7 The Soft-Tissue Anatomy of the Highly Derived Hand of *Perodicticus* Relative to the More Generalised *Nycticebus*

Marissa Boettcher, Kaitlyn C. Leonard, Anthony Herrel and
Adam Hartstone-Rose

7.1 Introduction

7.1.1 Characteristics of *Perodicticus*

The African lorisid subfamily Perodicticinae includes the slow-moving angwantibos (*Arctocebus*) and the pottos (*Perodicticus*) (Lambert, 2014), the focal taxon of this chapter. The distinguishing physical features of this subfamily include their short tails and vestigial manual second digit (Charles-Dominique, 1977a). *Perodicticus potto*, first described by Bosman in 1704 and further characterised by Müller in 1776 (Bosman, 1705; Müller, 1773; Smeenk et al., 2006), was originally placed in the genus *Nycticebus* by Geoffroy, but the subsequent rediscovery of the animal in Sierra Leone by Bennett in the early nineteenth century became the basis for his naming the genus *Perodicticus* (Bennett, 1831; Hill, 1953a; Smeenk et al., 2006).

Perodicticus is the largest of the African lorisids and has a geographical distribution that includes West and Central Africa, extending from Liberia to Kenya (Chiarelli, 1972; Fleagle, 1999; Nekaris and Bearder, 2007; Poindexter and Nekaris, 2017a). On average, across the three known species, the males have an average body length of 337–406 mm and tail length of 50–81 mm, while the females are slightly smaller, with an average body and tail length of 355–417 mm and 56–72 mm, respectively (Chiarelli, 1972). Like most primates, they are arboreal and often maintain a height of 30 m above the ground in the canopy (Lambert, 2014).

7.1.2 Locomotion and Limb Anatomy

The locomotion of *Perodicticus* is highly characteristic of the species. In an unstressed state, their limb movements tend to be slow and deliberate, with a constant rate maintained during each phase (i.e. movement of a limb towards or away from a substrate) and only one limb breaking contact at a time (Jouffroy et al., 1983). Even under stressful conditions, *Perodicticus* has been reported never to completely break contact with a substrate (Bishop, 1962; Oates, 1984). This maximises stability and this, along with its powerful grip, allows for very slow, deliberate motion (Charles-Dominique, 1977a).

The highly derived hands of *Perodicticus* (Figure 7.1) play an integral role in their distinctive locomotor habits and many of their anatomical apomorphies are likely related to their slow-moving, arboreal lifestyle. These relatively unique anatomical

Figure 7.1 *Perodicticus potto.* Note the extent to which the thumb directly opposes the fingers at 180°, and the highly reduced second ray (arrow inset).
Photos courtesy of David Haring, the Duke Lemur Center

features include their severely reduced second digit and hyper-abducted pollex (~180 degrees) (Bishop, 1962; Hill, 1953b; Jouffroy et al., 1983; Oates, 1984; Walker, 1979), as well as their reportedly strong grip (Lemelin and Jungers, 2007; Oates, 1984). These characteristics limit the possible orientations of the hand during substrate grasping in such a way that the branch always sits in the hand of *Perodicticus*, running from the base of the fifth metacarpal to the distal end of the second metacarpal (Bishop, 1962), as seen in Figure 7.1. During the initiation of grasping, the distal region of the palmar pad makes first contact with the substrate and, subsequently, digits I, III, IV and V wrap around the substrate, with the highly reduced second digit always pointing in the direction of motion when hand-over-hand locomotion is used (Bishop, 1962). Additionally, *Perodicticus* (along with the other Lorisidae primates; Grand, 1967) has specialised leg and fore-limb vasculature called *retia mirabilia* (Hill, 1953b; Wiens, 2002) that function to lower tissue temperature and, thus, the demand for oxygen in the muscles (O'Dea, 1990). In *Perodicticus*, this structure has been described as providing the oxygenation that allows them to maintain their strong grasp for hours (Lambert, 2014; Nekaris and Bearder, 2007; Poindexter and Nekaris, 2017a). Although locomotor adaptations are often considered in response to predation, this is likely not the case for lorisids as other nocturnal animals of similar size have not developed such anatomical features (Oates, 1984).

The locomotor patterns of *Perodicticus* have been previously studied (Bishop, 1962; Jouffroy et al., 1983), but current literature regarding their underlying soft-tissue anatomy is lacking. Of the minimal documentation that exists regarding their intrinsic and extrinsic hand muscle anatomy, the most thorough accounts were published over 50 years ago and lack photographic evidence to support their descriptions (Forster, 1933; Kanagasuntheram and Jayawardene, 1957; Murie and Mivart, 1869; Straus, 1942; Van Campen and Van der Hoeven, 1859). Furthermore, the previously published studies did not describe in detail the origins and insertions of the muscles and have failed to mention/describe certain muscles. Though the authors of these previous studies have included *Perodicticus* in their samples, few have given special attention to its musculature (see Table 7.1–7.6 for specific myological descriptions obtained from the existing literature), though Murie and Mivart (1869), Jouffroy (1962) and Kanagasuntheram and Jayawardene (1957) have been the most thorough.

7.1.3 Previous Descriptions of Muscle Functional Morphology

In the earlier study from 1869, Murie and Mivart examined an unspecified number of primates. Eight of the individuals (all of which belonged to *Loris* and *Galago* – *sensu lato*) included in their sample were dissected by the authors and the remaining were taken from earlier studies for comparison. Of the descriptions of the forearm and hand musculature of *Perodicticus* and *Nycticebus* provided by the authors, the most detail was given for the digital muscles (as opposed to the wrist extensors and flexors and the positional muscles) – specifically their insertions. The visual descriptions of the musculature and notes on the non-digital forearm and hand muscles were lacking. The study conducted by Kanagasuntheram and Jayawardene in 1957 gave myological descriptions for the intrinsic hand musculature with a much narrower sample including three individuals from the family Lorisidae: *Nycticebus coucang*, *Loris tardigradus* and *Perodicticus potto* (all *sensu lato*). Although the authors provided more substantial visual descriptions via diagrams of the musculature than were given by Murie and Mivart, minimal descriptions were given for the forearm musculature – specifically the non-digital forearm muscles. Finally, the most complete description of the myology of the forearm muscles in lemurs and strepsirrhines in general is that of Jouffroy (1962). She dissected two *Perodicticus*, two *Nycticebus*, one *Loris*, one *Otolemur*, two *Galagoides* and two *Galago*, in addition to a broad sample of lemurs and other primates. All the muscles of the forelimb were described in this study, but illustrations principally concern the muscles in lemurs.

Due to the confusion that exists and the contradictory information on the muscles of the forearm and hand in *Perodicticus*, the aim of our study is to provide a thorough account and illustrations of these muscles. To do this, we include photographic illustrations and detailed notes of the orientations and attachments of each muscle. We also note how this taxon's myology differs from typical primate anatomy and from previous descriptions of this species. We also conducted new dissections of the closely related *Nycticebus coucang* to contextualise further the derived morphology of *P. potto* in comparison to a more generalised lorisid. We use the taxonomy ascribed to the species in question based on their labelling from their relevant institutions, recognising that these may later be updated.

7.1.4 Hypotheses

1. Because the wrist flexors and extensors and the forearm positional muscles do not typically qualitatively vary in primates (Leischner et al., 2018), we do not expect to see considerable differences in these muscles between *P. potto* and *N. coucang.*
2. Because of its highly reduced second digit, however, we do expect to see differences in the muscular anatomy of the second digit between *P. potto* and *N. coucang*. Although Murie and Mivart (1869) and Forster (1933) previously reported that extensor indicis in *Perodicticus* extends to multiple digits (not just the second one) and is therefore not a true extensor indicis, we expect to see either the complete absence or reduction of a dedicated extensor indicis muscle in *Perodicticus*. We do not expect to see an insertion of the digital flexors and extensors on the second digit due to its reduced size and role in locomotion.
3. We also expect to see differences in musculature of *Perodicticus* associated with its hyper-abducted first digit – perhaps more differentiated or substantial extrinsic and intrinsic pollucial muscles.

7.2 Methods

We dissected the forearm region (physical compartment, not functional) and hands of two lorisids: a male, formalin-preserved potto (*Perodicticus potto – sensu lato*) from the Muséum National d'Histoire Naturelle in Paris, France (MNHN 1939-524) and a female, fresh/frozen Sunda slow loris (*Nycticebus coucang*) from the Duke Lemur Centre in Durham, NC (AHR 110005). The potto was a wild-caught lab specimen that was used in a behavioural study (Jouffroy et al., 1983) and the slow loris was born in captivity. Because we were only able to sample one *P. potto* specimen, it is difficult to determine whether some of our findings are attributable to species characteristics or intraspecific variation. To mitigate this, we observed the musculature of a second specimen (MNHN 1973-230) to confirm these qualitative findings, specifically those pertaining to brachioradialis.

We dissected each forearm and hand muscle in successive layers, including the elbow flexor *brachioradialis* as this muscle is superficial to the radial wrist extensors and must be removed to allow for further dissection. During each dissection, photographs and detailed notes were taken, including the origin and insertion points of each muscle. Particular note was made of how the two study taxa differ from each other and diverge from both typical primate morphology and from the previous descriptions of their musculature based on published descriptions (e.g., Kanagasuntheram and Jayawardene, 1957; Leischner et al., 2018; Lemelin and Diogo, 2016; Murie and Mivart, 1869).

We performed minimal quantitative analyses for this chapter. Rather, these types of analyses will be presented elsewhere (Boettcher et al., 2019). We did, however, calculate the percentage of each specimen's body weight that is composed of forearm and hand muscle tissue. Because there was no body weight associated with our dissection specimen of *Perodicticus*, we used the average body weight of the individuals of *Perodicticus* measured by Nekaris and Bearder (2007), who studied the largest *P. potto* sample presented in the literature. Our resulting body mass estimate was 1.03 kg. Fortunately, for our *N. coucang* specimen we were able to obtain its last living body weight: 0.843 kg.

7.3 Results

Contrary to our predictions of a conservative anatomical configuration, we found substantial differences between *Perodicticus* and *N. coucang*. Our observations also differ from the previously published literature on their wrist (Tables 7.1 and 7.2), digits (Tables 7.3 and 7.4), brachioradialis (Table 7.5) and intrinsic hand musculature (Table 7.6) (Figures 7.2–7.6). Muscles that did not present extraordinary anatomy have been relegated to the Appendix. However, we believe that these observations are still of value to provide a complete soft-tissue overview of the region. Unlike in previous literature, we are including them for completeness.

Table 7.1 Previously published descriptions, as well as our observations during dissection, of the *wrist extensors*.

Muscle (abbreviation)	Previous descriptions	Our observations
Extensor carpi radialis longus (ECRL)	***P. potto*** • As in other primates (Jouffroy, 1962) • Large structure (Miller, 1943)	***P. potto*** Origin: distal humerus (deep to BR) Insertion: base of MCII (typical variation)
	N. coucang • As in other primates (Jouffroy, 1962)	***N. coucang*** Tendon runs deep to EPL and APL Origin: distal, lateral humerus (deep to BR) Insertion: base of MCI (typical variation)
Extensor carpi radialis brevis (ECRB)	***P. potto*** As in other primates (Jouffroy, 1962)	***P. potto*** Origin: distal head of humerus (deep to BR and ECRL) Insertions: base of MCIII (typical variation)
	N. coucang As in other primates (Jouffroy, 1962)	***N. coucang*** Tendon runs deep to EPL and APL Origin: distal, lateral humerus (deep to BR and ECRL) Insertion: base of MCII (typical variation)
Extensor carpi ulnaris (ECU)	***P. potto*** • Relatively large with insertion on the pisiform and MCV (Hill, 1953b). • Large, with two tendons (Miller, 1943)	***P. potto*** Normal size for a primate Origin: proximal end of ulna (fibres also attach along the proximal one-third of the ulna) Insertion: base of MCV
	N. coucang N/A	***N. coucang*** Origin: lateral epicondyle of humerus Insertion: base of MCV

Table 7.2 Previously published descriptions, as well as our observations during dissection, of the wrist flexors.

Muscle (abbreviation)	Previous descriptions	Our observations
Flexor carpi radialis (FCR)	***P. potto*** N/A ***N. coucang*** N/A	***P. potto*** Origin: medial epicondyle of humerus Insertion: trapezium ***N. coucang*** Origin: medial epicondyle of humerus Insertion: base of MCII
Flexor carpi ulnaris (FCU)	***P. potto*** • Present with insertion on pisiform (Jouffroy, 1962; Nayak, 1933) • A tendinous slip inserts on the base of MCII (Miller, 1943) ***N. coucang*** N/A	***P. potto*** Origin: medial epicondyle of humerus and sheet along proximal ulna Insertion: pisiform ***N. coucang*** Origin: sheet along lateral, proximal half of ulna Insertion: pisiform and base of MCV

Table 7.3 Previously published descriptions, as well as our observations during dissection, of the digital extensors.

Muscle (abbreviation)	Previous descriptions	Our observations
Extensor digitorum (ED)	***P. potto*** • Has four tendons – one to digit III, two to digit IV and one to digit V (Murie and Mivart, 1869) • Did not insert on digit II (Straus, 1942) • As in other lemurs (Jouffroy, 1962) • Inserts on the lateral three digits; an insertion on the second digit is lacking (Miller, 1943)	***P. potto*** *Three separate muscle bellies (see Figures 7.2 and 7.3) *ED III,IV* Origin: merges with the main belly of extensor digitorum (~1.8 cm from the humerus) Insertion: sends tendons to digits III (on distal phalanx) and IV (tendon merges with the tendon from extensor digitorum). Three-quarters of the tendon mass goes to digit III. *ED IV,V* Origin: distal end of the humerus Insertion: one-third of the mass goes to digit IV only. The larger portion of the belly (two-thirds) further branches into two tendons of equal size (50 per cent to digit IV and 50 per cent to digit V). All tendons insert on the distal phalanx *ED III* Origin: lateral ulna along distal half Insertion: distal phalanx of digit III

Table 7.3 (cont.)

Muscle (abbreviation)	Previous descriptions	Our observations
	N. coucang ● Arises from the same belly as extensor digiti minimi (the two bellies remaining independent) and branches into five tendons (two of which go to digit IV – one radial and one ulnar) (Murie and Mivart, 1869). ● Extensor digiti quarti is not an independent muscle from extensor digitorum (Diogo and Wood, 2011)	***N. coucang*** Only one belly Origin: lateral epicondyle of humerus Insertion: distal phalanx of digits III–V
Extensor indicis (EI)	***P. potto*** ● Insertion varied from right to left limb; right: tendons to digits II and IV; left: tendons went to digits II and V (Murie and Mivart, 1869). ● Identified (also called extensor digitorum profundus) with insertion on digits II, III and IV (Forster, 1933) ● Insertions similar to *Daubentonia* on digits II and IV (Jouffroy, 1962) ● Sends tendon to base of MCII and to phalanges of digit II (Miller, 1943)	***P. potto*** *Exists, despite vestigiality of digit (see Figures 7.2 and 7.3) Origin: the distal region of the interosseous membrane Insertion: the distal end of the single phalanx of digit II
	N. coucang ● Insertion varied from right to left limb; right: tendons to digits II and IV; left: tendons went to digits II and V (Murie and Mivart, 1869) ● Inserts on digits II and III (Lemelin and Diogo, 2016)	***N. coucang*** Origin: lateral aspect of ulna (distal half) Insertion: distal phalanx of digit II
Extensor pollicis brevis (EPB)	***P. potto*** ● Deficient (Murie and Mivart, 1869) ● Absent (Jouffroy, 1962)	***P. potto*** None identified
	N. coucang Absent (Jouffroy, 1962)	***N. coucang*** None identified
Extensor pollicis longus (EPL)	***P. potto*** N/A	***P. potto*** Origin: proximal one-third of the ulna Insertion: base of the distal phalanx of digit I
	N. coucang N/A	***N. coucang*** Origin: lateral aspect of ulna (sheet along proximal half; some fibres originate on the interosseous membrane) Insertion: distal phalanx of digit I

Table 7.3 (cont.)

Muscle (abbreviation)	Previous descriptions	Our observations
Abductor pollicis longus (APL)	***P. potto*** As in *Lemur* (Jouffroy, 1962)	***P. potto*** Origin: radius and proximal half of interosseous membrane Insertion: medial aspect of base of MCI; deep to thenar group
	N. coucang N/A	***N. coucang*** Origin: medial, proximal half of radius and interosseous membrane Insertion: medial aspect of base of MCI
Extensor digiti minimi (EDM)	***P. potto*** ● Inseparable from extensor digitorum (Murie and Mivart, 1869).	***P. potto*** Origin: proximal head of radius (deep to ED muscles) Insertion: distal phalanx of digit V
	N. coucang ● Same origin as extensor digitorum; inserts on digit V only (Murie and Mivart, 1869). ● Inserts on digit V only (Lemelin and Diogo, 2016).	***N. coucang*** Independent extensor digiti minimi not identified

Note: Notable morphology is marked with an asterisk (*).

Table 7.4 Previously published descriptions, as well as our observations during dissection, of the *digital flexors.*

Muscle (abbreviation)	Previous descriptions	Our observations
Combined flexor digitorum superficialis (FDS), flexor digitorum profundus (FDP) and flexor pollicis longus (FPL)	***P. potto*** *Flexor digitorum superficialis* ● Well developed (Forster, 1933); no insertion on digit II (Kanagasuntheram and Jayawardene, 1957; Lemelin and Diogo, 2016; Straus, 1942) ● Gives tendinous slip to FDP; tendons emerge from a large tendinous plate; inserts on digit II (Miller, 1943) ● No tendon to digit II (Jouffroy, 1962)	***P. potto*** *Flexor digitorum superficialis* Independent belly from FDP Origin: medial epicondyle of humerus (deep to BR and radial extensors) Insertion: intermediate phalanges of digits III–V *Flexor digitorum profundus + flexor pollicis longus* Has three fused bellies. FPL is fused with the medial belly
	Flexor digitorum profundus ● Merges with flexor pollicis longus; some fibres from FDS innervating; insertion on all five digits (Murie and Mivart, 1869)	Origin: the radius, ulna and interosseous membrane in a sheet. Most proximal attachment is on the medial epicondyle of the humerus

Table 7.4 (cont.)

Muscle (abbreviation)	Previous descriptions	Our observations
	● Innervation of FDP and FPL; insertion points on digits I and III–V (Van Campen and Van der Hoeven (1859) ● Well developed; has two distinct muscle bellies (fibre contributions from FPL) with insertion points on proximal phalanx of digits I and III–V (Forster, 1933). ● No insertion on digit II (Lemelin and Diogo, 2016; Straus, 1942).	Insertion: distal phalanx of digits I and III–V
	Flexor pollicis longus ● Not distinct from other digital flexors (Murie and Mivart, 1869) ● Fibres contribute to FDP (Forster, 1933)	
	N. coucang *Flexor digitorum superficialis* ● Missing insertion on digit II (Straus, 1942) ● Flexors are primitive (Hill, 1953b) ● Inserts on digits II–V (Diogo and Wood, 2011) ● Does not give a tendinous slip to FDP; the digital flexor tendons emerge directly from the muscle belly (Miller, 1943) *Flexor digitorum profundus* ● Single head at origin with fibre contributions from FDS; inserts on all digits except third (Murie and Mivart, 1869) ● Has two well-defined muscle bellies (one from the ulnar side and the other from the radial side) that give rise to independent tendons that are distinct at the carpal tunnel; the radial head sends tendons to all five digits and the ulnar	***N. coucang*** A tendon from FDS dives into FDP and the two muscles are inseparable with the fibres innervating about halfway down the forearm Origin: proximal half of radius, ulna and interosseous membrane Insertions: (1) FDP: distal phalanx of digits I (fused FPL) and III–V. (2) FDS: intermediate phalanx of digits II–V (typical split insertion observed in digits III–V). Tendon to digit II fuses with tendon from FDP

Table 7.4 (cont.)

Muscle (abbreviation)	Previous descriptions	Our observations
	head to digits I, IV and V (Gyambibi and Lemelin, 2013; Lemelin and Diogo, 2016). • Large; originates on the proximal two-thirds of the ulna, the coronoid process and interosseous membrane; origin is adjacent to the insertion of brachialis; contributes to FPL; gives tendons to all five digits with tendon to digit II being most substantial (Hill, 1953b) *Flexor pollicis longus* • Considerably larger than FDP; inserts on digits I and II–IV (Murie and Mivart, 1869) • Present with fibres contributed from FDP; the total mass gives tendons to each digit (Hill, 1953b) • Not a distinct muscle (Diogo and Wood, 2011)	

Note: Notable morphology is marked with an asterisk (*).

Table 7.5 Previously published descriptions, as well as our observations during dissection, of brachioradialis.

Muscle (abbreviation)	Previous descriptions	Our observations
*Brachioradialis (BR)	***P. potto*** • Well developed (Jouffroy, 1962; Nayak, 1933) • Enormous; arises from lateral epicondylar ridge of humerus and attaches on lateral distal radius (Miller, 1943)	***P. potto*** *Extremely large, as seen in Figure 7.6 Origin: along nearly the entire length* of the humerus Insertion: lateral side of distal radius
	N. coucang Less developed than in *P. Potto* (Jouffroy, 1962; Nayak, 1933)	***N. coucang*** Origin: distal, lateral humerus Insertion: styloid process of radius

Note: Notable morphology is marked with an asterisk (*).

Table 7.6 Previously published descriptions, as well as our observations during dissection, of the intrinsic hand muscles.

Muscle (abbreviation.)	Previous descriptions	Our observations
Thenar group: opponens pollicis (OP), flexor pollicis brevis (FPB), and abductor pollicis brevis (AbdPB)	***P. potto*** ● No opponens identified (Forster, 1933) ● Opponens present (Lemelin and Diogo, 2016) ● FPB was regionally reduced and had undergone distal displacement (Kanagasuntheram and Jayawardene, 1957). ● FPB is larger and contributes to the 'pincer-like' appearance (Forster, 1933) ● OP reaches the distal portion of the metacarpal in lorisiformes (Diogo and Wood, 2011)	***P. potto*** *Abductor pollicis brevis* Origin: trapezium Insertion: base of the proximal phalanx of the digit I (via aponeurosis) *Opponens pollicis* *Three small bellies with identical origins and insertions. Origin: trapezium Insertion: distal end of MCI (palmar, lateral side) *Flexor pollicis brevis* Origin: trapezoid Insertions (2): base of proximal phalanx and base of distal phalanx of digit I
	N. coucang ● AbdPB is not well differentiated from the outer part of FPB (Hill, 1953b). ● A flexor brevis profundus was observed (completely distinct from FPB; not fused with intermetacarpal muscles); OP present and inserts almost exclusively on the distal portion of MCI (Lemelin and Diogo, 2016) ● OP is a distinct muscle in primates and, in lorisiformes, reaches the distal portion of MCI (Diogo and Wood, 2011)	***N. coucang*** *Abductor pollicis brevis* Three separate bellies Origin: palmar aspect of scaphoid Insertions: (1) radial side of MCI, (2) base of proximal phalanx of digit I and (3) radial aspect of distal end of proximal phalanx of digit I *Flexor pollicis brevis* Has two bellies adjacent to each other Origin: flexor retinaculum Insertions: (1) distal end of MCI and (2) base of proximal phalanx of digit I *Opponens pollicis* Origin: trapezium and flexor retinaculum Insertion: radial, distal end of MCI
Hypothenar group: opponens digiti minimi (ODM), flexor digiti minimi brevis (FDMB), and abductor digiti minimi (AbdDM)	***P. potto*** ● Comprised of the flexor and abductor muscles, but no opponens identified (Forster, 1933)	***P. potto*** *Abductor digiti minimi* Origin: pisiform Insertion: base of the proximal phalanx of digit V

Table 7.6 (cont.)

Muscle (abbreviation.)	Previous descriptions	Our observations
		Flexor digiti minimi Has four separate bellies Origin: hamate Insertions (4): (1; largest belly) distal end of the proximal phalanx of digit V; (2/3) proximal end of the proximal phalanx of digit V; (4) base of the proximal phalanx of digit V *Opponens digiti minimi* Three separate bellies Origin: hamate Insertions (3): (1; superficial belly) distal end of MCV; (2; middle belly) sheet along MCV; (3; deep belly) distal end of MCV
	N. coucang • FDMB's insertion extends to the middle or distal phalanx of digit V; ODM is one layer (not differentiated into superficial and deep layers) and inserts along the entire length of MCV (Lemelin and Diogo, 2016). • ODM is a distinct muscle (Diogo and Wood, 2011).	***N. coucang*** *Abductor digiti minimi* Origin: pisiform Insertion: medial aspect of base of proximal phalanx of digit V *Flexor digiti minimi brevis* Origin: hamate Insertion: distal end of the proximal phalanx of digit V *Opponens digiti minimi* Origin: hamate Insertion: sheet along medial aspect of MCV
Contrahentes and pollucial adductors	***P. potto*** • Reported for digits I (oblique and transverse heads; transverse head had attachment point on digit III), II and V; adductor pollicis (largest contrahentes) is present; contributes to hand's 'pincer-like' appearance (Forster, 1933) • Contrahentes IV is reduced (Kanagasuntheram and Jayawardene, 1957) • Present, well developed (Nayak, 1933)	***P. potto*** *Adductor pollicis transverse* Origin: ulnar side of MCII (distal end) Insertion: distal end of the proximal phalanx of digit I *Adductor pollicis oblique (larger head)* Origin: MCII Insertion: MCI

Table 7.6 (cont.)

Muscle (abbreviation.)	Previous descriptions	Our observations
	N. coucang - Adductor pollicis brevis has no distinct transverse or oblique head (Lemelin and Diogo, 2016) - Adductor pollicis muscle is well developed; mass is larger than all other taxa (Gyambibi and Lemelin, 2013) - Contrahentes of digit IV present but absent on digit III; variable between individuals (Jouffroy, 1962)	***N. coucang*** *Adductor pollicis oblique* Origin: base of MCII Insertions: (1) distal end of MCI and (2) proximal end of proximal phalanx of digit I *Adductor pollicis transversus* Origin: distal end of MCIII Insertion: distal end of proximal phalanx of digit I (some fibres inserted on the proximal end of the proximal phalanx)
Lumbricals	***P. potto*** - Deficiency in the first lumbrical (Kanagasuntheram and Jayawardene, 1957). - Absence of second lumbrical (Straus, 1942) - Only three lumbricals (Jouffroy, 1962; Nayak, 1933)	***P. potto*** *Second lumbrical* Origin: respective tendon of FDP Insertion: proximal end of distal phalanx (radial side) of digit III *Third lumbrical* Origin: respective tendon of FDP Insertion: proximal end of the distal phalanx (radial side) of digit IV *Fourth lumbrical* Origin: respective tendon of FDP Insertion: proximal end of the distal phalanx (radial side) of digit V
	N. coucang - Four radially inserted lumbricals were present (Murie and Mivart, 1869)	***N. coucang*** *Third lumbrical* Origin: respective tendon of FDP Insertion: distal end of proximal phalanx (ulnar side) of digit III *Fourth lumbrical* Origin: respective tendon of FDP Insertion: distal end of the proximal phalanx of digit IV

Note: Notable morphology is marked with an asterisk (*).

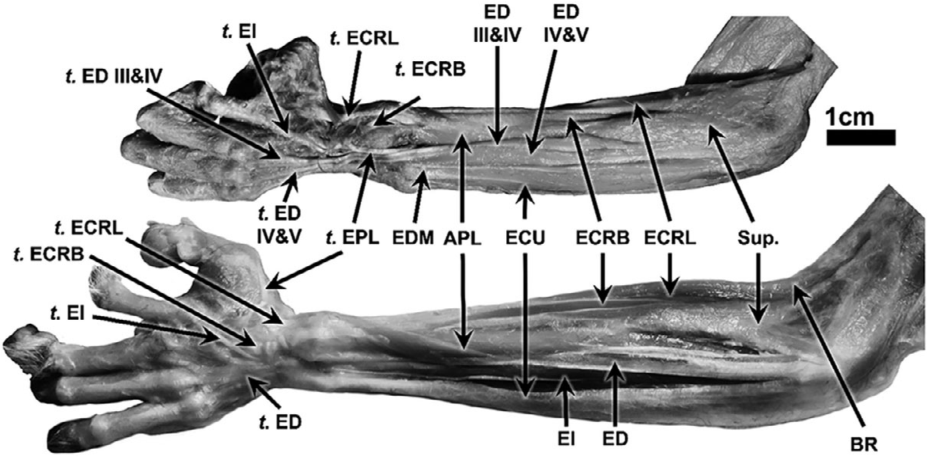

Figure 7.2 Superficial extensor muscles (and tendons 't') of the forearm and hand of *P. potto* (top) and *N. coucang*. See Tables 7.1–7.6 for abbreviations.

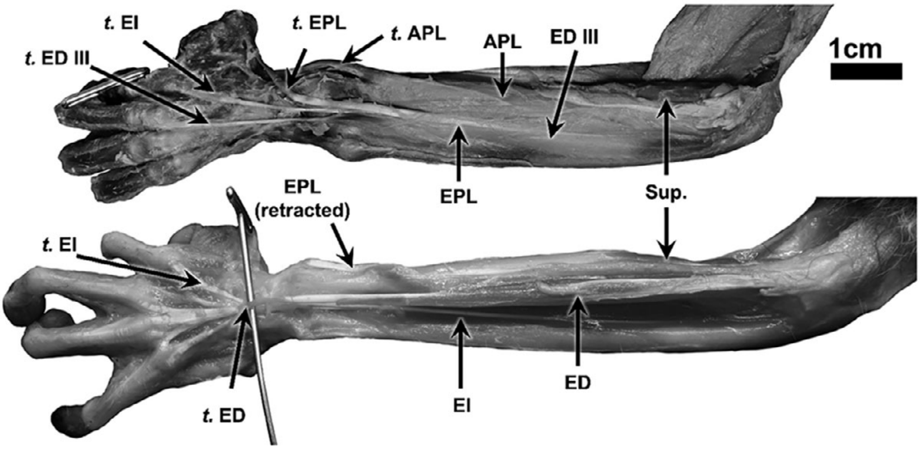

Figure 7.3 Deep extensor muscles (and tendons 't') of the forearm and hand of *P. potto* (top) and *N. coucang*. See Tables 7.1–7.6 for abbreviations.

7.4 Discussion

7.4.1 Our Findings vs the Literature

Murie and Mivart (1869) and Forster (1933) previously reported the presence of extensor indicis in *P. potto* with insertion points occurring on multiple digits, not just digit II (see Table 7.3 for further qualitative description). Thus, the muscle did not function as a true extensor indicis but rather a more general digital extensor. During our dissection, however, we observed the presence of a true extensor indicis (a muscle that inserts solely on digit II; see Figures 7.2 and 7.3). This was unexpected for two reasons: (1) our observation of the muscle's insertion differed from what was previously reported; and (2)

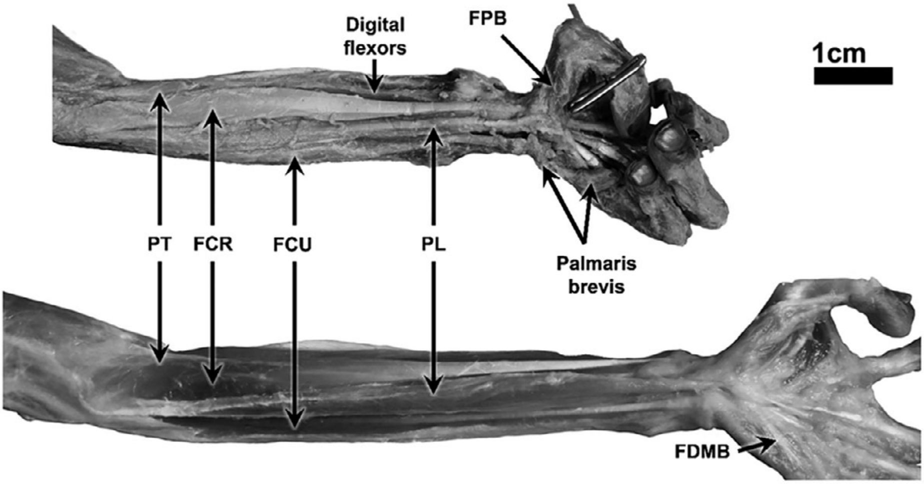

Figure 7.4 Superficial flexor muscles of the forearm and hand of *P. potto* (top) and *N. coucang*. See Tables 7.1–7.6 for abbreviations.

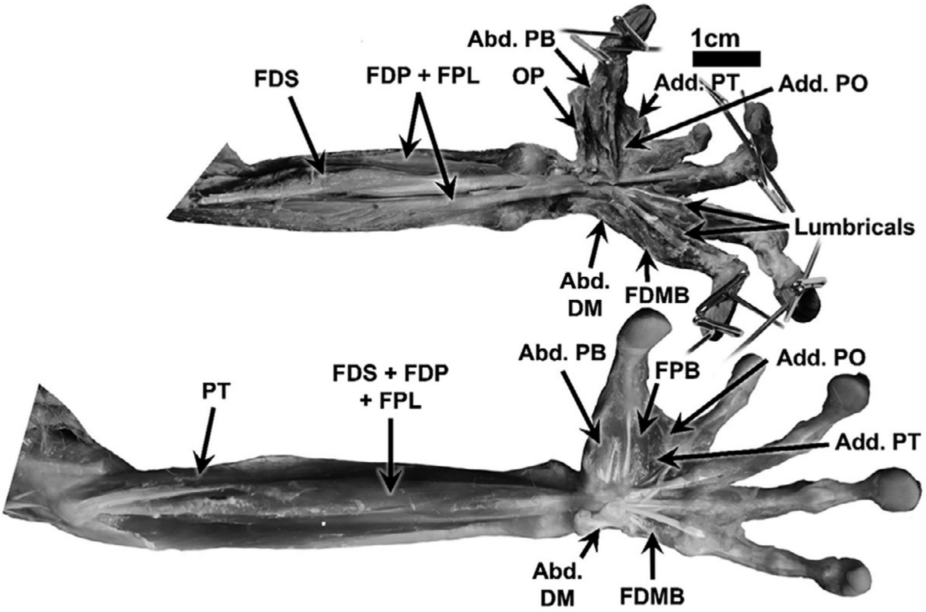

Figure 7.5 Deep flexor muscles of the forearm and hand of *P. potto* (top) and *N. coucang*. See Tables 7.1–7.6 for abbreviations.

the severe reduction of the second digit of *Perodicticus* would not intuitively indicate functionality; therefore, it seems minimal specific muscle control would be necessary – especially for a muscle dedicated solely to this vestigial digit.

In addition to our surprising findings pertaining to the extensor indicis, the entire extensor compartment of *Perodicticus* was observed to be highly differentiated –

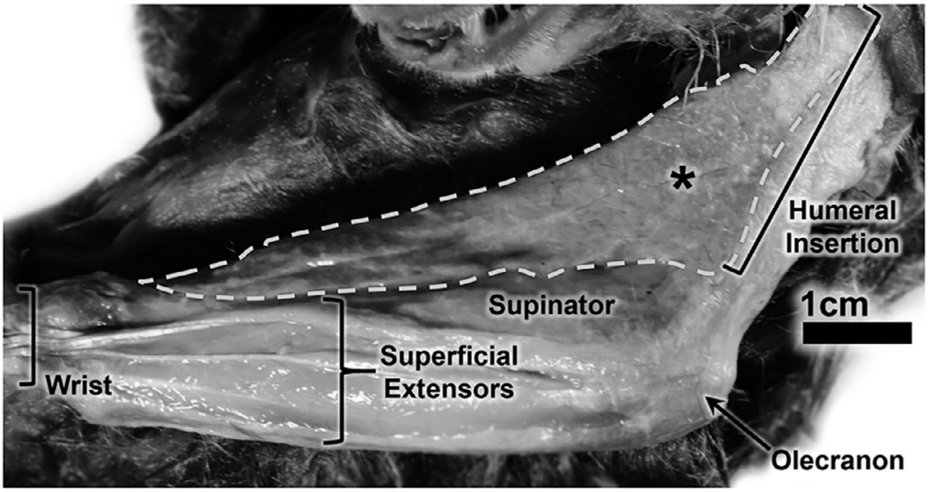

Figure 7.6 Lateral view of the exceptionally large brachioradialis (*, outlined with dashed line) of *P. potto*. Note that this muscle originates on nearly the entire length of the humerus (bracket). Despite the apparent split in the muscle (visible under the asterisk), the entirety of the brachioradialis had a single insertion on the distal radius.

a finding not unique to *P. potto*, but worth noting because differentiation implies high dexterity and fine control. It had been previously reported by Murie and Mivart (1869) and Straus (1942) that the extensor digitorum did not insert on the second digit. Our dissection confirmed this (as only the true extensor indicis inserted on digit II); however, we noted considerable differentiation within this compartment. As opposed to having a single extensor digitorum communis that inserted on each digit (as reported by Murie and Mivart, 1869), *P. potto* had multiple, differentiated bellies, including three extensor digitorum muscle bellies: extensor digitorum III; extensor digitorum III and IV; and extensor digitorum IV and V. Our potto specimen also presented a separate extensor digiti minimi and extensor pollicis longus (a finding not uncommon in primates), meaning that each digit other than the fourth had its own dedicated extensor muscles and most had multiple muscle bellies sending tendons to their extensor aponeuroses. Because other authors' reports have not confirmed this observation, it is possible that this finding could be a result of individual variation as opposed to an anatomical commonality of the species, as these muscles and their flexor counterparts are highly variable in primates (as has been observed in the sample published by Leischner and colleagues, 2018). Additional dissections of this species would therefore be valuable to clarify this matter.

The digital flexors were also notable in our dissections. For *Perodicticus*, we found the insertion of the superficial digital flexor to be on digits III through V, with the typical insertion on digit II being absent. This observation is consistent with the previous accounts of Straus (1942), Kanagsuntheram and Jayawardene (1957) and Lemelin and Diogo (2016). Additionally, our observation of the superficial digital flexor as a developed and distinct muscle from that of the deep digital flexor confirms reports by Forster (1933).

Our observations about the insertions of the deep digital flexor are consistent with reports by Straus (1942) and Lemelin and Diogo (2016), in that the insertion on digit II that represents the typical configuration observed within primates is missing in *P. potto*. We also noted the highly associated bellies of the deep digital flexor and flexor pollicis longus during our dissection. This observation was consistent with the findings of Murie and Mivart (1869), Van Campen and Van der Hoeven (1859) and Forster (1933).

In regard to the intrinsic hand musculature, our observations of lumbricals in *Perodicticus* confirmed previous reports. During our dissection, we noted the presence of lumbricals for digits III through V with origins and insertions typical of non-human primates. The specific digits for which lumbricals were present confirms the observations previously made by Kanagasuntheram and Jayawardene (1957) and Straus (1942).

We also confirmed the presence of two pollucial adductor heads. Although Straus (1942) noted the presence of this muscle in *P. potto*, he did not describe the two distinct heads (transverse and oblique) we observed.

7.4.2 *Perodicticus potto* vs *Nycticebus coucang*

The total combined muscle mass of each muscle in the forearm and hand compartments in *Perodicticus* and *N. coucang* is ~0.65 and 0.92 per cent of the total body mass, respectively. These are remarkably small total masses (Boettcher et al., 2019) considering the purported grip strength of these taxa, and it is somewhat surprising that *P. potto* has relatively less massive forearm and hand muscle mass than *N. coucang*, given the allusions in the behavioural literature to its extraordinary grip strength. We found other notable morphological features as well:

- Brachioradialis: our specimen of *Perodicticus* had a massive brachioradialis with an origin that spanned nearly the entirety of the humerus (Figure 7.6). Our specimen of *N. coucang*, on the other hand, had a brachioradialis more typical of primates (Boettcher et al., 2019). Of the differences noted between the forearm and hand of these individuals, the difference in the mass of the brachioradialis is most noteworthy. This muscle made up 27.27 and 5.41 per cent of the total forearm and hand muscle mass for *P. potto* and *N. coucang*, respectively. We were able to confirm this finding in another individual of *P. potto*. Because of this, as well as previous reports of this muscle's incredible size by Miller (1943), we believe this is a consistent feature of *P. potto*.
- Digital extensors: the extensor digitorum of *Perodicticus* was extremely differentiated (separated into three distinct bellies – extensor digitorum III and IV, extensor digitorum III, and extensor digitorum IV and V), while the extensor digitorum communis in *N. coucang* had only one belly that inserted on digits III, IV and V. The tendons inserted on the distal phalanx of the respective digit for each individual.
  - Extensor indicis: present in both species with origin in the distal forearm and insertion on the second ray (the single phalanx of digit II in *Perodicticus* and the distal phalanx in *N. coucang*).
  - Extensor digiti minimi: present in *Perodicticus* (with origins and insertions typical of primate myology), but not present in *N. coucang*.

- Flexors: our specimen of *Perodicticus* had a distinct superficial digital flexor (flexor digitorum superficialis) that inserted on digits III, IV, and V, but the deep digital flexor (flexor digitorum profundus) and flexor pollicis longus (flexor pollicis longus) had fused bellies (these deeper muscles sent tendons to digits I and III–V). Both the superficial and deep digital flexors and flexor pollicis longus were fused in *N. coucang*, with this collective muscle mass sending tendons to each digit. Contrary to behavioural observations noting exceptional grip strength in *P. potto*, the digital flexors do not appear to be exceptionally large, though analysis of its fibre architecture (which would indicate whether it is highly pennate and therefore relatively powerful for its size) is warranted.
- Extrinsic thumb muscles: flexor pollicis longus was fused with other digital flexors in both species, while the pollucial extensor and abductor (extensor pollicis longus and abductor pollicis longus) were present and distinct in each with typical origins and insertions.
- Thenar group: the origins and insertions were variable between the two species, but the most notable difference was in the degree of differentiation for different muscles. In *N. coucang*, the most highly differentiated thenar muscle was abductor pollicis brevis, which had three distinct bellies with similar origins and insertions, while this same muscle in *P. potto* had one belly. In *P. potto*, the opponens pollicis brevis was differentiated, having three separate muscle bellies. This same muscle was present in *N. coucang* with two bellies. The total mass of the thenar group also varied slightly between the two species. This group made up 1.43 per cent of the total forearm and hand muscle mass for *P. potto*, and 2.02 per cent for *N. coucang*.
- Hypothenar group: this group was highly differentiated in *P. potto*. Flexor digiti minimi brevis was composed of four separate muscle bellies and opponens digiti minimi was comprised of three. In contrast, each hypothenar muscle had only a single belly in *N. coucang*.
- Pollucial adductors: these muscles were similar in both individuals, varying only in total size. The mass of these two muscles made up 2.35 per cent of the total forearm and hand muscle mass in *P. potto*, and 3.30 per cent in *N. coucang*.

Based on our dissections, it is clear that *P. potto* presents some exceptional myological features. However, our findings contradict each one of our predictions. Namely, although the forearm muscles are relatively conserved across primates, we found notable variations present in our dissection specimens. The most distinctive example was the exceptionally large brachioradialis in our *P. potto* specimen – a morphology that we have confirmed in a second individual (MNHM 1973-230) and has been noted before (Jouffroy, 1962; Miller, 1943). Likewise, while we expected to find myological rearrangement related to the highly reduced second digit in *P. potto*, we observed a distinctive extensor indicis despite the seeming vestigiality of this finger. What makes this more remarkable is that this muscle is not present in many species of primates (unpublished findings from Leischner and colleagues and Boettcher et al.). Lastly, we expected to find highly derived thenar and hypothenar muscles reflective of the exceptional abduction of the digits in *P. potto*, and while we found interesting separation of these muscles into more distinctive bellies than is typical of many primates, there was no clear pattern relating to hyperabduction. The anatomy of *N. coucang* was also fairly distinctive, yet difficult to interpret functionally.

Beyond the reduced second digit and the hyperabducted thumb, the other manual distinction that comes up repeatedly in the literature is the exceptional grip strength of *Perodicticus* (Charles-Dominique, 1977a; Feldhamer et al., 2007; Lemelin and Jungers, 2007; Miller, 1943; Oates, 1984). While the intrinsic and extrinsic digital flexors of our specimen did not appear exceptionally large, further analysis of their fibre architecture is warranted. It is possible that these muscles are relatively pennate and therefore have relatively high physiological cross-sectional area – the myological variable that relates most directly to force. Therefore, in addition to this qualitative analysis and description, a quantitative study of these enigmatic animals and their highly derived hands is warranted in addition to studies measuring grip strength directly.

Acknowledgements

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Appendix

Table 7.7 Description of the forearm and hand muscles not discussed above.

Muscle (abbreviation)	Previous descriptions	Our observations
Supinator (Sup.)	***P. potto*** • No ulnar head in Lorisiformes (Diogo and Wood, 2011) • Has a superficial humeral head and a deep ulnar head (Miller, 1943) ***N. coucang*** • No ulnar head in Lorisiformes (Diogo and Wood, 2011)	***P. potto*** Origin: lateral aspect of proximal ulna Insertion: lateral aspect of midshaft of radius ***N. coucang*** Origin: lateral aspect of proximal ulna Insertion: lateral aspect of midshaft of radius
Pronator teres (PT)	***P. potto*** • As in other lemurs (Jouffroy, 1962) • Originates on the medial epicondyle of the humerus and inserts on the middle third of the radius (Miller, 1943)	***P. potto*** Origin: medial epicondyle of humerus and proximal ulna Insertion: lateral aspect of midshaft of radius

Table 7.7 (cont.)

Muscle (abbreviation)	Previous descriptions	Our observations
	N. coucang • As in other lemurs (Jouffroy, 1962) Originates on the medial epicondyle of the humerus and inserts on the middle third of the radius (Miller, 1943)	***N. coucang*** Origin: medial epicondyle of humerus and proximal ulna Insertion: lateral aspect of midshaft of radius
Pronator quadratus (PQ)	***P. potto*** N/A	***P. potto*** Origin: distal ulna (anterior aspect) Insertion: distal radius (anterior aspect)
	N. coucang N/A	***N. coucang*** Origin: distal ulna (anterior aspect) Insertion: distal radius (anterior aspect)
Palmaris longus (PL)	***P. potto*** • Small and large palmar muscles were identified (in typical locations of PL and FCR) (Forster, 1933)	***P. potto*** Origin: medial epicondyle of humerus Insertion: aponeurosis of palm
	N. coucang N/A	***N. coucang*** Origin: medial epicondyle of humerus Insertion: flexor retinaculum and skin of the hand
Palmaris brevis (PB)	***P. potto*** • Completely absent (Kanagasuntheram and Jayawardene, 1957) • Present (Nayak, 1933) ***N. coucang*** • Completely absent (Hill, 1953b). Present (Nayak, 1933)	***P. potto*** Origin: aponeurosis of palm (superficial to the hypothenar group) Insertion: skin on medial side of palm ***N. coucang*** None identified
Interossei	***P. potto*** • The third digit functions as the central axis in strepsirrhines (Lemelin and Diogo, 2016)	***P. potto*** *First dorsal interosseous* Origin: base of MCI (ulnar side) Insertion: distal end of proximal phalanx of digit II *Second dorsal interosseous* Origin: MCII and MCIII Insertion: proximal end of proximal phalanx of digit II *Third dorsal interosseous* Origin: MCIII and MCIV Insertion: proximal end of the proximal phalanx of digit III *Fourth dorsal interosseous*

Table 7.7 (cont.)

Muscle (abbreviation)	Previous descriptions	Our observations
		Origin: MCIV and MCV Insertion: proximal end of the proximal phalanx of digit IV *First and third palmar interosseous* Origin: distal end of respective metacarpal Insertion: proximal end of intermediate phalanx (ulnar side) of respective digit. *Second palmar interosseous* Origin: distal end of MCIV Insertion: proximal end of intermediate phalanx (radial side) of digit IV
	N. coucang • The dorsal interossei muscles attach on both sides of the fourth digit. This digit functions as the central axis; the third digit functions as the central axis in strepsirrhines (Lemelin and Diogo, 2016) • The fourth digit is the functional access for the dorsal interosseous muscles (Diogo and Wood, 2011) • Long interosseous of digit IV ranging to half of the first phalanx (Jouffroy, 1962)	***N. coucang*** *First dorsal interosseous* Origin: MCI and MCII Insertion: proximal end of proximal phalanx of digit II *Second dorsal interosseous* Origin: MCI and MCIII Insertion: proximal end of the proximal phalanx of digit III *Third dorsal interosseous* Origin: MCIII and MCIV Insertion: proximal end of the proximal phalanx of digit IV *Fourth dorsal interosseous* Origin: MCIV and MCV Insertion: proximal end of the proximal phalanx of digit IV *First palmar interosseous* Origin: ulnar side of MCII Insertion: proximal end of the proximal phalanx of digit II *Second palmar interosseous* Origin: palmar surface of MCIV Insertion: radial side of the base of the proximal phalanx of digit IV *Third palmar interosseous* Origin: middle/base of MCV Insertion: base of the proximal phalanx of digit V