus complex. Pectoralis major medially rotates the arm. Pectoralis abdminus also medially rotates the arm. There are three portions to the deltoideus complex, the clavicular, acromial and spinal portions. The clavicular portion moves the arm in the anterior direction. The acromial portion abducts the arm. The spinal portion laterally rotates the arm. The exact origins, insertions, and actions are summarized in
Table 3. Together, these muscles also allow for the raising and rotation of the forelimb. Taken with the rotator cuff observations, arboreal climbing behaviors (reaching above the body for more superior substrates to climb) are reinforced as a major part of the *Varecia* locomotor repertoire.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Origin</th>
<th>Insertion</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pectoralis major</td>
<td>Midline of anterior body from the clavicle to rib seven</td>
<td>Deltoid tuberosity</td>
<td>Medial rotation at the shoulder</td>
</tr>
<tr>
<td>Pectoralis abdominus</td>
<td>Midline of anterior body between ribs eight or nine to the caudal end of the sternum</td>
<td>Deltoid tuberosity</td>
<td>Medial rotation at the shoulder</td>
</tr>
<tr>
<td>Clavicular deltid</td>
<td>Inferior, distal aspect of the clavicle</td>
<td>Deltoid tuberosity</td>
<td>Anterior flexion of forelimb</td>
</tr>
<tr>
<td>Acromial deltid</td>
<td>Acromial end of the clavicle</td>
<td>Deltoid tuberosity</td>
<td>Abduction of forelimb</td>
</tr>
<tr>
<td>Spinal deltid</td>
<td>Ventral spine of the scapula</td>
<td>Deltoid tuberosity</td>
<td>Lateral rotation at the shoulder</td>
</tr>
</tbody>
</table>

The pelvis of *Varecia* has a well-developed anterior inferior iliac spine. This is the site of origin for the rectus femoris muscle which has the dual actions of flexing the thigh and extending the knee. This muscle is well developed in leaping prosimians, providing a strong force to propel the body to the next branch, and in *Homo sapiens* for use in bipedal walking (Sigmon and Farslow 1986). *Varecia* is known to leap from horizontal and vertical supports, and extends its hindlimbs during hindlimb suspension. Both of these activities would benefit from the presence of a strong rectus femoris.

The tibial tuberosity appears as a raised semicircular ridge on the anterior aspect of the tibia. It’s well developed appearance is due to the insertion of a group of several muscles,
referred to as the pes anserinus. The pes anserinus is composed of the gracilis, sartorius, and semitendinosus muscles. A summary of the origins, insertions, and actions of the pes anserinus is in Table 4. Used together these muscles act to flex and then medially rotate the leg. The lumber jack climbing movement observed by Pereira et al (1988) is a strategy Varecia uses to climb trees without the use of branches. The individual braces itself against the trunk with hands and feet. The hands release while the hindlimb is used to create a force to push the body upward. Then the hands and feet would regrip at the higher altitude. During this type of ascent the muscles of the pes anserinus would be very active, as an individual braces its hindlimb on either side of a vertical support.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Origin</th>
<th>Insertion</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gracilis</td>
<td>Pubic symphysis</td>
<td>Tibial tuberosity</td>
<td>Adduction of thigh and flexion of knee</td>
</tr>
<tr>
<td>Sartorius</td>
<td>Iliac crest</td>
<td>Tibial tuberosity</td>
<td>Flexion of thigh and flexion of knee</td>
</tr>
<tr>
<td>Semitendinosus</td>
<td>Ischial tuberosity</td>
<td>Tibial tuberosity</td>
<td>Extension of thigh and flexion of knee</td>
</tr>
</tbody>
</table>

**Discussion Muscular**

This section will discuss the muscular elements that stood out as unique or important to the locomotor behaviors previously documented for this species.

The panniculus carnosus is a highly superficial muscle, derived from skeletal musculature and present only in mammals, such as the cat, dog, hedgehog, echidna, and some primates (Langworthy 1924). This muscle in Varecia variegata is highly developed and spans
the entire dorsal and lateral thoracic and abdominal musculature. It is present in varying
degrees in some primates and completely lost in others, such as humans.

Panniculus carnosus can be identified in the rhesus macaque, *Macaca mulatta* (Howell
and Straus 1993). Macaques are terrestrial primates, only using arboreal support for selected
activities and feeding (Wells and Turnquist 2001). The population is widespread through
southern Asia, living in varied habitats that include rainforests, bamboo forests, and
coniferous forests (Howell and Straus 1993). The rhesus macaque is diurnal and omnivorous
(Howell and Straus 1993). The panniculus carnosus is highly developed in the Panamanian
night monkey, *Aotus zonalis*. These are nocturnal, arboreal quadrupeds that were once diurnal
but re-evolved nocturnal behaviors and abilities (Wright 1994). Their range extends from the
rainforests of Panama to Argentina and these animals feed on fruits, leaves, and insects
(Wright 1994). This muscle is less developed in the red-backed squirrel monkey, *Saimiri
oerstedii* (Langworthy 1924). This frugivorous and insectivorous monkey is an arboreal
quadruped, spending most of its time in the lower canopy of the forests of Costa Rica and
Panama (Wong, et al. 2014) Panniculus carnosus is present but very underdeveloped in the
white-throated capuchin, *Cebus capucinus* (Campbell 1937). The capuchin is an arboreal
quadruped inhabiting the middle canopy of the forest of Central America (Fragaszy,
Visalberghi and Fedigan 2004) They exist in a variety of habitats such as dry deciduous
forest, humid subtropical forest, and mangroves and their diet consists of fruits, insects, frogs,
and even small mammals (Cuasado, et al. 2014).

The existence of panniculus carnosus to varying degrees in species with different
locomotor habits, inhabiting different kinds of forests, and with varied diets is a possible
indicator that this muscle is conserved. All the examples provided here are of primates which are quadrapedal in some way (arboreal or terrestrial). Therefore it could also be important for quadrapedal mammals. The Panniculus carnosus is so thin and superficial that it is easily pulled away with the skin and overlooked by studies focusing on more prominent features. It could be that it has a greater presence in strepsirrhines and other primates but has yet to be recorded. Furthermore, panniculus carnosus is incredibly well developed in Varecia, so any studies based on the muscle itself could benefit greatly from use of this group.

The biceps femoris in Varecia variegata is particularly interesting because its origin is from the muscle belly of the semitendinosus. The muscle itself is thin but broad and inserts as a fascia to the tibia, much as in the rhesus monkey. However, in the rhesus monkey biceps femoris originates directly from the ischial tuberosity between the semitendinosus and the quadratus femoris (Howell and Straus 1993). This would mean that in the rhesus monkey this muscle will be an extensor of the thigh as well as a flexor of the knee. While in most primates this muscle cannot be said to be comprised of two separate heads, as it does in man, in Varecia there are two distinct portions of the muscle. Biceps femoris is a well developed hip extensor and knee flexor in Homo sapiens. However its unique origin combined with its thin, fascia like presence on the lateral side of the leg changes its action from either species previously mentioned. In Varecia, biceps femoris is has no action on the hip but will act as a weak knee flexor. Its lateral position though may help contribute to knee stabilization.

Semimembranosus is a single muscle in Varecia, however its composition varies among primate species. In humans and the red howling monkey, Alouatta seniculus, semimembranosus is a single muscle. The semimembranosus of the rhesus monkey and
baboon is composed of two parts, the semimembranosus propius and the semimembranosus accessorius (Swindler and Wood 1973) (Howell and Straus 1993).

Vastus lateralis presented as the largest of the quadriceps muscles dissected. In the brown lemur, *Lemur fulvus*, this muscle is what initiates leaping activity (Jungers, Jouffroy and Stern 1980). Vastus lateralis is highly developed in *Varecia* and most likely plays the same role, as a force generator for leaping behaviors. This would be especially important for the long descent leaps observed by Pereira et al. (1988).

Tibialis anterior displayed an interesting variation in the dissected specimen. In the right leg, the two inserting tendons were separable to the point just above the distal epiphyses of the tibia and fibula. Proximal to this, tibialis anterior is a single muscle belly. However, on the left leg the two inserting tendons were separable all the way up the muscle belly to its origin. The lateral portion of these two muscles has, at times, been referred to as the extensor hallucis longus (Howell and Straus 1993).
CHAPTER 3

PATHOLOGY

In this final chapter a pathological disorder found in a captive red-ruffed lemur, *Varecia rubra*, will be discussed. The initial diagnosis for this individual is a pathology of the periosteum called primary hypertrophic osteoarthropathy. This diagnosis was based on several symptoms see in patients diagnosed with primary hypertrophic osteoarthropathy: pachydermia, periostitis, and a genetic component.

This individual was ultimately euthanized and frozen for future study. The following will be a description of the subject’s symptoms in life and the periosteal reactions observed via dissection after its death. From this I drew the conclusion that hypertrophic osteoarthropathy was a misdiagnosis and will present an alternative possible diagnosis for the affected individual.

**Dissection**

The pathology exhibited itself as lesions of varying size along the long bones of the fore and hind limb. Dissection of the forelimb and hindlimbs revealed that the bony projections of the periosteum avoided areas of muscle origin and insertion.

In the forelimb, the lesions grew along the ulna, radius, metacarpals, carpals and phalanges (Figure 30, 31). The lesions along the ulna were by far the most prominent. The proximal and distal epiphyses of the radius presented with large lesions. The ulna also
presented with lesions, especially at its proximal epiphyses. Closer inspection of the hands and feet showed smaller lesions on the metacarpals, carpals, and the phalanges. In some areas the bone has completely overgrown the tendon.

![Figure 30. Right arm, lateral view.](image)

![Figure 31. Left wrist, lateral view.](image)

The hindlimb showed very similar results. Lesions appeared along the tibia and fibula (Figure 32). The most prominent lesions appeared at the distal epiphyses of these long bones. The metatarsals, tarsals, and phalanges had smaller lesions, some having completely
overgrown the tendon. The lesions did not seem to affect the left or right side of the body in different ways. In fact, many of the lesions presented in the same areas and to similar extent in the left and right limbs.

Figure 32. Right leg, anterior view.
Observations and photographs were taken of the skull to confirm the presence of pachydermia (Figure 33). It was determined that this individual showed no signs of pachydermia. Digital clubbing was not reported in the veterinary records nor was it observed in the preserved specimen.

![Figure 33. Anterior view of the faces of unhealthy Varecia rubra (left) and healthy Varecia variegata (right)](image)

**Hypertrophic Osteoarthropathy**

Hypertrophic osteoarthropathy is a condition which can be separated into two types, primary and secondary. Both types have been documented in humans and share many of the same symptoms. Primary and Secondary hypertrophic osteoarthropathy both cause pachydermia, which is a thickening of the skin. Periostitis, an inflammation of the periosteum, is also a common symptom. In these diseases periostitis appears as a symmetric osseus thickening, primarily affecting long bones such as the radius, ulna, tibia and fibula (Kachewar
This thickening is described as being laminated or applique in appearance (Rothschild and Martin 2006). This makes the bone appear as if new, thin irregular layers of bone have been laid on top of the existing bone. Also present in the two types of hypertrophic osteoarthropathy is clubbing of the digits in the hands and feet (Kachewar 2011, Rothschild, Neiffer and Marks 2011, Bhaskaranand, Shetty and Bhat 2001). This presents as a swelling in the tips of the phalanges, making them appear bulbous. Because primary and secondary hypertrophic osteoarthropathy share so many characteristics they can be commonly misinterpreted for one another. However, there are important differences that help to distinguish one from the other.

Secondary hypertrophic osteoarthropathy is most distinguishable by having an underlying pathology, which causes its common symptoms to present. Secondary hypertrophic osteoarthropathy has been attributed to nasopharyngeal and gastrointestinal diseases (Rothschild and Martin 2006). It has also been linked to underlying cardiovascular, hepatic, and endocrine disorders (Matucci-Cerinic, et al. 1991). The periosteal symptoms of this pathology avoid the epiphyses of the effected long bones (Kachewar 2011). Table 5 provides a list of the main (bolded) and minor symptoms of secondary hypertrophic osteoarthropathy and whether they presented in the subject of this study.

<table>
<thead>
<tr>
<th>Table 5 Secondary Hypertrophic Osteoarthropathy symptoms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symptoms</td>
</tr>
<tr>
<td>Clubbing in digits</td>
</tr>
<tr>
<td>Periostitis</td>
</tr>
<tr>
<td>Pachydermia</td>
</tr>
<tr>
<td>Presence of related pathology</td>
</tr>
<tr>
<td>Avoidance of epiphyses</td>
</tr>
</tbody>
</table>
Primary hypertrophic osteoarthropathy also referred to as Pachydermoperiostosis (Matucci-Cerinic, et al. 1991) is characterized by the fact that no other medical issues are present to cause bone overgrowth (Rothschild and Martin 2006). Finger clubbing is the most common symptom seen in this form and in the study performed by Matucci-Cerinic et al (1991) it was reported in every diagnosed case. The primary form also has a genetic component that distinguishes it from the secondary form. Often an officially diagnosed individual also had relatives which presented all or some of the same symptoms (Matucci-Cerinic, et al., 1991). This is most apparent with the appearance of finger clubbing. Finger clubbing is the symptom which most presented itself both in affected patients and their relatives who were also diagnosed with primary hypertrophic osteoarthropathy (Kachewar 2011).

Matucci-Cerinic et al (1991) listed the three most important symptoms for diagnosis of primary hypertrophic osteoarthropathy as finger clubbing, pachydermia, and periostitis. They also classified several forms in which the disease can present itself. The complete form is one in which all three main symptoms are present. The incomplete from is one on which two of the main symptoms present with some minor symptoms. The final form is the “forme fruste”, in which one main symptom is present with some minor symptoms. Their study further discusses the fact that pachydermia and periostitis may or may not be absent in a diagnosed patient. All cases presented with finger clubbing. Table 6 provides a list of main (bolded) and minor symptoms of primary hypertrophic osteoarthopathy and whether they present in the individual.
<table>
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<tr>
<td>Periostitis</td>
</tr>
<tr>
<td>Pachydermia</td>
</tr>
<tr>
<td>Epiphyseal widening</td>
</tr>
<tr>
<td>Genetic component</td>
</tr>
</tbody>
</table>

Periostitis is defined as an inflammation of the periosteum and technically applies here. However, in all other documented cases of primary hypertrophic osteoarthropathy it has applique-like, layered appearance. The specimen under question certainly has a reaction in the periosteum but it presents as bulbous lesions. Taking previous studies into account, it was determined that the periostitis that presents in hypertrophic osteoarthropathy is not present in the study individual.

Pachydermia was also given as a positive symptom in the initial diagnosis. In both forms of hypertrophic osteoarthropathy, pachydermia appears in the patient as a more prominent brow due to the thickening of skin in that area. Such a prominence of the brow was not seen during this investigation as seen in Figure 33.

The only symptom present in the study specimen that completely aligns with the diagnosis of primary hypertrophic osteoarthropathy is the presence of a genetic component. The daughters of the affected individual were observed to have similar symptoms, stiffening of the body and gait. However, the most often shared symptom of finger clubbing did not present itself in any of the individuals. Many diseases and conditions can be shared amongst family members who share a genetic susceptibility to it. This combined with the shared habitat of the individuals affected, leaves solely the genetic component as a poor indicator of the disease.
Nora’s Lesions

Originally described by and named for Frederick E. Nora bizarre parosteal osteochondromatous proliferation (BPOP) is a mineralization of soft tissue from the periosteum with intact cortex (Nora, Dhalin and Beabout 1983). They appear as rounded overgrowths of bone on the long bones, metacarpals, and metatarsals. These lesions occur most often in the phalanges, more so in the proximal than distal portions (Torreggiani, Munk and Al-Ismail 2001).

Dhon et al (2006) described the stages of the developing lesions from observations of radiographs. Nora’s lesions typically begin as a periosteal soft-tissue swelling or mass. The mass begins to undergo calcification until it reaches the point of being a completely ossified lesion. Noras’ lesions often goes unrecognized, misdiagnosed, and mistreated (Dhont, et al. 2006, Gursel, et al. 2008).

Pathology Conclusions

The lesions observed encompassing the tendons of the metatarsals, metacarpals and phalanges could have been particularly problematic in life. A contracting muscle in the fore or hindlimb acts on the skeletal digits through its tendinous insertion. The lesions overgrowing these tendons at different levels of the hands and feet could act as pseudo insertions, if the action of the muscle is unable to pass this point or simply weakened beyond this point. This would greatly reduce dexterity in the hands and feet. For an animal climbing and feeding in tree tops this could be devastating.
The largest lesions appearing at the epiphyses of the bones could also prove to be very problematic. For example the large lesions seen at the distal end of the ulna and radius would certainly have reduced the normal range of motion at the wrist joint. The same could be said for the lesions at the ends of the tibia and fibula.

A diagnosis of secondary hypertrophic osteoarthropathy is not supported because of the lack of underlying pathologies. If primary hypertrophic osteoarthropathy was the condition, then some major assumptions would have to be made. The type of periostitis see in the affected individual would have to have manifested in this case differently than in any other diagnosed individual, as lesions instead of applique type. The most common symptom, digital clubbing, is absent. It was noted in the veterinary records that the subject’s daughter began to exhibit similar symptoms, such as stiffness of gait. However, the symptom most commonly seen in the family members of individuals with primary hypertrophic osteoarthropathy, digital clubbing, is also absent in the daughter.

This work supports the diagnosis of Nora’s lesions for this individual. The shape, progression, and location of the periosteal growths described in Nora’s lesions, matches the lesions observed in the affected specimen described here. This diagnosis may have been overlooked by the veterinarians at the time because of the rarity of this condition, and its similarity to hypertrophic osteoarthropathy. This particular pathology has only been documented in humans thus far, and is absent from veterinary journals.
CHAPTER 4
CONCLUSIONS

The normal or healthy condition for the forelimb and hindlimb anatomy for Varecia was established through the dissection of a captive black and white ruffed, Varecia variegata, from the Pittsburgh Zoo. Observations from both the skeletal and muscular anatomy showed structures in concordance with what we understand about the behavior and lifestyle of Varecia, an arboreal adapted primate. For example, a dorsally curved humerus is an indication of quadrupedal movements and Varecia certainly moves in this manner. In a similar way, Varecia’s broad scapular fossae confirm its reliance on climbing movements through the tree tops. The overall forelimb and hindlimb musculoskeletal anatomy of Varecia fits with its arboreal lifestyle being largely an arboreal quadruped that spends much of its time in the canopy of rainforests.

This normal anatomical pattern in Varecia allows us to examine the main question of this study concerning the effects of a bone disease. Comparing the healthy individual to the affected specimen showed that periosteal reactions did not disrupt the origins and insertions of the forelimb or hindlimb musculature. This observation suggests that the lethargic behavior noted for the diseased individual cannot be explained in terms of simple muscle mechanics. Instead, the osteological lesions grew over the muscles and in most cases the tendons along the carpals, metacarpals, tarsals, and metatarsals in the hands and feet. This altered and weakened the gripping or grasping abilities in the hands and feet of the diseased individual, in
comparison to the healthy individual, and may explain why the diseased individual had a reluctance to climb. The large growths at the distal epiphyses would have compounded any movements by reducing the range of motion at those joints.

The initial diagnosis of primary hypertrophic osteoarthropathy was dismissed based on the absence of the three main symptoms associated with this disease: finger clubbing, pachydermia, and periostitis. It should be noted that while periostitis was present in the study individual it was in a form not seen in patients with primary hypertrophic osteoarthropathy. Instead, the presence of bony lesions on the long bones, carpals, metacarpals, tarsals, metatarsals, and phalanges make Nora’s lesions (bizarre parosteal osteochondromatous proliferation) a more likely diagnosis. Nora’s lesions begin as periosteal growths that then calcify. The continuously elevating ALP (Alkaline Phosphatase) levels further support this diagnosis. ALP increases in the blood are correlated with osteoblasts actively creating bone. As the lesions grew in size and number, calcifying along the way, rising ALP was being found in all blood tests performed on the diseased individual.

Future studies of Nora’s lesions in Varecia or other primates should be geared towards living individuals. A range of motion study at the joints could help determine the degree in which motion is lost at the epiphyseal sites of these lesions. Testing the dexterity and power grips for both the hands and feet would be important data to collect as well. All of this information could help determine the degree in which Nora’s lesions affect grip and dexterity of the affected individuals. In the end, this case study is the first example of Nora’s lesions found in a non-human primate.
REFERENCES


