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# Comparative Anatomical Study of the Forearm Extensor Muscles of *Cebus libidinosus* (Rylands et al., 2000; Primates, Cebidae), Modern Humans, and Other Primates, With Comments on Primate Evolution, Phylogeny, and Manipulatory Behavior

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## ABSTRACT

Despite its abundance in Latin America, and its remarkable ability to use tools, there are only a few myological studies on the capuchin monkey, *Cebus libidinosus*. In the present study, we dissected the forearm extensor muscles of six adult males and two adult females of this species. We describe these muscles and compare them with those of other primates dissected by us and by other authors. The forearm extensor muscles of *Cebus* monkeys are, in general, more similar to those of other platyrrhines than to distantly related taxa that use tools, such as chimpanzees and modern humans, with three main exceptions: contrary to most other platyrrhines, (1) in *Cebus*, chimpanzees and modern humans the extensor pollicis longus usually inserts onto Digit I, and not onto Digits I and II; (2) in *Cebus* the abductor pollicis longus has two separate tendons, as is the case in chimpanzees, and in modern humans (where one of these tendons is associated with a distinct belly, forming the muscle extensor pollicis brevis); (3) in *Cebus*, and in modern humans and chimpanzees, the extensor pollicis longus is not deeply blended with the extensor indicis. Therefore, the *Cebus* monkeys provide an illustrative example of how phylogenetic constraints and ecological adaptations have been combined to develop a specific myological configuration that, associated with their sophisticated neurological organization, allow them to easily navigate in their arboreal habitats and, at the same time, to finely manipulate objects in order to search for food and to prepare this food for ingestion. Anat Rec, 293:2056–2070, 2010. © 2010 Wiley-Liss, Inc.

**Key words:** anatomy; *Cebus libidinosus*; chimpanzees; forearm extensor muscles; modern humans; manipulatory behavior; monkeys; primates

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Analyses of the comparative anatomy of primates are crucial to increase our understanding about functional morphology, behavior, and phylogeny of these mammals. Despite this, detailed comparative myological studies of primates are rather spotty in the literature (Gibbs et al., 2000, 2002). An example of a primate that has been insufficiently studied in terms of its myology is *Cebus libidinosus*, a common New World monkey (Senft, 1907; Erickson, 1948; Dunlap et al., 1985; Aziz and Dunlap, 1986; Aversi-Ferreira et al., 2005a,b, 2006, 2007a,b,c). As stressed by Barros et al. (2003), a better knowledge of the comparative anatomy of the *Cebus* monkeys would help to better understand the functional morphology and evolution of this fascinating primate taxon. Detailed information of the forelimb myology of *Cebus* species would allow a better understanding of the behavior, social interaction, feeding habits, and the reproduction of these species, and, thus, help contributing to their preservation in the wild and in captivity. This is particularly important because the habitats of these species are increasingly in danger due to human activities (Santini, 1983; Auricchio, 1995).

The *C. libidinosus* monkey—a prominent representative of the platyrrhines—has yet to be the subject of a comprehensive monograph on its anatomy, like the one that was published by Hartman and Straus (1933) about the catarrhine rhesus monkey (*Macaca mulatta*). There are some unpublished doctoral dissertations on *Cebus apella* (e.g., Senft, 1907; Erikson, 1948) but these are not readily available. Schön (1968) provided some useful, but general, comments on the anatomy of the forelimb of *C. libidinosus* in his monograph of the howler monkey. Dunlap et al. (1985) investigated the comparative forelimb myology of 12 genera of Platyrrhini, two genera of Cercopithecoidea, and one genus of Hominoidea, concluding that “the forelimbs of *Cebus apella* and *Callicebus moloch* represent good models of ancestral anthropoid morphology.” Although their article contains some comments about the forelimb muscles of *Cebus apella*, they did not provide a detailed, systematic description of these muscles. The monograph “The Complete Capuchin” (Fragaszy et al., 2004) includes a few statements about the anatomy of *Cebus*, but this publication is essentially focused on the behavior and ecology of the members of this genus.

*Cebus* is a member of the subfamily Cebinae, which, together with the subfamilies Saimirinae, Aotinae, and Callitrichinae, form the family Cebidae. According to the results of recent genetic phylogenetic studies, the Cebinae and the Saimirinae form a clade that is closely related to the Callitrichinae and the Aotinae; in turn, the cebids are the sister-group of atelids (including the subfamilies Atelinae and Alouattinae), the clade including these two families being the sister-group of pitheciids (comprising the subfamilies Callicebinae and Pitheciinae), which are thus the most plesiomorphic extant new world monkeys (for recent reviews on this subject, see, e.g., Fabre et al., 2009; Wildman et al., 2009).

In his comprehensive analysis of tool use (“culture”) amongst non-human primates McGrew (1998) listed the following genera which use tools of various kinds: *Macaca*, *Cebus*, *Pongo*, *Gorilla*, and *Pan* (for specific information, see, e.g., Boesch and Boesch, 1980; Galdikas, 1982; Wood, 1984; Huffman and Quiatt, 1986; Goodall,

1986; Chapman and Fedigan, 1990; Janson and Boinski, 1992; Fragaszy and Boinski, 1995; Visalberghi, 1997; Visalberghi and McGrew, 1997; van Schaik, 2004). That is, within all the living new world monkeys, *Cebus* is the only one in which tool use has been reported.

The scarce anatomical data available suggest that the nerves, muscles, and blood vessels of the shoulder and arm of *C. libidinosus* are more similar to those of other new world monkeys and of old world monkeys that do not use tools, such as baboons, than to those of taxa that use tools, such as chimpanzees and modern humans. This points out the importance of phylogenetic constraints in the evolution of these structures.

However, recent data have also indicated that, with regard to certain flexor forearm muscles, *C. libidinosus* appears to be more similar to taxa such as chimpanzees and modern humans than to other new world monkeys and to old world monkeys such as baboons (Aversi-Ferreira et al., 2005a,b, 2006a,b, 2007a,b; Aversi-Ferreira, 2009; Marin et al., 2009). According to Aversi-Ferreira and his colleagues, this seems to indicate that adaptations to a similar behavior (tool use) might have also played an important role in the evolution of primate musculature. Interestingly, these similarities exist despite differences of the detailed central nervous system controls and their specific peripheral neural connections in *Cebus* and in taxa such as chimpanzees and modern humans. In addition, there are also noteworthy differences in the blood supply of these muscles in *C. libidinosus*, modern humans, and other hominoids (Aversi-Ferreira et al., 2007a,b).

As a general statement, it can be said that in modern humans the hand moves more freely, being mainly used to grab and to manipulate, whereas in *Cebus* this structure is mainly used in feeding, grooming and, when necessary, in locomotion (Straus, 1941a,b; Erikson, 1948; Moore and Dalley, 2001). According to Paiva (1998), *Cebus* presents an encephalic index that is somewhat identical to that of chimpanzees and higher than that of gorillas, orangutans, and many Old World monkeys. *Cebus* exhibits complex cultural behavior (Lopes, 2004) and well-developed use of memory (Tavares and Tomaz, 2002) and of tools (Antinucci and Visalberghi, 1986; Chapman and Fedigan, 1990; Janson and Boinski, 1992; Fragaszy and Boinski, 1995; Visalberghi, 1997; Visalberghi and McGrew, 1997). Interestingly, in *Cebus* the use of tools is not associated with a high mobility of the thumb (Napier, 1980).

To better understand the movements of the wrist, the hand, and the digits in *Cebus* monkeys, we will describe in detail the forearm extensor muscles of *C. libidinosus*, compare the origins, insertions, vascular supply and innervation of these muscles with those of the muscles of other new world monkeys and other primates that do not use tools, as well as of primates that do use tools, such as chimpanzees and modern humans, and then examine our anatomical findings and comparisons in a broader phylogenetic, functional and evolutionary context. The main hypotheses that we want to explore are: if the forearm extensors of *Cebus* are more similar to those of other new world monkeys and other non-hominoid primates that do not use tools, such as baboons (thus indicating the importance of phylogenetic constraints), or are instead more similar to distantly related taxa that do use tools, such as chimpanzees and modern

humans (thus indicating the importance of ecological adaptations to a same behavior, i.e., using tools).

## MATERIAL AND METHODS

The forearms of eight specimens (six adult males and two adult females) of *C. libidinosus* weighing from 1 to 2 kg, were dissected for this project. These animals died in zoos in the 1970s and were donated by the Brazilian Institute of the Environment (IBAMA, Sete Lagoas, Minas Gerais, Brazil), being recently deposited in the anatomical collection of the Federal University of Goiás, Campus of Catalão, where they were dissected and studied. This work was previously approved by the Institutional Ethical Committee from the Federal University of Goiás (CoEP-UFG 81/2008, authorization from the IBAMA No. 15275).

To undertake the anatomical observations for the present work, after receiving the specimens at the anatomical collection of the Federal University of Goiás each specimen was processed, by the first author, as follows: (1) it received an injection of latex 601-A (Dupont) stained with Wandalar red diluted in ammonium hydroxide in the abdominal aorta in order to facilitate the visualization of small arteries; (2) it was incubated in water at room temperature for 10–12 hr; and then (3) it received a perfusion of 10% formaldehyde with 5% glycerin through the femoral vein for fixation. The monkeys were preserved in 10% formaldehyde in closed opaque boxes to avoid light penetration and formaldehyde evaporation. The dissections were documented with a digital camera. The first author of the present paper dissected both sides of the eight specimens of *C. libidinosus*; the other authors have dissected numerous other primate and non-primate mammalian species in the past (see, e.g., the list of specimens provided by Dunlap et al., 1985, which were dissected by Aziz, and the list of specimens dissected by Diogo et al., 2009, which were dissected by Diogo). The nomenclature of the forelimb muscles follows, whenever it is possible, that used in human anatomy (The Federative Committee on Anatomical Terminology, 1998; see Diogo et al., 2009).

Our description of the forearm extensor muscles of *C. libidinosus* mainly follows the basic scheme outlined by Schafer et al. (1923) and Parsons Schaeffer (1942), which takes into account the evolutionary paradigm established by Brooks (1889; see also, e.g., Howell and Straus, 1933; Lewis, 1966, 1989; Schön, 1968; however, a more elaborate classificatory scheme is presented in the discussion). This scheme takes into consideration the location, nerve supply, vascular supply, function, ontogeny, and phylogeny of the muscles, recognizing the following groups: (1) the radial group (brachioradialis, extensor carpi radialis longus, extensor carpi radialis brevis, and supinator); (2) the superficial dorsal group (extensor digitorum and extensor digiti minimi); (3) the ulnar group (anconeus and extensor carpi ulnaris); and (4) the deep dorsal group, which can be subdivided into a superficial lamina (extensor pollicis longus and the extensor indicis) and a deeper lamina (abductor pollicis longus and extensor pollicis brevis). In our discussion, we have also made use of Tuttle's (1969) functional groupings of the forearm extensors, which are: (a) the wrist extensors (extensor carpi radialis longus, extensor carpi radialis brevis, extensor carpi ulnaris); (b) digital

(D II–D V) extensors (extensor digitorum, extensor indicis, extensor digiti minimi); Digit I extensors (abductor pollicis longus, extensor pollicis brevis, extensor pollicis longus); and the supinator. This grouping is useful in the functional analysis of the forearm-wrist-hand musculature.

## RESULTS

The textual description of the attachments, innervation, and blood supply of the forearm extensor muscles of the *C. libidinosus* specimens dissected by us is complemented with the information summarized in Tables 1 and 2 and the photographs shown in Figs. 1–6.

### The Radial Group

In *C. libidinosus*, the brachioradialis, which is located at the antero-lateral portion of the forearm (Fig. 1), presents a flat and elongated shape and a slender distal portion with a short tendon. It originates on the latero-distal portion of the humerus, namely on the supracondylar ridge, and inserts on the styloid process of the radius. This muscle is innervated by the radial nerve and vascularized by the radial artery, which is covered by the muscle at the proximal and medial portions of its trajectory in the forearm.

The extensor carpi radialis longus is located on the postero-lateral portion of the forearm (Fig. 1). It has a flat and elongated shape, originating from the latero-distal portion of the humerus, on the supracondylar ridge just below the origin of the brachioradialis. It passes deep to the extensor retinaculum (second compartment) and inserts below the tendon of the abductor pollicis longus muscle, distal to the wrist and on the dorsal surface of metacarpal II. It is innervated by the radial nerve and vascularized by the radial artery.

The extensor carpi radialis brevis (Fig. 1) is found at the postero-lateral portion of the forearm, having a cylindrical and elongated shape. It extends from the lateral epicondyle of the humerus, in common with the extensor digitorum and extensor digiti minimi, and inserts on the dorsal surface of metacarpal III. It is innervated by the radial nerve and supplied by the radial artery. The tendon of this muscle passes through the second extensor compartment at the wrist.

The supinator (Fig. 6) originates from two sources. One head originates from the lateral epicondyle (and contiguous areas) whereas the other begins on the lateral aspect of the proximal ulna. The muscle is inserted on the proximal part of the shaft of the radius. It is perforated by the deep radial nerve, which also supplies it. Upon its exit from the supinator, the deep radial nerve is called the posterior interosseous nerve. The supinator receives its blood supply from the posterior interosseous artery.

### The Superficial Dorsal Group

Located at the median portion of the forearm, the extensor digitorum (Fig. 1; note that this muscle is often designated as “extensor digitorum communis”), has a flat and elongated shape; it mainly originates from the lateral epicondyle of the humerus and inserts on the dorsal aponeurosis of Digits II–V (Fig. 2). At the wrist, it

**TABLE 1. Forearm extensor muscle attachments and their nerve supply in *C. libidinosus***


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Brachioradialis
Origin: Lateral supracondylar ridge
Insertion: Styloid process of radius
Nerve: Radial (usually C5 and C6 in modern humans)
Extensor compartment: --
Extensor carpi radialis longus
Origin: Lateral supracondylar ridge below brachioradialis
Insertion: Base of metacarpal II
Nerve: Radial (usually C6 and C7 in modern humans)
Extensor compartment: 2
Extensor carpi radialis brevis
Origin: Lateral epicondyle
Insertion: Base of metacarpal III
Nerve: Radial (usually C7 and C8 in modern humans)
Extensor compartment: 2
Supinator
Origin: Elbow joint capsule and sigmoid cavity of ulna, lateral epicondyle
Insertion: Proximal part of shaft of the radius
Nerve: Deep radial (usually C5–C7 in modern humans)
Extensor compartment: --
Extensor digitorum
Origin: Common extensor tendon, lateral epicondyle, muscular intersepta, antebrachial fascia
Insertion: D II, D III, D IV, D V; P2, P3 (extensor mechanism)
Nerve: Radial (usually C6–C8 in modern humans)
Extensor compartment: 4
Extensor digiti minimi
Origin: Common extensor tendon, lateral epicondyle, extensor digitorum communis, intermuscular septa
Insertion: D IV, D V (expansion mechanism)
Nerve: Radial (usually C6–C8 in modern humans)
Extensor compartment: 5
Anconeus
Origin: Distal part of triceps brachii, lateral epicondyle
Insertion: Lateral aspect of olecranon process
Nerve: Radial (usually C6 and C7 in modern humans)
Extensor compartment: --
Extensor carpi ulnaris
Origin: Common extensor tendon, lateral epicondyle
Insertion: Metacarpal V
Nerve: Posterior interosseous (usually C6–C8 in modern humans)
Extensor compartment: 6
Extensor pollicis longus
Origin: Middle third of ulnar shaft, interosseous membrane
Insertion: Proximal and distal phalanges of the thumb
Nerve: Posterior interosseous (usually C6 and C7 in modern humans)
Extensor compartment: 3
Extensor indicis complex
Origin: Body of ulna, interosseous membrane
Insertion: D II, D III, D IV (expansion mechanisms)
Nerve: Posterior interosseous (usually C6–C8 in modern humans)
Extensor compartment: 4
*Main body of abductor pollicis longus
Origin: Posterior surface of ulna, interosseous membrane, body of radius
Insertion: Trapezium, sesamoid bone, metacarpal I
Nerve: Posterior interosseous (usually C6 and C7 in modern humans)
Extensor compartment: 1
*Portion of abductor pollicis longus that probably corresponds to extensor pollicis brevis of modern humans
Origin: Proximal third of radius, interosseous membrane
Insertion: Articular capsule between metacarpal I and trapezium, base of metacarpal I
Nerve: Posterior interosseous (usually C6 and C7 in modern humans)
Extensor compartment: 1

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The passage of muscle tendons through specific compartments of the extensor retinaculum is also included (note: by the 8th week of development the myotomic blocks which participate in the formation of the upper limb muscles are arranged into a proximo-distal series as follows: C5, C6, C7, C8, and T1; all extensor muscles are formed from contributions of myotomes C5–C8; they are either supplied directly by the main radial nerve, the deep radial nerve, or the posterior interosseous nerve; extensor muscles which originate more proximally receive C5–C6 contributions, those which are located more distally receive C6–C8 spinal nerves; this information pertains to modern humans but it probably also applies to other anthropoids; see, e.g., Brooks and Zeitman, 1998).

TABLE 2. Distribution of forearm extensor muscles in the hominoids

	Homo	Pan	Gorilla	Pongo	Hylobates	Macaca	Colobus	Papio	Cebus	Saimiri	Callithrix	Alouatta	Aotus	Pithecia	Tarsius	Lemur	Loris
Brachioradialis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor carpi radialis longus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor carpi radialis brevis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Supinator	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor digitorum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor digiti minimi	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Anconeus	X	X	X	X	UNP	X	X	X	X	X	X	X	X	X	X	X	X
Extensor carpi ulnaris	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor pollicis longus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor indicis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Abductor pollicis longus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Extensor pollicis brevis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Distribution of forearm extensor muscles in the hominoids *Homo*, *Pan*, *Gorilla*, *Pongo*, and *Hylobates*, in the old World monkeys *Macaca*, *Colobus*, and *Papio*, in the New World monkeys *Cebus* (Cebidae, Cebinae), *Saimiri* (Cebidae, Callitrichinae), *Callithrix* (Cebidae, Callitrichinae), *Alouatta* (Atelidae), *Aotus* (Aotidae), *Pithecia* (Pitheciidae), in *Tarsius*, and in the strepsirrhines *Lemur* and *Loris*, based on an extensive review of the literature and on the dissections of the first author and also on the dissections of various hominoid and non-hominoid primates by the second and third authors: X means that the muscle is usually present in the respective taxon; UNP means that the anconeus is usually not present as a distinct muscle in *Hylobates* (see, e.g., the recent reviews of Diogo et al., 2009 and Diogo and Wood, 2009).

passes through the fourth compartment of the extensor retinaculum. The aponeurosis from which its tendons arise lies near to the bases of the phalanges in *C. libidinosus*. The tendons of the extensor digitorum are diverse in shape, and more than one tendon may be attached to each finger (Fig. 2). Each tendon contributes to the formation of the digital dorsal extensor tendon. A ramification of the tendon to Digit II occasionally attaches on the thumb. The extensor digitorum is innervated by the radial nerve and supplied by the radial artery.

The extensor digiti minimi, often named “extensor quinti digiti proprius,” lies at the postero-medial portion of the forearm (Figs. 1–4). It has a cylindrical and elongated shape and mainly originates from the lateral epicondyle of the humerus, inserting on the dorsal portion of Digits V and IV. It is supplied by muscular branches of the radial artery and innervated by the radial nerve.

### The Ulnar Group

The anconeus is a triangular muscle which mainly originates from the lateral epicondyle and inserts on the lateral margin of the olecranon process. It is supplied by the radial nerve and the recurrent radial artery. Some of its fibers interdigitate with the extensor carpi ulnaris.

The extensor carpi ulnaris (Fig. 6) is located at the postero-medial surface of the forearm (Figs. 1, 3, and 6). It mainly originates from the lateral epicondyle of the humerus, and does not originate directly from the ulna; after passing through the sixth compartment of the extensor retinaculum, it inserts on the metacarpal of Digit V. It is innervated by the posterior interosseous nerve and vascularized by branches of the posterior interosseous artery.

### The Deep Dorsal Group

As explained above, this group can be subdivided into a superficial lamina (extensor pollicis longus and extensor indicis) and a deep lamina (abductor pollicis longus; in *C. libidinosus* the extensor pollicis brevis is not present as a separate, distinct muscle: see text below and Table 2). The extensor pollicis longus (Fig. 3) originates from the medial third of the posterior surface of the ulna and from the interosseous membrane; distally, its tendon is bifurcated, inserting on both the proximal and the distal phalanges of the thumb. It is innervated and supplied by the posterior interosseous nerve and artery, respectively. At the wrist, its tendon passes through the third compartment of the extensor retinaculum.

The extensor indicis originates from the body of the ulna and the interosseous membrane, near the extensor pollicis longus, and passes through the fourth compartment of the extensor retinaculum, inserting on the dorsal aspects of the distal-most phalanges of Digits II, III, and IV. In fact, the extensor indicis may be seen as a structure including distinct bundles: an “extensor digiti secundi proprius” (to Digit II), an “extensor digiti tertii proprius” (to Digit III), and an “extensor digiti quarti proprius” (to Digit IV). This muscle (part of the “extensor digitorum profundus” sensu authors such as Schön, 1968, and Aziz and Dunlap, 1986) receives its nerve supply from the posterior interosseous nerve; it is vascularized by the posterior interosseous artery.



Fig. 1. Left forearm of a *C. libidinosus* specimen showing the extensor superficial muscles: (1) brachioradialis; (2) extensor carpi radialis longus; (3) extensor carpi radialis brevis; (4) extensor digitorum; (5) extensor digiti minimi, and (6) extensor carpi ulnaris (Bar = 1 cm).

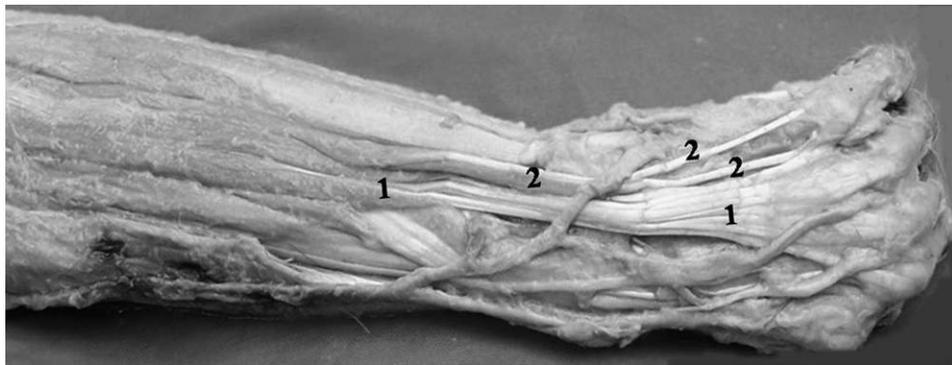


Fig. 2. Fleshy bellies and tendons of extensor digitorum (1) and extensor digiti minimi (2) of the left forearm of a *C. libidinosus* specimen (Bar = 1 cm).

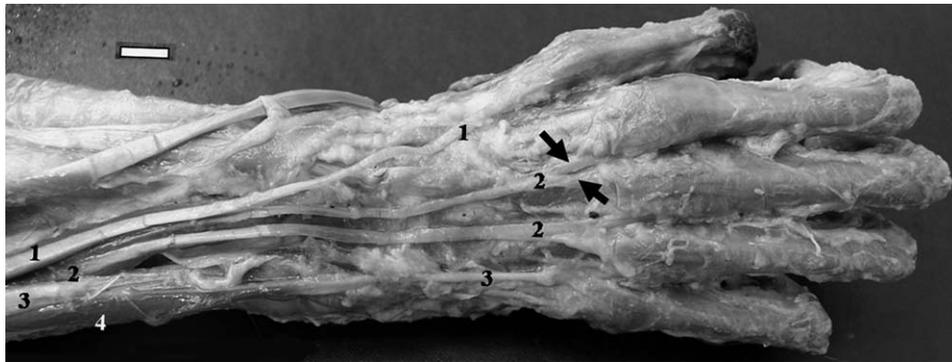


Fig. 3. Deep aspect of right forearm of a *C. libidinosus* specimen showing the: (1) extensor pollicis longus; (2) extensor indicis (going to Digits II and III [arrows] and IV); (3) extensor digiti minimi; (4) extensor carpi ulnaris (Bar = 1 cm).

The abductor pollicis longus (Figs. 4 and 5) originates from the posterior surface of the ulna, the radius, and the interosseous membrane. Its tendon passes through the first compartment of the extensor retinaculum and inserts on the base of metacarpal I, on the trapezium, and on the sesamoid bone situated near these two osteological structures. It is innervated by the posterior interosseous nerve and vascularized by the posterior interosseous artery. A small bundle of this muscle origi-

nates from the proximal third of the radius and the interosseous membrane, passes through the first compartment of the extensor retinaculum, and inserts on the articular capsule lying between the trapezium and the metacarpal I and on the base of this latter bone, being also supplied by the posterior interosseous nerve and artery (Figs. 2–4). However, the fleshy portion of this bundle, which seems to correspond to the extensor pollicis brevis of modern humans, is deeply blended with

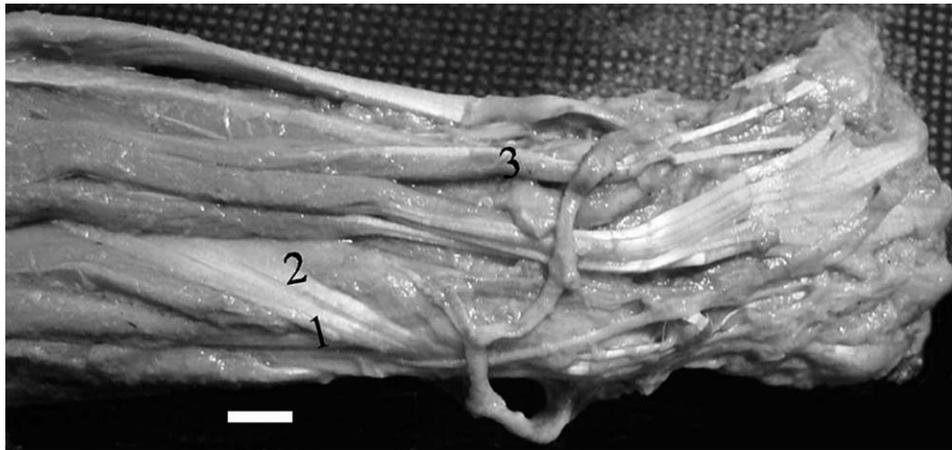


Fig. 4. Right forearm of a *C. libidinosus* specimen showing the abductor pollicis longus (1 and 2 represent the parts of the muscle that correspond to the abductor pollicis longus and to the extensor pollicis brevis of modern humans, respectively, which are not as differentiated as they are in

modern humans: that is, in *C. libidinosus* the extensor pollicis brevis is not present as a separate, distinct muscle, as is also the case in the vast majority of other non-human primates, with exception to hylobatids: see text and Table 2 for more details) and the extensor digiti minimi (3) (Bar = 1 cm).

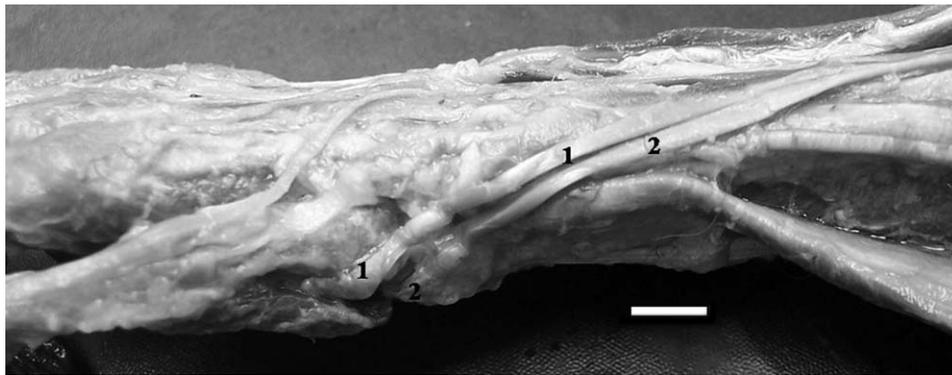


Fig. 5. Lateral view of the right forearm of a *C. libidinosus* specimen showing the tendons arising from the mainly undivided fleshy belly of the abductor pollicis longus (2 and 1 represent, respectively, the tendons that correspond to the tendon of the abductor pollicis longus of modern

humans, here inserting onto the base of metacarpal I, and to the tendon of the extensor pollicis brevis of modern humans, here inserting onto the base of metacarpal I and also onto the capsule of the articulation between this bone and the trapezium [white arrow]) (Bar = 1 cm).



Fig. 6. Medial view of the right forearm of a *C. libidinosus* specimen showing the supinator (1) and the extensor carpi ulnaris (2) (Bar = 1 cm).

the main body of the abductor pollicis longus, although its insertion tendon can be easily distinguished from the tendon arriving from this main body (Figs. 2–4; Table 1).

## DISCUSSION

Following Brook's (1889) initial systematization of the tetrapod extensor muscles, Howell (1936) and Haines

(1939) undertook a major update of the homologies of these muscles of the upper limb. Straus (1941a,b) revised the scheme by adding fresher data, including his own numerous investigations of old and new world monkeys and of hominoids. The latter work included analyses of morphology in relation to observed behavioral/functional observations of these primates. In 1989, Lewis revised Straus's work by including up-to-date critical data on the ontogeny of specific muscles and on his own research on the forearm-wrist-hand muscles of primates. Diogo et al (2009) have recently summarized the contemporary information regarding the evolution and homologies of the pectoral and forelimb muscles, from bony fish such as coelacanths and dipnoans to modern humans.

The comparisons provided below between *C. libidinosus* and other primates, particularly new world monkeys and other anthropoids, are complemented with the information given in Table 2, which summarizes the distribution of the forearm extensor muscles in the hominoids *Homo*, *Pan*, *Gorilla*, *Pongo*, and *Hylobates*, in the Old World monkeys *Macaca*, *Colobus*, and *Papio*, in the New World monkeys *Cebus* (Cebidae, Cebinae), *Saimiri* (Cebidae, Saimiriinae), *Callithrix* (Cebidae, Callitrichinae), *Aotus* (Cebidae, Aotinae), *Alouatta* (Atelidae), *Pithecia* (Pitheciidae), in *Tarsius*, and in the strepsirrhines *Lemur* and *Loris*. Therefore, in the present work we provide data for all the four subfamilies of Cebidae (Cebinae, Saimiriinae, Aotinae and Callitrichinae), as well as for the two other extant families of New World monkeys, Atelidae and Pitheciidae (for a short summary on the current systematics and the phylogenetic relationships of New World monkeys, see Introduction above; for more details on these subjects, see the recent reviews of Fabre et al., 2009 and Wildman et al., 2009).

In the paragraphs below, we will contrast the data obtained by our dissections of *Cebus* and of various other primate taxa, including the new world monkeys *Aotus*, *Saimiri*, *Pithecia*, and *Callithrix*, the old world monkeys *Macaca*, *Colobus*, *Papio*, and *Cercopithecus*, and the five extant hominoid genera. It should be noted that we have detailed information about these taxa, as well as about *Tarsius* and the strepsirrhines *Loris*, *Nycticebus*, *Lemur*, and *Propithecus*, because one of us, Rui Diogo (RD), has dissected all the head, neck, pectoral, and upper limb muscles of various specimens of these 19 primate genera. Those dissections were part of a project that was done with other colleagues with the main aim of providing the first phylogenetic analysis of primates based on muscular characters, which will be published in the near future (in the form of a book, by Taylor & Francis). Interestingly, the results of that cladistic analysis (which has a total of 212 muscular characters) has corroborated the platyrrhine relationships shown in the cladograms obtained in the recent genetic phylogenetic studies of Fabre et al. (2009) and Wildman et al. (2009): *Saimiri* and *Cebus* appear together, and are more closely related to *Callithrix* and to *Aotus* than to *Pithecia*, which appears as the most plesiomorphic new world monkey included in the cladistic analysis.

In modern humans, the brachioradialis usually originates from the proximal two-thirds of the lateral supracondylar ridge of the humerus and from the anterior surface of the lateral intermuscular septum, inserting on the lateral aspect of the styloid process of the radius (e.g., Di Dio et al., 2003; Netter, 2006). This muscle

bends towards the forearm and maintains the hand at an intermediate position between pronation and supination. It is usually innervated by branches of the radial nerve which contain fibers of the fifth and sixth cervical spinal nerves (C5 and C6). It is vascularized by the anterior radial recurrent artery, proximally, and by the radial artery, distally (Testut and Latarjet, 1959; Gray, 1979; Netter, 2006). It forms a protective muscular sheath over the superficial radial nerve and the radial artery. Swindler and Wood (1973) describe the brachioradialis as a broad and powerful muscle in baboons and chimpanzees; in the latter group it mainly occupies the radial edge of the ventral surface of the forearm. They state that, in these two primate groups, the brachioradialis is innervated by the radial nerve and supplied by the radial artery, which is covered by the muscle. In the 5 *Cebus apella*, 4 *Saimiri sciureus*, 1 *Aotus* sp., 1 *Callithrix moloch*, 1 *Callimico goeldii*, 2 *Callithrix argentata*, 1 *Callithrix jacchus*, 1 *Saguinus geoffroyi*, 1 *Saguinus myxtax*, 1 *Leontopithecus rosalia*, 1 *Callithrix pygmaea*, 1 *Lagothrix lagotricha*, 2 *Ateles geoffroyi*, and 1 *Alouatta palliata* specimens dissected by Dunlap et al., 1985, the brachioradialis connected the lateral supracondylar ridge of the humerus to the distal portion of the radius. However, in *Saimiri* there was an additional head that took origin from the pectoral ridge of the humerus, medial to the insertion of the pectoralis major. According to Straus 1941a,b, in *Saguinus geoffroyi* and *Cebus albifrons* the brachioradialis is inserted just proximally to the styloid process of the humerus. Senft 1907 and Beattie 1927 stated that in *Callithrix jacchus* the brachioradialis runs from the epicondylar ridge of the humerus to the styloid process, but sometimes also to the carpal region. Ziemer (1972) reported that in *Pithecia monachus* this muscle is innervated by the deep branch of the radial nerve and connects the epicondylar ridge of the humerus to the styloid process only. These latter observations were corroborated, respectively, in the *Callithrix jacchus* and the *Pithecia pithecia* specimens dissected by RD.

According to Moore and Dalley (2001), the human brachioradialis is particularly active during fast movements of the forearm flexion when made against resistance. Testut and Latarjet (1978) report that, besides bending, in modern humans the brachioradialis may also semi-pronate the forearm when in forced supination. In *Cebus paella*, the brachioradialis is the largest forearm extensor, with a muscular mass of 30.4% of the total mass of the forearm extensors (12.8% of the total mass of the muscles of the forearm), whereas in *Papio hamadryas*, a mainly terrestrial quadruped species, the mass of the brachioradialis represents 24% of the mass of the forearm extensors and 8.4% of the mass of the forearm muscles (Kikuchi, 2010). By taking into account the position, mass, and attachments of the remarkably robust brachioradialis muscle in *Cebus* (Fig. 1) suggests that this muscle is associated with forearm flexion, semi-pronation, and supination, and that its main action is restricted to the first part of the forearm flexion movement. The robustness of the brachioradialis in *Cebus* is very likely related to the crucial role played by these muscles in the arboreal activities of the members of this taxon.

In modern humans, the extensor carpi radialis longus usually originates from the lower third of the lateral

supracondylar ridge of the humerus and in front of the lateral intermuscular septum and inserts on the radial aspect of the dorsal surface of the base of metacarpal II (e.g., Di Dio et al., 2003; Netter, 2006). It is innervated by the radial nerve (usually by fibers from C6 and C7) and vascularized by branches of the anterior radial recurrent artery. The extensor carpi radialis brevis usually originates from the lateral epicondyle of the humerus and inserts on the dorsal surface of the base of metacarpal III, and basically helps to perform the same movements promoted by the extensor carpi radialis longus, that is, the extension and abduction of the wrist (e.g., Gray, 1979; Di Dio et al., 2003; Netter, 2006). It is usually supplied by the radial recurrent artery, the elbow joint arterial circle, and the posterior interosseous artery, being usually innervated by the posterior interosseous nerve, which originates in C7 and C8 (Table 1). In phylogenetic plesiomorphic mammals such as monotremes, the extensor carpi radialis longus and brevis are united in a singular muscle, the extensor carpi radialis sensu Diogo et al. (2009). In mammals such as rodents, tree-shrews and flying lemurs these two muscles are usually present as distinct structures (Diogo et al., 2009). In primates these two muscles are usually also separated, promoting the movements such as the abduction and the extension of the wrist, which are particularly important in arboreal taxa such as *Cebus*. According to Swindler and Wood (1973), in Old World monkeys exhibiting a habitual terrestrial quadrupedalism, such as baboons, there is no clear differentiation between the extensor carpi radialis longus and the extensor carpi radialis brevis. In New World monkeys such as *Callithrix jacchus* and *Pithecia monachus* the extensor carpi radialis longus usually runs from the lateral supracondylar ridge of the humerus to the metacarpal II, as is the case in *C. libidinosus* (e.g., Senft, 1907; Ziemer, 1972). This configuration was also found in all the *Callithrix*, *Pithecia*, *Aotus*, and *Saimiri* specimens dissected by RD. In all the New World monkeys dissected by Straus (1941a,b), the extensor carpi radialis brevis originated from the lateral epicondyle of the humerus and inserted onto metacarpal III (as is also the case in *C. libidinosus*), except in *Saguinus geoffroyi*, in which the origin was entirely from the distal part of the lateral supracondylar ridge of the humerus, and in *Cebus albifrons*, in which the insertion was onto both metacarpals II and III. According to Senft (1907) and Ziemer (1972) in *Callithrix jacchus* and *Pithecia monachus* this muscle usually runs from the lateral supracondylar ridge and lateral epicondyle of the humerus to the metacarpal III. It is thus interesting to note that regarding the insertion of the extensor carpi radialis brevis, *C. libidinosus* is more similar to New World monkeys from other genera and even families (e.g., *Pithecia*, from the family Pitheciidae, in which this muscle usually also inserts onto metacarpal III only) than to other species of *Cebus* such as *C. albifrons* (in which this muscle often goes to metacarpals II and III).

In modern humans, the extensor digitorum commonly originates on the lateral epicondyle (and its vicinity) of the humerus and is inserted on the middle and distal phalanges of Digits II–V; before attachments of each tendon on its respective digital phalanges, each tendon becomes a part of the extensor (dorsal) expansion mech-

anism (e.g., Netter, 2006). As described above, we encounter a similar arrangement in *C. libidinosus*. A similar arrangement was also found in all the New World monkeys dissected by authors such as Straus (1941a,b), Ziemer (1972), and Kaneff (1979, 1980a,b), and by RD. Senft (1907) also reported an origin from the lateral epicondyle and an insertion onto Digits II–V in *Callithrix jacchus*, but other authors (e.g., Beattie, 1927; Hill, 1957; Nagashima, 1976) stated that in at least some *Callithrix* specimens the extensor digitorum actually inserts onto Digits I–V. In modern humans, the innervation of this muscle is usually by the posterior interosseous nerve (fibers of C6–C8) and vascularization is by the radial artery (e.g., Llorca, 1963; Grant and Basmajian, 1965; Cunningham, 1976; Erhart, 1976; Gray, 1979; Gardner and Osburn, 1980; Lockhart et al., 1983; Snell, 1984; O’Rahilly, 1985; Hollinshead and Rosse, 1991; Spence, 1991; Sobotta, 2000; Netter, 2006). In chimpanzees and baboons the fleshy portion of the extensor digitorum is usually not as divided as in modern humans, its tendons mainly separating after crossing the fourth compartment of the extensor retinaculum (Swindler and Wood, 1973). They display a considerable intra-specific variation in these primates (Swindler and Wood, 1973). As explained above, in general, modern humans, chimpanzees, baboons, and *C. libidinosus* are similar in what respects the origin, insertion, vascularization, and innervation of the extensor digitorum, but in modern humans, contrary to the other groups, there is no accentuated ramification and multidirectional insertions of the tendons of this muscle. Behavioral studies have not reported differentiated movements of the fingers in *Cebus*, that is, the movements of the different fingers are usually combined and associated with the opening and closing of the hand (see, e.g., Straus, 1941a,b); the individual actions of fingers often require a large number of neuro-muscular synapses and more individualized muscles with less accentuated ramifications of the insertion tendons, as seen in modern humans (e.g., Machado, 2000).

In modern humans, the extensor digiti minimi usually originates from the common extensor tendon of the lateral epicondyle via a slender fascicle and from intermuscular septa, passes through the fifth compartment of the extensor retinaculum, and inserts on the extensor expansion of the tendon of that digit (e.g., Gibbs, 1999; Netter, 2006). Here, it is often joined by the tendon of the extensor digitorum to Digit V, that is, this digit receives two extensor tendons, one from the extensor digitorum and one from the extensor digiti minimi. In a few modern humans the extensor digiti minimi attaches to both Digits 4 and 5, as it usually does in *Cebus* and in most non-human anthropoids, including the vast majority of New World and Old world monkeys (e.g., Senft, 1907; Beattie, 1927; Straus, 1941a,b; Ziemer, 1972; Kaneff, 1980a,b; Lewis, 1989) and *Pongo*, but not *Hyllobates*, *Gorilla* and *Pan*, in which the muscle usually goes to Digit 5 only (e.g., Swindler and Wood, 1973; Diogo et al., 2009; Diogo and Wood, 2009). An insertion onto Digits 4 and 5 was found in all the *Callithrix*, *Pithecia*, *Aotus*, and *Saimiri* specimens dissected by RD.

In modern humans, the extensor carpi ulnaris usually originates from the ulna, the lateral epicondyle of the humerus and from the common extensor tendon and inserts on the base of metacarpal V and, in some cases,

to the proximal phalanx of this digit; it mainly acts with the radial extensors and the ulnar flexors to extend and adduct the wrist (e.g., Gibbs, 1999; Netter, 2006). A bony origin from both the ulna and humerus is also found in other hominoids, in *Tarsius*, in strepsirhines and in numerous other mammals, including marsupials (e.g., Jouffroy, 1971; Gibbs, 1999; Diogo et al., 2009). As described above, in *C. libidinosus* the origin is from the lateral epicondyle of the humerus and from the common extensor tendon, but not from the ulna; this is also the case in New World monkeys such as *Pithecia*, *Aotus*, *Callithrix* and *Saimiri* (e.g., Ziemer, 1972; dissections by RD) and in Old World monkeys such as *Macaca*, *Papio*, *Cercopithecus*, and *Colobus* (Howell and Straus, 1933; Straus, 1941a,b; Swindler and Wood, 1973; Lewis, 1989). As is the case in *C. libidinosus*, in modern humans the extensor carpi ulnaris is supplied by a branch of the posterior interosseous nerve (usually C6–C8) and the posterior interosseous artery. As stressed by Gibbs (1999), in some modern humans and in some chimpanzees this muscle may attach on the proximal phalanx of Digit V, forming an “ulnaris digiti quinti.” It is possible that within the evolution of mammals some of the attachments of the superficial ulnar extensor muscular sheath were lost, whereas the radial extensors located close to the thenar compartment have undergone considerable differentiation (see e.g., Tuttle, 1969; Aziz and Dunlap, 1986).

In modern humans, the extensor pollicis longus usually originates from the dorsum of the ulnar shaft, between the origin of the abductor pollicis longus/extensor pollicis brevis and the extensor indicis. It is regarded as one of the so-called “out cropping” forearm muscles which form the boundaries of the anatomical “snuff box,” being usually inserted to the base of the distal phalanx of Digit I and supplied by the posterior interosseous nerve (usually C6 and C7) and artery (e.g., Gibbs, 1999; Netter, 2006). One frequently encounters, in numerous new world monkeys, connections between the extensor pollicis longus and the extensor indicis (e.g., Schafer et al., 1923). Straus (1941a,b) and Schön (1968) have described the structure formed by these two muscles as the “extensor pollicis et indicis longus” in some New World monkeys (e.g., *Alouatta fusca* and *Saguinus Geoffroyi*). This points to a developmental relationship between these neighboring muscles that control the thumb and the forefinger, two digits that are critical for the precision grip. This idea is supported by the recent review of Diogo et al. (2009), which defends that both these mammalian muscles derive phylogenetically from the extensores digitorum breves of other tetrapods. Actually, in the cladistic analysis undertaken by RD (see above), one of the features that appears as a synapomorphy of new world monkeys is precisely the deep blending between the extensor indicis and the extensor pollicis longus: such a blending is consistently found in *Pithecia*, *Aotus*, *Saimiri*, and *Callithrix*, but not in any of the other 14 non-platyrrhine primate genera included in that analysis. Interestingly, in the *C. libidinosus* specimens dissected by us, as well as in specimens of other *Cebus* species dissected by authors such as Lewis (1989; e.g., *Cebus capucinus*), the extensor pollicis longus is well separate from the extensor indicis; this appears as a secondary reversion in RD’s cladistic analysis. This is thus a feature in which *Cebus* is more similar to chim-

panzees and modern humans (in which these two muscles are also usually well separated) than to most other new world monkeys. Another aspect in which the extensor pollicis longus of *Cebus* is also more similar to that of humans and chimpanzees than to that of most other new world monkeys is that in the former taxa this muscle usually goes to Digit 1 only, while in the latter taxa it usually goes to both Digits I and II. It should be noted that in the *Cebus albifrons* specimen dissected by Straus (1941a,b) there is an insertion onto Digits I and II, and that this is also the case in one of the five specimens of *Cebus apella* dissected by Dunlap et al. (1985) and one of the three specimens of *Cebus apella* dissected by Kaneff 1980a,b. However, the condition found in all the other *Cebus* specimens dissected by these latter authors is similar to that found by us in *C. libidinosus*, indicating that the usual condition for *Cebus* is effectively that in which the muscle goes to Digit I only. As an insertion onto both Digits I and II is consistently found in members of all the major taxa of Platyrrhini, including its most plesomorphic living group, the Pitheciidae (e.g., Straus, 1941a,b; Dunlap et al., 1985; dissections by RD), it is thus more parsimonious to consider that an insertion to Digits I and II represents a synapomorphy of new world monkeys; the insertion to Digit 1 only that is usually found in *Cebus* represents a derived condition (i.e., a secondary reversion) within these monkeys (this hypothesis was corroborated by the phylogenetic analysis of RD).

In modern humans, the extensor indicis usually originates from the dorsal aspect of the ulna and the interosseous membrane and inserts on the extensor expansion of Digit II, being supplied by the posterior interosseous nerve (usually C6–C8) and artery (e.g., Gibbs, 1999; Netter, 2006). Aziz and Dunlap (1986) have provided a review of the presence of “expanded” versions of this muscle which, in addition to supplying the index finger, also sends tendons to Digits I, III, IV, and even V. Authors such as Schön (1968) refer to the “extensor indicis complex”, which is often also named “extensor digitorum profundus” and may be divided into an “extensor digiti tertii proprius” (to Digit III), an “extensor digiti quarti” (to Digit IV) and an “extensor digiti quinti profundus” (to Digit V). As recently stressed by Diogo et al. (2009), the presence of muscles such as the “extensor digiti quarti” and/or the “extensor digiti tertii proprius” is common for mammals, the latter being for instance present in monotremes, and the former in placental mammals such as rodents. In *Tarsius*, strepsirhines such as *Loris* and *Nycticebus*, and catarrhines such as *Macaca*, *Papio* and *Pongo* the “extensor indicis complex” usually goes to Digits II and III, whereas in gorillas and *Pan* the insertion is usually onto Digit II only, as is often the case in modern humans (e.g., Jouffroy, 1971; Kaneff, 1980a,b; Diogo et al., 2009). However, in hylobatids, strepsirhines such as *Lemur* and *Propithecus* and in the vast majority of new world monkeys (e.g., Straus, 1941a,b; Jouffroy, 1971; Kaneff, 1980a,b; Dunlap et al., 1985; Diogo et al., 2009), the insertion is onto Digits II, III, and IV, as is the case in the *C. libidinosus* specimens dissected by us (see above). An insertion to Digits II, III, and IV was also found in the *Aotus*, *Saimiri*, and *Callithrix* specimens dissected by RD, but not in the *Pithecia* specimen dissected by him, in which the muscle inserted onto Digits II and III only, as it did in one of the 10

*Pithecia* specimens dissected by Ziemer (1972). However, in all the other nine *Pithecia* specimens dissected by Ziemer (1972), as well as in the *Pithecia* specimens dissected by Barnard (1875), there was an insertion onto Digits II, III, and IV, indicating that this is very likely the usual condition for *Pithecia*. It should be noted that occasionally in some specimens of other species of *Cebus* the extensor indicis might also go to Digits II and III only (e.g., *C. albifrons*: Straus, 1941a,b). However, the condition found in most members of this genus is clearly that in which the muscle goes to Digits II, III, and IV, as found in our *C. libinosus* (e.g., this condition was also found in the three *C. apella* dissected by Kaneff, 1980a,b, in the five *C. apella* reported by Dunlap et al., 1985, and in the *C. capucinus* specimens dissected by Lewis, 1989). Therefore, the plesiomorphic condition for new world monkeys clearly seems that in which the extensor indicis goes to Digits II, III, and IV; this was corroborated by the cladistic analysis of RD.

In modern humans, the abductor pollicis longus (“extensor ossis metacarpi pollicis” sensu authors such as Champneys, 1871) usually originates from the dorsal aspect of the ulna and the radius and the neighboring interosseous membrane and inserts on the base of metacarpal I and, in some cases, on the trapezium, being supplied by the posterior interosseous nerve (usually C6 and C7) and artery (e.g., Gibbs, 1999; Netter, 2006). The abductor pollicis longus and the extensor pollicis brevis are amongst those “outcropping” muscles of the forearm that emerge from the deep aspect of the extensores carpi radialis longus and brevis and cross obliquely over the distal radial shaft (here they conceal the insertion tendon of the brachioradialis; e.g., Gibbs, 1999; Netter, 2006). The human extensor pollicis brevis (“extensor primi internodii pollicis” sensu authors such as Champneys, 1871) usually originates on the proximal third of the dorsal aspect of the radial shaft and on the neighboring interosseous membrane and inserts on the base of the proximal phalanx of the thumb, being also supplied by the posterior interosseous nerve (usually C6 and C7) and artery. In some modern humans, the extensor pollicis brevis is not differentiated from the abductor pollicis longus (e.g., Gibbs, 1999; Diogo et al., 2009).

As explained in the recent review of Diogo et al. (2009), the plesiomorphic condition for mammals, often seen for example in phylogenetically plesiomorphic taxa such as platypus, is that in which the abductor pollicis longus has a single tendon, that is, in which there is no sign of a differentiation of a portion of this muscle into an extensor pollicis brevis. In tree-shrews such as *Tupaia* and flying lemurs such as *Cynocephalus* the abductor pollicis longus has two tendons, which usually attach on the metacarpal I and on the trapezium and surrounding structures, and which probably correspond to the tendons of the extensor pollicis brevis and of the abductor pollicis longus of modern humans. However, strepsirrhines often have a single tendon. Some authors have described an extensor pollicis brevis in hominoids such as *Pan* and *Pongo*, whereas authors such as Lewis (1989) consider that the only hominoids that have a “true” extensor pollicis brevis such as that found in modern humans are the gorillas. This is because gorillas are the only non-human hominoids in which the structure that corresponds to the undivided abductor pollicis longus of the platypus is usually divided into a portion that

attaches of the metacarpal I (which corresponds to the abductor pollicis longus of modern humans) and into a portion that attaches on the proximal phalanx of Digit I (which corresponds to the extensor pollicis brevis of modern humans). However, Diogo and Wood (2009), based on their own dissection of numerous specimens of all five extant hominoid genera and a review of the literature, have shown that in *Gorilla*, as well as in *Pongo* and *Pan*, the extensor pollicis brevis is not really present as a distinct muscle, and that the only non-human hominoids in which there is a distinct, separate muscle extensor pollicis brevis are actually the hylobatids (the muscle usually going to the metacarpal/carpal region in these primates, and not to the proximal phalanx of the thumb, as is the case in modern humans; see Table 2). In *Pan* and *Pongo*, as well in the *Cebus* specimens dissected by us and by other authors (e.g., *C. albifrons*: Straus, 1941a,b; *C. capucinus*: Lewis, 1989) the structure that corresponds to the undivided abductor pollicis longus of platypus may be divided into two portions, but none of these portions actually attaches directly on the proximal phalanx of Digit I, as does the extensor pollicis brevis of modern humans and gorillas (e.g., Swindler and Wood, 1973; Lewis, 1989; Gibbs, 1999; Gibbs et al., 2002; Diogo et al., 2009). In *Cebus* the portion corresponding to the extensor pollicis brevis of modern humans usually attaches mainly onto the metacarpal I; such an insertion thus allows the extension of the thumb. It is important to note that within the vast majority of new world monkeys dissected by RD, as well as by other authors (e.g., Straus, 1941a,b; Kaneff, 1980a,b; Dunlap et al., 1985), the abductor pollicis longus has a single tendon of insertion. The presence of two separate tendons thus clearly represents a derived character within extant new world monkeys, and is another feature in which *Cebus* is more similar to chimpanzees and modern humans (which have a further differentiation of the abductor pollicis longus, where the tendon going to the metacarpal I becomes associated to an also separated fleshy belly, forming the peculiar muscle extensor pollicis brevis) than to most other new world monkeys.

The main functions of the forearm extensors of *Cebus* can be summarized as follows: (1) elbow flexion (brachioradialis), (2) elbow extension (anconeus, extensor carpi radialis longus, extensor carpi radialis brevis, extensor digitorum, extensor digiti minimi, and extensor carpi ulnaris), (3) wrist extensors (extensor carpi radialis longus, extensor carpi radialis brevis, and extensor carpi ulnaris), (4) wrist adductor (extensor carpi ulnaris), (5) wrist abductors (extensor carpi radialis longus and extensor carpi radialis brevis), (6) thumb abductor (abductor pollicis longus), (7) thumb extensors (extensor pollicis longus and portion of the abductor pollicis longus that corresponds to the extensor pollicis brevis of modern humans and gorillas), (8) extensors of the fingers (extensor digitorum, extensor digiti minimi, and extensor indicis). From the comparisons above, it can be said that the configuration of the extensor muscles of the forearm of *Cebus* is, in general, more similar to that of other platyrrhines (which do not use tools) than to that of distantly related taxa that also use tools, such as chimpanzees and modern humans. In fact, the overall configuration, divisions and attachments of the brachioradialis, extensor carpi radialis brevis, extensor carpi radialis longus, extensor carpi ulnaris, extensor carpi

radialis and extensor digitorum is remarkably similar within the taxonomically very diverse new world monkeys. This is clearly an indication that phylogenetic constraints did play (and very likely continue to play) a major role in the evolution of these forearm muscles. In fact, all the three cases in which there are major differences between *Cebus* and other new world monkeys, and similarities between this genus and taxa that use tools such as chimpanzees and modern humans, are found in a single group of these muscles, the deep dorsal group. These three features may be summarized as follows: (1) in *Cebus*, chimpanzees and modern humans the extensor pollicis longus usually inserts onto Digit I only, and not onto Digits I and II as is the case in most new world monkeys; (2) contrary to most other new world monkeys, in *Cebus* the anterior portion of the abductor pollicis longus is differentiated into two separate tendons, as is the case in chimpanzees and modern humans (as explained above, in modern humans the abductor pollicis longus is actually further differentiated into a separate muscle, the extensor pollicis brevis); (3) also contrary to most other platyrrhines, in *Cebus*, as well as in modern humans and chimpanzees, the extensor pollicis longus is not deeply blended with the extensor indicis.

Interestingly, all these three features are related to the movements of the thumb. In most other new world monkeys, the extension of the thumb is functionally closely associated to the extension of not only Digit II (because the extensor pollicis longus usually goes to Digits I and II) but also to Digits III and IV (because this latter muscle is deeply blended with the extensor indicis, which usually sends tendons to Digits II, III, and IV). Moreover, in most other new world monkeys the single tendon of the abductor pollicis longus goes to metacarpal I, but also to carpal bones, thus resulting in a close functional connection between the movements of the thumb and the movements of the carpus. However, in *Cebus* the extensor pollicis longus usually goes exclusively to Digit I and is not deeply blended to the extensor indicis, thus resulting in a functional uncoupling between the extension of the thumb and the extension of the other digits. Also, in *Cebus* the abductor pollicis longus has two separate tendons, and one of these tendons is also essentially associated with the movements of metacarpal I (see Fig. 5 and above), thus resulting in another functional uncoupling, that is, between the movements of the thumb and the movements of the carpus. With respect to these three features, *Cebus* is remarkably similar to chimpanzees. A particularly remarkable uncoupling between the movements of the thumb and the movements of the adjacent hand structures is found in modern humans, in which there are three separate dorsal muscles of the forearm going exclusively to Digit I. These are the extensor pollicis longus, the extensor pollicis brevis, and the abductor pollicis longus, which go to the distal phalanx, the proximal phalanx, and the metacarpal of the thumb, respectively. This configuration has been explicitly related to the peculiar human ability to manufacture and use tools (e.g., Napier, 1980; Marzke, 1997; Susman, 1998).

Could the relationship between the myological features that we reported above for *Cebus* be explained in view of what we know about the lifestyle of the members of this genus? The members of this genus are widely dis-

tributed in wooded areas of central and upper South America, and it has been stated that they are "wholly arboreal but descend to ground to drink and raid plantations" (Napier and Napier, 1967). Parker and Gibson (1977) made the following observation regarding their feeding habits: "they are omnivorous," their "diet including nuts, buds, flowers, leaves, shoots, stems, and pith of many plants, and significant amount of animal matter, including ants, wasps, spiders, insect larvae, eggs, and small vertebrates including baby squirrels, fledgling birds, frogs, and lizards (...)" many of these food sources are highly seasonal." Frigaszy et al. (2004) stated, in turn, that the diet of *Cebus* specimens is mainly based in fruits and invertebrates, but is also correlated with the body mass of the specific animal that chooses and eats the food. The capuchins spend a great deal of time foraging, and usually they eat as they move from tree to tree. They do, however, also spend time at the ground level when necessary (e.g., Napier and Napier, 1967). They are mainly quadrupedal, although they were placed by Erikson (1963) in a "climber" locomotory group. These monkeys are known to also adopt bipedal postures; as many other New World monkeys, they also have a prehensile tail which is used, when necessary, as a "fifth limb." In addition, *Cebus* also adopts a squatting posture of the kind seen in some Old World monkeys. According to Napier and Napier (1967) the hand of the capuchin monkey is prehensile with a pseudo-opposable thumb, which makes sense in the light of the three features listed above that are related to functional uncouplings between the thumb and other hand structures, in which *Cebus* is more similar to chimpanzees and to modern humans than to other new world monkeys.

Parker and Gibson (1977) provided a comprehensive review of (1) object manipulation, (2) tool use, and (3) sensorimotor intelligence in relations to feeding adaptations in capuchin monkeys and in the great apes. According to these authors, there is an "intelligent type of tool use" and an "unintelligent type of tool use." Regarding the capuchins, they stated that these monkeys: (1) display proto-tool use in the wild and "true" tool use in captivity and (2) exhibit "tertiary circular sensorimotor intelligence." Within Piaget's sensorimotor intelligence series, the capuchins were found to actually show Stages 3 through 6 (and possibly, Stages 1 and 2 as well; see Parker and Gibson, 1977). Parker and Gibson (1977) also found a positive correlation between *Cebus*' omnivory and the seasonality of their food supply. They extended Hamilton's hypothesis to propose that "tertiary sensorimotor intelligence arose in the common ancestor of *Cebus* monkeys and independently in the common ancestor of the great apes and hominids as an adaptation for feeding on a variety of seasonally available foods susceptible to extraction from a matrix of case through intelligent complex object manipulation, and for discovering and remembering their spatial and temporal location." They added that "the majority of evidence indicates that *Cebus* monkeys surpass all other monkeys and compare favorably with chimpanzees in the amount and scope of their complex object manipulation." According to authors such as Blumenthal (1987), the remarkable manual dexterity of the capuchins is testified by their successful training to be helpers of quadriplegic modern humans.

Stephan and Andy (1969) and Stephan (1972) noted that, in comparison with other monkeys, and even with non-human hominoids, capuchin monkeys have remarkable neurological capacities. They computed the following indices of the CNS of *Cebus*: (1) encephalization index of 9.8 (human: 12; chimpanzee: 11.5; atelid monkeys: 9.5); (2) progression index of the neocortex: 55 (human: 156; chimpanzee 60; atelid monkeys: 48); (3) progression index of striatum: 14 (human: 18; chimpanzee: 7). Stephan (1972) further stressed that *Cebus* monkeys have “especially well developed optic centers (...) whereas in *Homo* they (the optic centers) do not exceed the average for simians” (see also, e.g., Paiva, 1998).

The capuchin monkeys may be grouped with those platyrrhines that engage in “climbing and suspensory posturing in terminal branches” of trees, just like the hylobatids, the orangutans, and the chimpanzees (Tuttle, 1969). These monkeys spend a great deal of time in active manipulation to search for food and to prepare it for ingestion, and it does appear that they may use their wrist and hand—in equal measure—in locomotion and in manipulation. The importance of manipulation in these monkeys may thus be related to the fact that the muscles of their thenar aspect of the wrist and hand regions exhibit, in general, a greater partition than those of the ulnar side (see above). Stephan (1972) and Paiva (1998) stated that the fine manipulation of objects displayed by primates such as the capuchin monkeys, including “object-substrate manipulation,” “complex object manipulation,” and “social-object manipulation,” is only possible due to the remarkable neurological organization of these monkeys (e.g., the evolution of higher learning centers in the cerebral cortex). Interestingly, the fact that *Cebus* monkeys have at least two complete sets of digital extensors, as do most other monkeys and also the highly arboreal Asian apes (see above), also indicates that these monkeys are able to navigate in arboreal habitats with confidence and ease.

In summary, on the one hand *Cebus* has many features in common with the other new world monkeys (e.g., the extensor indicis usually going to Digits II, III, and IV; the extensor digiti minimi going to Digits IV and V; the extensor carpi ulnaris not originating from the ulna), which are examples of the important role played by phylogenetic constraints. These features are probably the ones that allow the *Cebus* monkeys to easily navigate in its arboreal habitat, as do other new world monkeys. On the other hand, there are three features in which *Cebus* is clearly different from most other new world monkeys and more similar to distantly related taxa that also use tools, such as chimpanzees and modern humans (i.e., extensor pollicis longus going to Digit I only; separation between this muscle and the extensor indicis; abductor pollicis longus with two separate tendons). All these features are related with the movements of the thumb, and are thus very likely related to the ability to finely manipulate objects; they thus indicate that specific, homoplastic ecological adaptations towards a similar behavior (tool use) have also played an important role in the evolution of the primate forearm muscles. Therefore, the *Cebus* monkeys provide an illustrative example of how phylogenetic constraints and ecological adaptations have been combined to develop a specific myological configuration that, associated with their sophisticated neurological organization, allow them

to easily navigate in their arboreal habitats and, at the same time, to finely manipulate objects to search for food and to prepare this food for ingestion.

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