

Functional specialization in the intrinsic forelimb musculature of the American badger  
(*Taxidea taxus*)

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## ABSTRACT

Evaluation of relationships between muscle structure and digging function in fossorial species are lacking. We quantified muscle architecture in the forelimbs of American badgers (*Taxidea taxus*) and estimated force, power, and joint torque of their intrinsic musculature as these functional properties relate to their scratch-digging behavior. For comparison with the badger, muscle properties of the generalist opossum (*Didelphis virginiana*) were also quantified. Architectural properties measured included: muscle mass, length, volume, physiological cross-sectional area, fascicle length and pennation angle. Badgers showed significantly more massive shoulder flexors, elbow extensors and digital flexors. The triceps brachii for badger was the most massive muscle group studied and displayed long fascicles with little pennation, an architecture consistent with appreciable shortening capability and higher power. In addition to elbow extension, uniquely two biarticular heads (long and medial) of the triceps are capable of applying large flexor torques to the shoulder to retract the forelimb throughout the power stroke. The massive and complex digital flexors showed relatively greater pennation and shorter fascicle lengths in addition to compartmentalization of muscle heads for both force production and range of shortening to flex the carpus and digits. Muscles in other functional groups with short muscle moment arms showed some specialization for high force production, and are likely important for resistance against high limb forces imposed by interaction of the forelimb with the substrate. Collectively, the muscle specializations observed for badger indicate important differences between the forelimbs of fossorial and non-fossorial species, and indicate mechanisms for application of large out-forces during scratch-digging in badgers.

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## **DEDICATION**

I dedicate my Thesis to my parents who have taught me the value of education and my friends who have taught me the value of fun, without which I would never I have been able to finish this Thesis.

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## LIST OF ABBREVIATIONS

$\theta$  - pennation angle (in deg)

$\sigma$  - maximum isometric muscle stress

$\rho$  - skeletal muscle density

$\propto$  - proportional to

AI - architectural index

$F_{\max}$  - maximum isometric force

FL - fiber length

$FL\ s^{-1}$  - fiber shortening velocity in fiber lengths per second

DDF - deep digital flexor

$l^F$  - fascicle length

$l^M$  - muscle length

$M$  - muscle moment (torque)

$M$  - muscle mass (in g)

MTU - muscle-tendon unit

N - Newton

PCSA - physiological cross-section area (in  $cm^2$ )

$Q_{10}$  - temperature rate coefficient (10°C interval)

$r_m$  - muscle moment arm

SDF - superficial digital flexor

$V$  - muscle volume ( in  $cm^3$ )

$V_{\max}$  - maximum shortening velocity

W - Watts (unit of power)

## INTRODUCTION

Our understanding of animal structure and function often focuses on detailed studies of muscle-tendon architecture in the limbs of cursorial animals (Alexander et al. 1982; Sacks & Roy, 1982; Hermanson, 1997; Biewener, 1998; Brown et al., 2003; Payne et al. 2004, 2005; Zarucco et al. 2004; Smith et al. 2006; Watson & Wilson, 2007; Williams et al. 2007, 2008a; McGowan et al. 2008; Butcher et al. 2009; Hudson et al. 2011). However, locomotion is only one behavior critical to the survival of animals. Many animals are specialized for non-locomotor, or adaptive behaviors, for success in the niches they occupy. Digging is a behavior important to a large number of phylogenetically and functionally diverse groups spanning subterranean, semi-fossorial and fossorial lineages. In particular, animals specialized for the fossorial habit (Hildebrand & Goslow, 2001) have a lifestyle whereby digging provides them with microhabitats for socializing, raising young, hunting and escaping predation, but they do not live permanently beneath the surface (Quaife, 1978; Long, 1999; Lindzey, 2003). Fossorial specialists most commonly dig by scratch-digging (Hildebrand & Goslow, 2001), where the forelimbs are alternately flexed and extended to move soil rearward for removal of debris either behind or posterolateral to the animal by the hindfeet (Quaife, 1978, Hildebrand & Goslow, 2001).

Despite the prevalence and utility of scratch-digging for survival, evaluation of relationships between muscle structure and digging function in fossorial species (e.g., Stahlheim-Smith, 1984; Thewissen & Badoux, 1986; Ebensperger & Bozinovic, 2000; Vizcaíno & Milne, 2002; Lagaria & Youlatos, 2006; Endo et al. 2003, 2007), including the American badger (Quaife, 1978), is still limited. The American badger (*Taxidea taxus*) is a member of the family *Mustelidae* (Long, 1973) and is commonly found throughout of plains of North America (Lindzey, 2003; Eads & Biggins, 2008). The badger is one of a few carnivores that hunt primarily by scratch-digging (Hildebrand, 1985). Badgers actively hunt by excavating the burrows of tunneling rodents (e.g., pocket gophers, prairie dogs, ground squirrels) (Long, 1973), and strike to kill by a single bite to the thorax (Michener & Iwaniuk, 2001). Badgers have even been observed to manipulate tools (e.g., wood blocks) with their forepaws to plug up exits to burrows, thereby trapping their prey inside (Michener, 2004). Corresponding with these adaptive behaviors are

several distinctive morphological features of badgers for the fossorial habit: First, a nictitating membrane (i.e., third eyelid) that protects the eyes from dirt and debris that might compromise vision during digging (Long, 1973). Second, large hindfeet (~10.5 cm in length) that are shovel-shaped (Lindzey, 2003), with toes that are partially webbed for excavating soil dislodged by powerful digging strokes of forelimbs (Quaife, 1978). Third, forefeet that have five long, sharp foreclaws (~5 cm in length) that are used to cut through compact soil. Fourth, robust forelimbs with a particularly large humerus displaying large bony processes for strong muscular attachment (Quaife, 1978). Finally, shorter distal limb bones (e.g., radius, metacarpals and phalanges) and a long olecranon process are both viewed as fundamental adaptations for increasing mechanical advantage of the forelimb musculature and application of high out-forces during scratch-digging (Hildebrand & Goslow, 2001).

In order to dig through the substrate, badgers must be able to generate high power and large joint torques with their digging apparatus. Forelimb muscles specialized for shortening and generation of high power would be expected to have long and fast fascicles in a parallel fiber architecture (Zajac, 1989, 1992), whereas muscles specialized for large torque should also have large muscle moment arms, defined as the perpendicular distance between the line of muscle action and joint centre of rotation. Conversely, other muscles in the digging apparatus (e.g., humeral stabilizers, wrist flexors) would have to resist large joint torques caused by high forces the limb experiences during scratch-digging (Quaife, 1978). Muscles specialized for this function would be expected to have pennate architecture with larger physiological cross-sectional area (PCSA), and appreciable muscle moment arms for added leverage to resist joint rotations (Hudson et al. 2011). Architectural measurements of muscle mass, fascicle length and fiber pennation angle permit estimation of maximum isometric force ( $F_{\max}$ ) and mechanical power, both key indicators of functional performance in muscles. Musculoskeletal anatomy has been described for numerous digging lineages: moles (Parsons, 1901; Yalden, 1966; Bou et al. 1990), rodents (Lehman, 1963; Gasc et al. 1985; Lessa, 1990, Lessa & Stein 1992; Lagaria & Youlatos, 2006; Morgan & Verzi, 2011; Elissamburu & De Santis, 2011), tenrecs (Endo et al. 2007), aardvarks (Thewissen & Badoux, 1986; Endo et al. 2003), armadillos (Miles, 1941; Gaudin & Biewener, 1992; Vizcaíno et al.

1999; Vizcaíno & Milne, 2002). However, skeletal adaptation in forelimb bones continues to be the primary focus of these studies. General findings characterize robust humeri capable of resisting high bending forces, massive triceps inserting on a relatively long olecranon process, large pronators, carpal flexors and digital flexors originating from a prominent medial epicondyle, and robust carpals/metacarpals capable of resisting high forces. Two studies have previously described musculoskeletal anatomy for the American badger (Hall, 1927; Quaipe, 1978), but neither quantified muscle architectural properties of the digging apparatus, nor the functional significance of their forelimb muscle morphology. Here we investigate muscle properties in the forelimbs of badgers as they relate to their scratch-digging behaviors.

### **Objectives & Hypotheses**

The objective of this study is to quantify muscle architectural properties of the intrinsic forelimb musculature of the fossorial American badger and compare them with similar data from the forelimbs of the non-fossorial Virginia opossum (*Didelphis virginia*). Comparative analysis of muscle architecture in the forelimbs of the badger with that of the generalist opossum, should provide additional insight into the evolution of their degree of fossorial specialization for applying large out-forces with their digging apparatus. The opossum has been previously used as comparative species for studies involving digging animals (Stalheim-Smith, 1989; Gaudin & Biewener, 1992), thus despite their phylogenetic distance, statistical comparison of a fossorial species with a species representing a basal mammalian condition can highlight functional differences (Garland & Adolf, 1994) associated muscle specializations for digging. We hypothesize that most forelimb muscles will have long fascicles in a parallel fiber architecture, allowing for significant shortening and force production over a large range of joint motion. This muscle architecture and functional capacity is expected to be optimized for powerful scratch-digging motions. Specifically, the *triceps* group is expected to have the highest power and joint torque capacity of all intrinsic forelimb musculature. Flexors of the wrist and digits are also hypothesized to show a high concentration of limb muscle mass, and have muscle architecture consistent with high work and power capacity.

## **Materials and methods**

### **Specimens**

Forelimbs from six American badgers (obtained from licensed fur trappers belonging to the North Dakota Fur Hunters & Trappers Association) and six Virginia opossums (forelimbs obtained from animals trapped for another study in accordance with YSU, IACUC protocol: 03-09; PI: M.T. Butcher) were used for this study. Badger forelimbs were freshly removed from the carcass post-mortem and immediately frozen. Unfortunately, extrinsic forelimb muscles were unavailable for dissection due to this procedure and thus were not included in any analysis. Specimens were stored at  $-20^{\circ}\text{C}$  until experimentation. Limbs were allowed to thaw for 24-36 h at  $4^{\circ}\text{C}$  prior to dissection and measurement. Morphometric data from animals used are presented in Table 1.

### **Muscle measurements**

Forelimbs were dissected and the musculoskeletal anatomy of their intrinsic musculature (excluding the manus) was described and quantified using established methods (Payne et al. 2005; Smith et al. 2006; Williams et al. 2007, 2008a). Muscle name, origin and insertion followed nomenclature of Hall (1927) and Quaiife (1978) for badger, and that of Kirsch (1973) and Jenkins & Weijs (1979) for the opossum. Muscle action was estimated by the line of action of the muscle about the joints it crossed. In total, 33 muscles from the badger forelimb, and 28 muscles from the opossum forelimb were systematically dissected from a distal-to-proximal orientation. Muscle moment arm ( $r_m$ ) was measured using digital calipers (Mitutoyo, Japan, accurate to 0.01 mm) for select muscles with attachments about the wrist, elbow and shoulder joints (with each joint in a neutral position) prior to their removal (see Fig. 1). Following muscle removal from the forelimb, any associated free tendons were removed, and muscle mass was measured using an electronic balance (Mettler-Toldeo, USA, accurate to 0.01g). Fascicle length ( $l^F$ ) was measured at 5-10 sites along the muscle belly using digital calipers and the mean was calculated. Fiber pennation angle ( $\theta$ ) was also measured at 5-10 sites along the muscle belly using a protractor and the mean was calculated. Muscles were periodically moistened with PBS (phosphate buffered saline) to prevent desiccation during dissection and measurement.

## Calculations & Normalization

Muscle volume was calculated by dividing mean muscle mass by a muscle density of  $1.06 \text{ g cm}^{-3}$  (Mendez & Keyes, 1960). Physiological cross-sectional area (PCSA) was calculated according to Zarucco et al. (2004) as

$$(V/l^F) \times \cos \theta, \quad (1)$$

where  $V$  is muscle volume (in  $\text{cm}^3$ ),  $l^F$  is mean fascicle length (in cm), and  $\theta$  is mean pennation angle (in deg). Pennation angle was used in our calculations of PCSA to correct for more accurate estimates of isometric force (Williams et al. 2008a). Maximum isometric force ( $F_{\max}$ ) was estimated by multiplying PCSA and a maximum isometric stress of  $30 \text{ N cm}^{-2}$  (Woledge et al. 1985; Medler, 2002). Joint torque was calculated by multiplying  $F_{\max}$  and  $r_m$ , while power was estimated according to Hill (1938) as

$$0.1 (F_{\max} \times V_{\max}), \quad (2)$$

where  $V_{\max}$  (in fiber lengths per second:  $\text{FL s}^{-1}$ ) is maximum shortening velocity of single muscle fibers. Size-specific values of  $V_{\max}$  were predicted for badger and opossum using published slack test data for fast MHC-2A fibers at  $12^\circ\text{C}$  (Toniolo et al. 2007). Relative values of  $1.87 \text{ FL s}^{-1}$  for a 7.6 kg badger, and  $2.12 \text{ FL s}^{-1}$  for a 2.1 kg opossum were determined at  $12^\circ\text{C}$  (Fig. 2). Accounting for a  $Q_{10}$  of 2-6 for  $V_{\max}$  (Ranatunga, 1984; Pate et al. 1994), values of  $7.5 \text{ FL s}^{-1}$  and  $8.5 \text{ FL s}^{-1}$  were estimated at near physiologic temperatures for badgers ( $38^\circ\text{C}$ : Harlow, 1981) and opossums ( $35^\circ\text{C}$ ; Higgenbotham & Koon, 1955), respectively.

Muscle architecture measurements were determined as both absolute and normalized values to allow comparison between species and individuals. Muscle data were assumed to scale isometric with body mass ( $M$ ), and thus were normalized accordingly (Alexander et al. 1981; Payne et al. 2004). Masses were normalized directly to  $M^{1.0}$ , areas to  $M^{0.66}$ , and lengths to  $M^{0.33}$ . Mass of each muscle studied was also normalized to total forelimb muscle mass and presented as an architectural index (AI) of proximal-to-distal forelimb muscle mass distribution (Smith et al. 2006; Williams et al. 2008a). For this part of the statistical analysis (see below), muscles were categorized into functional groups (e.g., shoulder flexors, elbow extensors, digital flexors) where grand means were used to calculate group averages. Data reported for  $l^F$  and  $\theta$  for individual muscles also represent

grand means. Ratios of fascicle length to muscle length (Zarucco et al. 2004; Butcher et al. 2009), and PCSA to muscle mass (Williams et al. 2007, 2008a) were additionally calculated (badger only) to indicate muscle function.

### **Digging observations**

Observations of digging behavior representative of the American badger were made previously on two captive badgers (unpublished data acquired from A.P. Russell at the University of Calgary; Quaife, 1978). One badger (male) was observed while housed in sand filled enclosure at the Calgary Zoo. The second badger (female, 6.5 kg) was obtained from Calgary Animal Control, and housed at the University of Calgary Animal Care Facility. Patterns of forelimb motion for this animal were filmed at 100 frames s<sup>-1</sup> in a laboratory enclosure and in the field for kinematic assessment of scratch-digging behavior. Descriptive observations of digging behavior were made on a total of 200 digging sequences between the two animals. Kinematic analysis was confined to 12 sequences that clearly depicted stereotypical digging for each scratch-digging pattern described. Measurements of joint angles and timing variables were combined with both descriptive observations of forelimb motion and estimated muscle properties to evaluate muscle function during scratch-digging in badgers.

### **Statistical analysis**

Descriptive statistics for architecture measurements are reported as means and SD (standard deviation) unless otherwise specified. Species comparisons were made using Multivariate Analysis of Variance (MANOVA) performed on normalized muscle data from badgers and opossums using PASW Statistics 18 (IBM, SPSS). Variables tested were pennation angle and normalized: muscle mass, fascicle length, and PCSA. Functional muscle group mass distributions for badgers and opossums were compared using an ANOVA. Statistical significance for all tests was accepted at  $P < 0.05$ .



## RESULTS

### Functional distribution of forelimb muscle mass

The badger forelimb has 33 intrinsic forelimb muscles (excluding muscles of the manus) for which their origins, insertions, actions and fiber architecture have been described and verified (Table 2). Overall, the badger shows robust forelimb musculature; subscapularis, flexors of the shoulder, elbow extensors and digital flexors are all massive muscles of the digging apparatus (Table 3; Fig. 3). Mean total forelimb muscle mass for badger was  $218 \pm 66.4$  g, accounting for 2.8% of body mass. Comparatively, mean total forelimb muscle mass for opossum was  $50.7 \pm 12.4$  g, accounting for a similar percentage of body mass at 2.5 %. The largest muscle group in the forelimbs of both animals was the triceps brachii, which specifically for badger, accounted for 30% of intrinsic forelimb muscle mass. In the badger, the triceps has three large and distinct muscle heads: medial, long, and lateral which decrease in size in that order. Notably, the long head of triceps brachii (TBLO) and the medial head of triceps brachii (TBM) both originate from the scapula.

The distribution of muscle mass relative to total forelimb muscle mass for badger and opossum is shown in Fig. 4. Biarticular muscles, for example TBLO, were included in more than one functional group, in this case it is both a shoulder flexor and elbow extensor. The largest functional group for badger was the elbow extensors, which were significantly ( $P \leq 0.001$ ) more massive than those for opossum, and accounted for  $31.7 \pm 1.1\%$  of total intrinsic forelimb muscle mass (Fig. 4). Additionally, each head of the triceps alone was significantly more massive than the corresponding head for opossum. The second largest group was the shoulder flexors, which were also significantly ( $P < 0.05$ ) more massive for badger compared with opossum, and accounted for  $30.1 \pm 0.9\%$  of total intrinsic forelimb muscle mass (Fig. 4). From this group, the long and medial heads were significantly more massive than the those for opossum, yet the teres major for opossum was larger than that for badger ( $P \leq 0.001$ ) (Tables 4, 5). Digital flexors for badger also accounted for a large portion of total forelimb muscle mass at  $17.7 \pm 0.4\%$  and were significantly ( $P \leq 0.001$ ) more massive than opossum digital flexors (Fig. 4). Flexor digitorum superficialis (SDF) alone was significantly more massive than the SDF for opossum ( $P \leq 0.001$ ), as were two heads (radial and ulnar) of the flexor digitorum profundus (DDFU and DDFR,  $P < 0.05$ ; Tables 3, 5).

### **Muscle architectural properties**

Overall, architectural properties for the majority of intrinsic forelimb muscles did not show statistical differences between badger and opossum. Fascicle pennation angles ( $\theta$ ) in the forelimb of the badger ranged on average from 0-21°, with most muscles displaying parallel-fiber architecture. Notably, several muscles for badger including teres major, TBLO, and biceps brachii, each show no pennation (Table 3). The DDFR for badger also showed no pennation and thus was significantly ( $P \leq 0.001$ ) different from the DDFR for opossum, which had a mean pennation angle of  $14 \pm 7^\circ$  (Tables 4, 5). Badger muscles with the highest degree of pennation were the unipennate DDFU ( $21 \pm 6^\circ$ ) and the multipennate subscapularis ( $21 \pm 5^\circ$ ) (Table 3). Compared with badger, the subscapularis for opossum had a fundamentally different muscle architecture, showing long, parallel fascicles with no pennation. Mean values of  $\theta$  for badger were also relatively high for the bipennate SDF at  $19 \pm 8^\circ$ , and PCSA for this muscle was also significantly higher ( $P \leq 0.001$ ) than for the SDF for opossum (Tables 3, 5).

Ratios of PCSA to muscle mass for badger only are shown in Fig. 5A, with high values indicating higher force production capability. Subscapularis was found to have the highest ratio, estimated to be capable of producing an estimated  $F_{\max}$  of 434 N (Table 3). Flexors of the carpus and digits generally showed intermediate PCSA:muscle mass ratios ranging between 0.36 and 0.55. Of these muscles FCR, FCU, and SDF each had ratios  $> 0.5$  (Fig. 5A). The SDF had a relatively high estimated  $F_{\max}$  at 122 N, while each of five muscle heads of DDF had lower PCSA:muscle mass ratios and no head was estimated to produce greater than 100 N of isometric force (Table 3). Notably, the elbow flexors and extensors for badger had the lowest PCSA:muscle mass ratios. In particular, TBLO and brachioradialis had ratios of approximately 0.10, with  $F_{\max}$  estimates of 54.2 N and 17.6 N, respectively (Table 3; Fig. 5A).

Intrinsic muscles for badger showed a range of fascicle lengths that did not change systematically from proximal-to-distal portions of the forelimb. The longest mean fascicle lengths were found in the TBLO ( $9.3 \pm 1.3$  cm) for badger and these were significantly longer ( $P \leq 0.001$ ) compared with the TBLO for opossum (Tables 3, 5). Other muscles for badger having relatively long fascicles were the TBM, TBLA, and teres major, each having a mean fascicle length greater than 4 cm (Table 3). In the

antebrachium, two of the digital flexors had relatively long fascicle lengths, DDFR ( $3.7 \pm 0.8$  cm) and DDFHC ( $3.8 \pm 0.9$  cm) (Table 3), however, neither was significant compared with opossum (Table 5).

Figure 5B shows ratios of fascicle length to muscle length for badger intrinsic forelimb muscles. Here high values indicate higher levels of fascicle shortening capability. TBLO and brachioradialis had high ratios (range: 0.6 – 0.9) as did several other elbow flexor and extensor muscles, including the TBLA, TBM and brachialis. Digital flexors DDFHC and DDFR also had high fascicle length:muscle length ratios approaching 0.70, while other heads of this functional group were calculated to have ratios  $< 0.30$  (Fig. 5B). Subscapularis had the lowest ratio of all intrinsic muscles. Muscles with both relatively high PCSA:muscle mass and fascicle length:muscle length ratios also are suggested to have higher work and power capacity. The muscles with the highest estimated power in the badger were the TBM (5.36 W) and TBLA (5.01 W) heads of the triceps group (Table 3), although these massive muscles showed low PCSA:muscle mass ratios. In addition to elbow extensors, two heads of the digital flexor complex, SDF (1.89 W) and DDFR (1.71 W), also had relatively high power generation capacity (Table 3), and these muscles both showed intermediate ratios of force and shortening capability. For comparison, the TBLO for opossum was estimated to generate 1.62 W of power (Table 4), and this was the highest of any intrinsic forelimb muscle in this species.

Several muscles for badger had large muscle moment arms ( $r_m$ ) and large estimated joint torques (Table 6). With origins from the scapula, the biarticular TBLO and TBM each had the largest  $r_m$  at the shoulder joint and consequently, joint torques at the shoulder were estimated to be the largest for each muscle. Despite having a shorter mean  $r_m$  ( $2.8 \pm 0.6$  cm) at the shoulder, TBM had the highest joint torque of any muscle measured with a estimated value of 477 N.cm (Table 6). Similarly, subscapularis, had a small mean  $r_m$  at the shoulder ( $0.9 \pm 0.2$  cm), but had the capacity to apply a substantial shoulder joint torque. At the elbow, the long olecranon process for badger resulted in relatively long mean  $r_m$  ( $\sim 2$  cm) for each muscle of the triceps group (Table 6). The more massive and slightly pennate TBM and TBLA, were estimated to be able to apply large joint torques at 361 and 244 N.cm, respectively, while that of the TBLO was

considerably lower at the elbow. SDF and DDF (all heads combined with a common tendon of insertion) each had estimated values of joint torque at the carpus that exceed 200 N.cm. Surprisingly, despite a relatively long mean  $r_m$  ( $1.5 \pm 0.3$ ) at the carpus due to the long pisiform bone, the small FCU for badger was estimated to have the lowest joint torque of any muscle measured.

### **Scratch-digging behavior**

Badgers were observed to dig most frequently by one of two patterns: soil shifting or soil cutting. Soil shifting, was most common and was usually carried out in loosely packed soil. Soil cutting, was used for entry into compact soil and was accomplished by initially piercing the substrate with large foreclaws. Figure 6 shows a typical limb sequence from contact of the forelimb to removal at the end of the power stroke during soil shifting. Motion at each joint was largely similar for each digging pattern, with distinctions noted for soil cutting. To begin the limb cycle, pads of the manus contact the soil first followed closely by the long foreclaws, whereas during soil cutting, the foreclaws are presented to the soil first. Initial interaction of the manus with substrate causes the carpus to become hyperextended (Fig. 6A-B). At this time, the shoulder joint is extended to 130-140° (forelimb near maximum protraction) and the elbow extended to approximately 120° (see Fig. 1 for angular convention). The antebrachium is pronated to ensure a broad contact of the manus, and the wrist is radially flexed 20°. Furthermore, the brachium is abducted approximately 50° and digits are also abducted. Forelimbs show much less abduction at the time of contact during soil cutting, and both the shoulder (100°) and elbow (115°) are relatively less extended. Just prior to delivery of the power stroke, the carpus flexes to allow the large foreclaws better purchase of the soil.

The power stroke (retraction of the forelimb) begins with flexion of the digits (~30°). During the initial phases of the power stroke, the forelimb is drawn posteroventral as a result of simultaneous brachial adduction, shoulder flexion and elbow extension (Fig. 6C-D). The brachium continues to be adducted as the forelimb is retracted, pulling the manus further beneath the trunk. Concurrently, the antebrachium is partially supinated, while the wrist further flexes (up to 60°) and the digits are adducted, forming a shovel-shaped manus as soil is moved progressively towards the hindlimbs (Fig. 6E-F). Accompanying

wrist flexion, badgers tend to concentrate more body mass over the digging apparatus during soil cutting in particular, which allows them to push the tips of the foreclaws deeper into the substrate. This is facilitated by extension of the hindlimbs to shift the centre-of-mass (CoM) over the forelimbs. When less wrist flexion is observed, badgers kept their body mass shifted more caudally, and entry to the soil was gained by cutting the surface with faster power strokes. Lateral flexion of the trunk also aids in the delivery of the power stroke by the ipsilateral forelimb regardless of the digging pattern employed (Fig. 6G-H). At the end power stroke, the shoulder is flexed to 80°, the brachium is slightly abducted, and the elbow extended to 150° (Fig 6I). The power stroke takes on average 400 ms to complete. Average duration of the power stroke is shorter (260 ms) for soil cutting, owing to more rapid limb cycles where the shoulder and elbow are less extended at the time of contact, but both joints are flexed to a greater extent (shoulder, 75°; elbow, 90°) at the completion of the power stroke.

## **DISCUSSION**

Forelimb muscle architecture of the fossorial badger was quantified and compared with properties from forelimbs of the generalist opossum in order to better understand what muscle architectural properties reflect fossorial specialization. Overall, massive shoulder flexors, elbow extensors and digital flexors were observed in the forelimb of the badger which supported our hypotheses. Based on architectural properties, the multipennate subscapularis was specialized for high force production and application of large joint torques about the shoulder for humeral stabilization during digging. The architecture of most intrinsic muscles was consistent with relatively high power and large joint torque capability, particularly in the triceps brachii. The digital flexors were massive, but showed more diverse architecture than was anticipated, which did not support our hypothesis that these muscles would have long fascicles in a parallel architecture. These muscle groups are discussed below in relation to their function during the power stroke in scratch-digging.

## **Gross anatomy**

Musculoskeletal anatomy has been previously described for the American badger (Hall, 1927; Quaiife, 1978). Observations made in this study were largely in accord with reported descriptions with two exceptions: (1) Neither of the previous studies reported the presence of teres minor, but our specimens showed a distinct muscle belly that was easily separated from the infraspinatus and inserted on the greater tubercle of the humerus. (2) Hall (1927) reported the SDF inserted on the distal phalanges and DDF inserted on the middle phalanges. Our dissections agreed with those of Quaiife (1978) indicating a traditional insertion of SDF and DDF tendons on the middle and distal phalanges, respectively (Table 2). Most muscle origins for badger appeared fleshy with no discernable tendonous attachment to the bone. Muscle insertions were largely via short, thin tendons except the digital flexor tendons, which were substantially longer and thicker.

The forelimb of the badger was distinctive by its robust musculature about the scapula, the brachium, and flexor compartment of the antebrachium. Notably, the triceps brachii has two heads (TBLO and TBM) originating from the scapula, which is unusual among fossorial species previously studied including the prairie dog (Stahlheim-Smith, 1984), ground squirrel (Lagaria & Youlatos, 2006), groundhog (Bezuidenhout & Evans, 2005), aardvark (Thewissen & Badoux, 1986), and armadillo (Miles, 1941). An additional head of the triceps originating from the scapula can substantially increase the flexor torque applied at the shoulder during power stroke resulting in more powerful forelimb retraction. In this way, a substantial amount of the triceps group mass (~64%) can function synergistically with the latissimus dorsi, portions of the deltoideus, and teres major as forelimb retractors, as opposed to elbow extensors during scratch-digging. Powerful retraction of the forelimb would impose high bending forces on the humerus. The humerus of the badger was also robust, which takes into account large areas of muscular attachment as well as a relatively large cross-section. We calculated a humeral robusticity index (humeral mid-shaft width:humeral length) of 0.13, which is relatively high compared with a number of burrowing rodents (range: 0.08-0.12) for which similar data has been tabulated (Lagaria & Youlatos, 2006). A higher index here is suggestive of appreciable resistance to bending in the badger humerus.

At the elbow, the long olecranon process gives the each head of the massive triceps brachii a relatively long muscle moment arm (Table 6). Large moment arms for the triceps is a feature fundamental to digging species and is directly related the ability of the triceps to apply extensor torques at the elbow and thus apply large out-force to the substrate. The mechanical advantage of the triceps is related by a standard index of fossorial ability (Hildebrand, 1985). A value of 0.38 for badger is substantially higher than that determined for opossum (0.22), and is higher than fossorial ability indices reported for burrowers (range 0.17-0.25: Lagaria & Youlatos 2006). However, fossorial ability for the badger by this index is comparatively low relative to golden moles (0.68-0.77: Hildebrand, 1985) and armadillos (0.58-0.93: Vizcaíno & Milne, 2002), which both display extremely derived ulnae. Similarly, a triceps out-force index (Lagaria & Youlatos 2006) estimates downward force at the point of contact with the substrate per unit triceps in-force. For badger, this index was calculated at 0.29, which was well above a values of 0.16 for opossum, and those previously determined to be high in marmots (0.21) and prairie dogs (0.20) (Lagaria & Youlatos 2006). Collectively, robust musculature, a long olecranon process, and foreshortened ulna and metacarpals, underscore a high mechanical advantage of the triceps brachii and suggest a high degree of fossorial specialization in the forelimbs of badgers.

Additionally, the badger has massive digital flexor muscles in the antebrachium, accounting for 17.7% of total intrinsic forelimb muscle mass (Fig. 4). This marks a departure from the condition seen in cursorial animals where there is an overall proximal-to-distal reduction in forelimb muscle mass (Payne et al. 2005; Smith et al. 2006; Hudson et al. 2011). The DDF was a particularly large and complex muscle, displaying five heads, a range of fiber architectures, and a strong, thick tendon of insertion. Due to sizable  $r_m$  and high force production capabilities of SDF and DDF (Fig. 5A), the digital flexors can apply a large flexor torque at the carpus and the digits, which can augment the out-force applied to the substrate during scratch-digging.

### **Functional roles of intrinsic musculature**

The power stroke begins with simultaneous adduction of the brachium, flexion of the shoulder, and extension of the elbow (see Fig. 6). It is likely that high force is translated through the shoulder due to the interaction of the limb with the substrate opposing humeral retraction. Although it has a short muscle moment arm, subscapularis is capable of large joint torque because of its high PCSA and isometric  $F_{\max}$ , and thus is well suited to function as a medial humeral stabilizer producing high counterforce. Humeral adduction is also important during the power stroke, but the short fascicles and multipennate architecture of subscapularis limit this functional role. Therefore, adduction is likely performed by pectoralis, which has a large moment arm due to its broad insertion on the robust pectoral ridge of the humerus (Quaife, 1978). This difference in subscapularis muscle architecture between badger and opossum may suggest that high stabilizing forces at the shoulder may not be as important during scansorial behaviors or slow terrestrial locomotion (e.g., walking, trotting). A stabilizing function was also proposed for the multipennate subscapularis of the hare (Williams et al. 2007), which demonstrates both galloping and digging behavior, lending support to our functional interpretations.

Kinematic evaluation of scratch-digging showed that the shoulder is flexed through a range of  $60^\circ$ , suggesting that a substantial muscle shortening is required of the shoulder flexors (and limb retractors) during the power stroke. Large extrinsic muscles such as latissimus dorsi would be expected to provide the majority of power for this movement, however, TBM and TBLO are massive muscles with relatively long fascicles, and likely contribute significant work and power for humeral retraction. Moreover, elbow extension is limited to a range of  $30^\circ$  during the power stroke for soil shifting, and undergoes approximately  $30^\circ$  of flexion during soil cutting. This suggests that the biarticular TBLO and TBM may function more effectively as humeral retractors than elbow extensors. Despite the muscle moment arm of TBM being half the length of that of TBLO, its high mass and  $F_{\max}$  allow TBM to provide a substantial flexor torque (477 N.cm) at the shoulder. The long, parallel fascicles of TBLO provides this muscle with high shortening capability (Fig. 5B) and is likely important for contribution of high power (3.80 W) to retract the humerus quickly. A similar function has been suggested for the TBLO in the



scratch-digging aardvark (Thewissen & Baddoux, 1986) and a number of cursorial animals during running (English 1978; Goslow et al. 1981; Hoyt et al. 2005; Carroll & Biewener, 2009), where the long head is the only biarticular head of the triceps capable of applying a torque at the shoulder for humeral retraction. No muscle in the badger forelimb had extremely high power capacity, but high contractile velocity may not be required for digging, as forelimb muscles of prairie dogs have been shown to have long contractile times and high fatigue resistance (Stalheim-Smith, 1984). Myosin heavy chain (MHC) isoform analyses would allow for more accurate estimates of power, and preliminary (unpublished) data show that badger forelimb muscles have primarily oxidative fiber types (slow, MHC-1 and fast, MHC-2A). It may be that slower fibers are not particularly prohibitive for digging because of the high mechanical advantage of many intrinsic muscles in the badger forelimb, particularly the triceps brachii.

It was surprising to find that badgers extend the elbow only 30° throughout the power stroke for commonly used soil shifting digging pattern. However, limited kinematics data available for digging prairie dogs (Stalheim-Smith, 1984) and aardvarks (Thewissen & Baddoux, 1986) indicate a similar range of shoulder flexion but less elbow extension during the power stroke than was observed for badger, suggesting the massive badger triceps must actively extend the elbow while performing humeral retraction. Therefore, the functional roles of the triceps appear to be diverse and compartmentalized, with the biarticular TBLO and TBM primarily acting as shoulder flexors/limb retractors and secondarily as elbow extensors during stereotypical digging behavior in badgers. Recent studies of *in vivo* function in the triceps of goats (Carroll et al. 2008; Carroll & Biewener 2009) provide insight into this type of functional compartmentalization. The biarticular long head was shown to actively shorten throughout stance phase during running, while the monoarticular lateral head lengthened and shortened as expected with patterns of elbow flexion and extension (Carroll & Biewener 2009). The ability of the triceps long head to continuously shorten irrespective of elbow joint motion indicates the ability biarticular muscles with a similar architecture (high mass, long fascicles) to contribute substantial work and power to limb cycle, and exert relatively large torques about the shoulder and elbow simultaneously. In badgers, a similar pattern of shortening in TBLO and TBM during the power stroke would be expected. Significant fascicle shortening

would result in shoulder flexion and elbow extension, although the amount of elbow extension will be constrained by resistance offered by the substrate that will vary with hardness of the soil. The function of the monoarticular TBLA, however, is restricted to elbow extension, and fascicle shortening may likely mirror patterns of elbow flexion and extension as it does goats (Carroll et al. 2008). The mechanical advantage of TBLA allows it to exert a relatively high extensor torque (244 N.cm) at the elbow, which may also be important for resisting flexion of the elbow ( $\sim 25^\circ$ ) during soil cutting in hard soil. The high power capacity of TBLA (5.01 W) indicates it also has the capability to shorten to actively extend the elbow during the power stroke. Measurements of EMG and sonomicrometry are needed to verify these functional roles for the badger triceps group.

Opossums show a different apportioning of their musculature about the shoulder and elbow joints. Compared with badgers, overall less intrinsic muscle mass is dedicated to shoulder flexors (TBM is not a shoulder flexor in opossum) and more is accounted for by elbow flexors (Fig. 4). Large joint torques and out-forces produced by the biceps brachii have been previously shown to distinguish elbow flexor function between climbers (fox squirrel, raccoon) and diggers (prairie dog), as more massive elbow flexors provide the needed propulsion to move up a vertical substrate (Stahlheim-Smith, 1984, 1989). Significantly more massive biceps brachii in the Virginia opossum may then be explained by its scansorial abilities. Conversely, our limited analysis of scratch-digging forelimb kinematics in badgers suggests the elbow flexors may have an important role in counterbalancing extensor torques applied at the elbow by the triceps brachii during the power stroke, and roles in shoulder extension and elbow flexion initiating recovery phase (limb protraction) (Quaife, 1978). High shortening capability (Fig. 5B) and moderate power (Table 4) of the biceps brachii, brachialis, and brachioradialis are consistent with performing muscle work to flex the elbow when lifting the forelimb off the substrate following the power stroke, and extension of the shoulder with anterior swing of the limb.

Lastly, flexion of the carpus and digits is critical to scratch-digging in badgers. Interestingly, carpal flexors did not show the high concentration of limb muscle mass that was expected. However, carpal flexors had relatively high force production capability for their mass (Fig 5A) suggesting that these muscles may play a role in resisting carpal hyperextension caused by the force of interaction of the manus with the substrate. Of

note, FCU was significantly more massive and had significantly higher PCSA for opossum (Tables 4, 5). This finding may be related to the importance of ulnar deviation at the carpus when climbing vertical substrates. Despite lower PCSA, the badger carpus has a long pisiform bone which serves as the insertion for FCU (Hall, 1927; Quaife, 1978), and thus substantially increases its mechanical advantage (Hildebrand & Goslow, 2001) and joint torque (Table 6). The purpose of the long pisiform may be to compensate for the short  $r_m$ , and lower force and power properties of FCR and palmaris longus, which both appear to be less suited for wrist flexion during the power stroke.

The clear disparity between the mass of the digital flexors and carpal flexors indicates the importance of the digital flexors for scratch-digging. Moreover, compared to the generalist opossum, significantly more mass is dedicated to the digital flexors than the digital extensors in the fossorial badger (Fig. 4). To cut through compact soil, badgers have to powerfully flex their digits to pierce the soil with the foreclaws and concentrate a higher percentage of their body mass over the forelimbs (Quaife, 1978). Not only are the digital flexors massive and capable of applying relatively large joint torque at both the carpus and digits, but they also show a diversity of muscle architectures across the complex, which was also unexpected. The bipennate SDF has significant PCSA and is capable of producing high force (Fig. 5A). The massive and complex DDF shows a range of fascicle lengths and pennation. The unipennate DDFHA, DDFHB, and DDFU have architecture consistent with higher force production capability (Fig. 5A), whereas parallel-fibered DDFR and DDFHC have architecture consistent with high shortening capability (Fig. 5B). Overall, these functional properties combined with sizable muscle moment arms about the digits, suggest appreciable work and power from this muscle complex when flexing the digits during the power stroke, which is consistent with our original hypotheses. It may also be suggestive of compartmentalization for different functional tasks. Digital flexor heads specialized for high shortening can substantially flex the digits, while muscles with high  $F_{max}$  may allow badgers to maintain their digits in a flexed position as their large foreclaws cut through hard soil. Furthermore, their relatively large moment arms at the carpus indicates SDF and DDF are mechanically well suited to flex the carpus along with FCU, and augment out-force applied to the substrate by the triceps brachii.

### **Study limitations & Future directions**

The badger specimens obtained possessed only intrinsic forelimb muscles, but we recognize that measurements from extrinsic muscles including deltoideus, trapezius, latissimus dorsi, rhomboideus and pectoralis would provide a more complete view of functional specialization in the badger digging apparatus. Because little is known about digging performance and muscle function, *in vivo* data would be very helpful to better understand contractile activity of forelimb muscles during digging behaviors. Additional studies of the biomechanics in the limb systems of diggers are also needed to confirm muscle function based on measurements of architectural properties alone. Estimates of force and power are useful but, force can also be measured by direct means, and muscle power depends more on MHC isoform fiber type than directly on measurements of fascicle length. Architectural gear ratios (Azizi et al. 2007) also influence instantaneous muscle power output. Determination of MHC fiber types is currently being conducted and preliminary analysis indicates a high percentage of slow, oxidative MHC-1 and fast, highly oxidative MHC-2A fibers. These data will be used to refine estimates of muscle power. Use of CT scanning technology may also provide more accurate measurements of muscle fascicle length and pennation which would improve calculations of muscle force. It is also possible that some of the differences observed between these species may result from phylogenetic distance rather than function. Future comparisons of badger muscle properties with those of other digging specialists and more closely related species such as the raccoon (*Procyon lotor*) or otters (*Lutrinae*), should elucidate muscle properties selected for fossorial ability.

### **CONCLUSIONS**

The American badger displayed robust musculature capable of high joint torques at the shoulder, elbow, and wrist. Muscles in multiple functional groups were specialized for power generation or resistance against high limb forces during digging behavior. Collectively, the muscle specializations observed for badger indicate important differences between the forelimbs of fossorial and non-fossorial species, and indicate mechanisms for application of large out-forces during scratch-digging. The badger appears to species highly specialized for fossorial behavior.

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## **APPENDIX**

### **Literature Review**

Animals display a variety of anatomical adaptations that allow them to survive in their particular niche. Anatomical adaptations are reflected in a diversity of limb morphologies that indicate specializations for a particular habit (i.e. behavior) for example running, or other adaptive behaviors such as climbing and digging. In order to understand function of limb systems as it relates behavioral performance and survival, it is important to study the structure of animal limbs. Studies of structure/function relationships in the limbs of animals commonly involve analyses of limb bone geometry, muscle architecture and muscle fiber type composition.

### **Limb Muscles**

Muscles have evolved to meet a variety of functions demanding gross differences in performance. Skeletal muscle is a contractile tissue that when recruited by the nervous system, produces force and performs mechanical work. As such, muscles have traditionally been viewed exclusively as work and power generating machines or actuators (Bagshaw, 1982; McMahon, 1987). However, it is now well known that limb muscles can be specialized for a variety of functional tasks that do not involve the generation of high work and power (Biewener & Roberts, 2000; Alexander, 2003). Locomotion is an example of a behavior where distal limb muscles perform little-to-no mechanical work (e.g., Biewener et al., 1998, 2004) during running by contracting isometric, or undergoing lengthening contractions (Butcher et al., 2007, 2009). The arrangement and orientation of muscle fibers (i.e. muscle architecture), in addition to muscle fiber type composition (i.e. slow *versus* fast fibers), reflect functional specializations of muscle. Thus, quantification of muscle architectural properties is essential to an understanding of muscle function and how functional performance is integrated with the anatomy of animal limbs.

Limb muscles show remarkable diversity in the arrangement and orientation of their muscle fibers. Some muscles have long fibers arranged in parallel (parallel fiber architecture) indicating a specialization for substantial shortening and force production over a large range of contraction (Williams et al., 2007b). These muscles have a high capacity for performing positive work and generating power. Other muscles have short

fibers arranged at angles to the long axis of the muscle (pennate fiber architecture) indicating a specialization for higher force production (Biewener & Roberts, 2000; Zarucco et al., 2004; Butcher et al., 2009), but a low capacity for performing work and generating power. Fundamental measurements of muscle mass, muscle volume, fascicle (fiber) length, pennation angle ( $\theta$ ), and physiological cross-sectional area (PCSA; in  $\text{cm}^2$ ) are predictive of the maximum force muscles can produce, and work and power muscles can generate. Specifically, *peak* force production (in Newtons) of a muscle is determined by the PCSA of the fiber fascicles, which takes into account the angle or pennation of muscle fibers (McMahon, 1987; Alexander 2003).

Limb muscles typically display one of four types of fiber architecture: parallel, unipennate, bipennate and multipennate. Parallel-fibered muscles have lower PCSA due to long fascicles arranged at pennation angles of  $0\text{-}15^\circ$ , thus nearly all the force of contraction is transmitted along the long axis of the muscle to the distal tendon of insertion (Vogel, 2001; Smith et al., 2006; Williams et al., 2007a). Muscle fascicle (fiber) length and fiber orientation relative to the long axis of a muscle determine *relative* force production and range of contraction. In addition to a large range of contraction, parallel-fibered muscles are often composed of faster myosin heavy chain (MHC) fiber types (e.g., MHC-2X, 2B: Schiaffino & Reggiani, 1996) capable of producing a more forceful contraction and generating high power. However, these fibers are glycolytic and fatigue rapidly (Bagshaw, 1982; Vogel, 2001). Muscle fiber type (i.e. MHC isoform) is a critical factor for work and power generating capability of muscles because it is the primary determinant of the velocity at which muscle fibers shorten (Bottinelli & Reggiani, 2000). Mechanical work is defined as the product of force and range of contraction (shortening distance) and the rate at which work is performed is mechanical power. Power is commonly expressed as the product of force and shortening velocity (in Watts). Therefore, muscles with longer and faster fibers have an advantage for high power generation.

Pennate-fibered muscles have higher PCSA due to shorter fascicles arranged at pennation angles of  $15\text{-}55^\circ$ . Thus, only a percentage (equal to the  $\cos \theta$ ) of the force of contraction is transmitted from the fiber fascicles to the distal tendon of insertion (Vogel, 2001; Smith et al., 2006; Williams et al., 2007). Despite a reduction in muscle-tendon

force transfer, pennation allows for a substantial increase in force production capability because more fibers contract at one time creating more force without a consequent increase in muscle volume. This is important evolutionarily as animal function (e.g., running, digging) is constrained by limb muscle size (Alexander, 2003), thus pennation of limb muscles is a strategy to meet functional demands of higher force without maintenance of extremely large and metabolically expensive muscles. There are several levels of pennate fiber architecture typically observed in limb muscles: unipennate, bipennate, and multipennate. Unipennate muscles have relatively long muscle fibers attaching at an angle to one side of both the tendon of origin and tendon of insertion. Bipennate muscles have shorter muscle fibers attaching at an angle to two sides of the tendon of insertion. Multipennate muscles are highly complex by displaying multiple levels of pennation. Multipennate muscles have very short muscle fibers attaching between numerous tendon inscriptions (i.e. aponeurotic tendon) passing longitudinally throughout the muscle belly. In general, the higher the degree of pennation, the more specialized muscles are for high force production (and not mechanical work) due to progressive decrease in fascicle length and increase in number of fibers contracting per unit volume. Pennate muscles sacrifice range of contraction and power generation for high force production, especially during locomotor behaviors (Biewener & Roberts, 2000; Payne et al., 2005; Butcher et al., 2009). The energetic benefit of recruitment of a lower total volume of muscle fibers for a given amount of force is an advantage of pennate muscles over parallel-fibered muscles (Roberts et al., 1997). In addition, pennate-fibered muscles are often composed of slow, MHC-1 (slow oxidative) or fast, MHC-2A (fast oxidative) fiber types (Butcher et al., 2007) capable of sustained force production due to their aerobic and fatigue resistant properties (Bagshaw, 1982). As an example, several studies have indicated horse limb muscles are primarily composed of MHC-2A fibers (Snow, 1983; Kawai et al., 2009; Butcher et al., 2007, 2009, in press). MHC-1 and MHC-2A fibers generate low amounts of work and power (Bottinelli & Reggiani, 2000), however, slow muscles with short, pennate fibers produce high force economically (Biewener et al., 2004; Butcher et al., 2009).

Given the diversity of muscle architecture present in the limbs of animals, studies of muscle architectural properties alone may suggest the functional role of muscles in the



limb system, especially in an animal highly specialized by evolution for a given behavior. These types of analyses have traditionally been emphasized in animals specialized for running or the cursorial habit (Hildebrand, 1985), and are far less common in animals specialized for non-locomotor capabilities or adaptive behaviors.

### **Anatomical Specializations in Cursorial Animals**

Much of what is known about animal structure as it relates limb function has come from detailed studies of muscle architecture and fiber type composition in the limbs of cursorial animals. Cursorial animals are skilled runners that display differing degrees of morphological specializations in their limbs for high-speed running. Whereas speed is calculated as the product of stride length and stride frequency, the main way to increase speed is to increase the length of the stride by lengthening the distal limb relative to other portions of the body. Indeed, the imprint of evolution is most notable in the feet of cursorial animals (Hildebrand, 1960). Cursorial animals increase limb length by (i) elongation of the distal limb segment, namely the metacarpals and metatarsals, and (ii) changes in foot posture. A progressive increase in distal limb length and foot posture specialization is demonstrated in a diversity of cursors spanning humans (*Homo sapien sapien*), canids (e.g., greyhound: *Canis lupus familiaris*), big cats (e.g., cheetah: *Acinonyx jubatus*), and ungulates such as pronghorns (*Antilocapra americana*) and horses (*Equus caballus*) (Hildebrand, 1960). Humans display a plantigrade foot posture whereby the metatarsal bones contact the substrate during locomotion. More specialized high-speed runners such as greyhounds and cheetahs display a digitigrade foot posture whereby only their phalanges contact the substrate during locomotion. Finally, extremely specialized cursors like horses and pronghorns display a unguligrade foot posture whereby only the distal ends of their digits contact the substrate during locomotion (Hildebrand & Goslow, 2001).

Corresponding with an increase in distal limb length, the distal skeletal elements are as well often reduced in number and size in cursorial animals. As an example, the radius and ulna are commonly fused to decrease the overall mass of the limb (Hildebrand & Goslow, 2001). This is the general condition in digitigrade canids and felids. In addition to fusion of these two bones, the ulna can also be significantly reduced in size. In ungulates for example, the ulna is reduced to nothing more than an olecranon process

forming the posterior aspect of the elbow joint, serving as an attachment site for the large triceps brachii muscles (Hildebrand, 1960; 1985; Thomason, 1991). Decreasing mass of the distal limb enables cursors to expend less metabolic energy to overcome limb inertia, and thus they are able to cycle their limbs at faster rates during the swing phase of the running stride (Hildebrand, 1960). Furthermore, muscles in the distal portion of the limb once used for pronation/supination of the foot or abduction/adduction of the digits are reduced or eliminated altogether. This extreme level of morphological specialization further decreases distal limb mass and helps economize locomotion of large fast running animals (Hildebrand, 1960).

### **Muscle Architecture in Cursors**

One feature common to the limbs of cursorial animals is a concentration of the large, fast muscles in the proximal portion of the limb. As power is the rate at which mechanical work performed, the proximal limb would be expected to compartmentalize large volume muscles with relatively long, fast muscle fibers arranged in either a parallel or unipennate architecture (Panye et al., 2004; Smith et al., 2006). Compartmentalization of the largest muscles in the limb system about the hip or shoulder joints is also an evolutionary limb design for economizing locomotion (Hildebrand, 1960). This feature is well demonstrated in the forelimbs and hindlimbs of horses (e.g., Brown et al., 2003; Payne et al., 2004, 2005; Watson & Wilson, 2007), with the highest total muscle mass found in the proximal portion of the equine hindlimb. This is understood as the hindlimbs of horses, and most cursorial animals, are the propulsive limbs, while the forelimbs are used for braking and stability to redirect the center of mass (CoM) prior to the flight phase of each running stride (Merkens et al., 1993; Ruina et al., 2005). Specifically, the fast gluteus medius (Serrano et al., 1996; 2000) and biceps femoris muscles of the equine hindlimb have been shown to have the highest mass of all muscles in horse limbs at 8577 g and 7928 g, respectively (Payne et al., 2005). In the same study, fascicle lengths were extremely long averaging 20.3 cm in the gluteus medius and 25.8 cm in the biceps femoris (vertebral head), two muscles that act to powerfully extend the hip joint during running (Panye et al., 2005). Despite having a different functional role in locomotion, the forelimbs of horses also display large proximal limb muscles. For example, the massive triceps brachii (average mass: 4059 g) has long (average fiber length: 22.2 cm) and fast MHC-2X fibers

(Ryan et al., 1992) capable of supplementing mechanical power for each running stride during fast locomotion (Watson & Wilson, 2007).

A second feature common to the limbs of cursorial animals is a proximal-to-distal *decrease* in muscle mass and fascicle length. These features are exemplified in the limb muscles of dogs (Williams et al., 2008a, b) and horses (e.g., Brown et al., 2003a; Zarucco et al., 2004; Payne et al., 2004, 2005; Watson & Wilson, 2007). In the hindlimb of the greyhound, the biceps femoris muscle has been reported to have the highest mass of any hindlimb muscle (18% of total limb muscle mass) along with long, parallel fibers with a mean fascicle length of 14.3 cm (Williams et al., 2008a). Comparing this large hamstring muscle with a distal digital flexor muscle demonstrates a significant reduction in both muscle mass and fiber length. The flexor digitorum superficialis (SDF) muscle of the greyhound hindlimb was shown to be a relatively small muscle with an average mass of 53.4 g and mean fascicle length of 1.2 cm (Williams et al., 2008a), just 11% and 8% of biceps femoris mass and fascicle length, respectively. A similar distribution of muscle mass and fascicle length can also be observed in the forelimbs of greyhounds. For example, the long head of the large triceps brachii was reported at a mass of 341 g and mean fascicle length of 6.5 cm, compared to 18.3 g (muscle mass) and 1.2 cm (fascicle length) measured from the forelimb SDF (Williams et al., 2008b). Because of their shared cursorial habit, ungulates, like dogs, also demonstrate a significant proximal-to-distal reduction in muscle mass and fascicle length. In fact, this morphological feature is perhaps most extreme in the forelimbs of horses. Compared to the massive muscles with long fascicle lengths in the proximal portions of limbs in horses (see data above), the SDF in the distal forelimb has consistently been shown to have extremely short muscle fibers with mean fascicle lengths ranging from 3-8 mm (Hermanson & Cobb, 1992; Biewener, 1998; Brown et al., 2003; Zarucco et al., 2004; Butcher et al., 2009), for a relatively small muscle with an average mass of approximately 250 g (Brown et al., 2003; Zarucco et al., 2004; Butcher et al., 2009).

A third feature common to the limbs of cursorial animals is a proximal-to-distal *increase* in pennation and insertion tendon length. While massive, long-fibered muscles of the proximal portion of the limbs supply propulsive power for locomotion, short-fibered pennate muscles with long, compliant tendons function as biological springs that

store and return elastic strain energy to reduce metabolic energy consumption during running (Alexander, 1984; Biewener, 1998; Biewener & Roberts, 2000; Butcher et al., 2009). Metabolic energy savings directly result from the springy tendons undergoing the majority of length change (i.e. strain) as the whole muscle-tendon unit (MTU) elongates under the load of the animal (Wilson et al., 2001), thus allowing the muscle fibers to produce high resisting force by isometric or lengthening contractions which consume less metabolic energy than shortening contractions (Curtin & Davies, 1975). Energy returned via tendon recoil contributes mechanical work to the running stride at no additional metabolic cost to the animal; work that would otherwise have to be performed by the muscle fascicles (Biewener & Roberts, 2000). Muscle-tendon architectural property data from the horse is well studied and epitomizes the described functional morphology. Proximally, the massive gluteus medius and gluteus superficialis muscles display a moderate degrees of pennation ( $28-36^\circ$ ) and have relatively short (9.0 cm), stiff tendons attached to the greater trochanter and third trochanter of the femur (Payne et al., 2005). Distally, the ankle flexors (e.g., gastrocnemius), digital flexors (e.g., SDF) and digital extensors (e.g., extensor digitorum longus) all exhibit higher degrees of pennation and significantly longer, more compliant tendons. For example, the hindlimb SDF was found to have the highest mean pennation angle at  $52^\circ$  and longest insertion tendon length at 74.8 cm (Payne et al., 2005). A proximal-to-distal increase in muscle pennation and insertion tendon length is perhaps even more pronounced in the forelimbs of horses when comparing the complex digital flexor muscles (SDF and deep digital flexor) with architectural properties of the proximal forelimb musculature (Brown et al., 2003; Zarucco et al., 2004; Watson & Wilson, 2007; Butcher et al., 2009).

### **Non-locomotor Adapted Animals**

Locomotion is one behavior critical to the survival of animals, however, many mammals are specialized for non-locomotor or adaptive behaviors for success in the niches they occupy. Digging is a behavior important to both a phylogenetic and functional diversity of animal groups spanning numerous lineages and taxa of vertebrates and invertebrates. Animals specialized for digging or the fossorial habit (Hilebrand & Goslow, 2001) typically have a subterranean lifestyle whereby their digging behavior provides them with microhabitats for socializing, raising young, hunting and escaping predation.

Fossorial animals display numerous anatomical specializations for digging. In general, digging animals must be able to provide large out-forces or joint torque with their forelimb muscles, especially via substantial shortening of the triceps brachii to translate into powerful extension at the elbow joint. Static equilibrium analysis dictates that in order to balance torque at a given joint, out-force is equal to the product of in-force (muscle force) and the in-lever (muscle moment arm) divided by the out-lever (load moment arm) (Hildebrand & Goslow, 2001). In this mathematical relation, the muscle moment arm is the perpendicular distance from the muscle insertion to the joint center of rotation, while the load moment arm is the length of the limb segment from the joint center of rotation to the distal end of the limb bearing the load. It follows from this simple relationship that one way to increase joint torque, and thus mechanical power output of the triceps brachii for example, would be to decrease the length of the out-lever, that is the portion of the forelimb distal to the elbow joint extending to the distal ends of the digits. In contrast to cursorial animals, which display increased distal limb length, fossorial animals have evolved a shorter radius (compared with humerus) and short metacarpals and phalanges in order to *decrease* distal limb length (Hildebrand & Goslow, 2001). Another way to increase joint torque and power output of the forelimb musculature is to increase in-lever length, for which the triceps brachii is the olecranon process of the ulna. Thus, many fossorial animals display a very long olecranon processes. Percentage values of olecranon-to-ulna length (in-lever vs. out-lever) are 28% for the anteater (*Myrmecophaga*), 35% for the badger (*Taxidea*), 51% for the pangolin (*Manis*), 75% for the golden mole (*Amblysomus*), and 97% for the marsupial mole (*Notoryctes typhlops*) (Hildebrand, 1985). These data compared with a value of 12% for a closely related, but non-fossorial raccoon (*Procyon lotor*) (Hildebrand, 1985).

Anatomical specializations of increased muscle moment arm are not adaptations exclusive to muscles about the elbow joint. By application of the static equilibrium equation, it is evident that fossorial animals display similar specializations in the antebrachium of the forelimbs. For example, the pisiform bone (proximal carpal bone of the wrist joint) in a badger is elongated in order to increase the muscle moment arm, and therefore joint torque and power output, of the flexor carpi ulnaris muscle (Stein, 2000; Hildebrand & Goslow, 2001). Powerful flexion at the wrist joint is a key motion for the

scratch digging (see below) mode of fossorial behavior. Numerous fossorial animals also display relatively large forefeet with long foreclaws (Hildebrand & Goslow, 2001). While the mechanical relationship of the large and powerful flexor digitorum profundus muscle (i.e. deep digital flexor; DDF) does not change about the wrist joint, the relatively long forefeet in badgers for example, increase the moment arm of the DDF as it inserts at the distal ends of the digits. A relatively long muscle moment arm of the DDF, combined with long, stiff tendons that insert on all five digits, allows for a large range of contraction for powerful flexion of the digits and foreclaws. Like wrist flexion, powerful flexion of the digits is a key motion for scratch digging.

Other adaptations displayed in the limbs of fossorial animals are specializations of the limb muscles rather than changes in limb bone geometry (Hildebrand, 1985). These anatomical specializations are evaluated as muscle architectural properties. As force production and mechanical work performance of limb muscles are critical to translation of motion at a distal limb joint, another way to increase joint torque is to increase muscle work. Fossorial animals can do this by having massive muscles with long fascicles in a parallel fiber architecture. Large proximal muscles such as the triceps in the brachium should have the capacity to both produce large amounts of force and shorten over a large range of contraction, and thus will be able to perform large amounts of mechanical work and generate high power. Consequently, not only do the bony processes have to be large for the attachment of such powerful muscles, but the limbs require robust bones capable of withstanding the bending and torsional loading resulting from high muscle forces (Stein, 2000; Hildebrand & Goslow, 2001).

### **Fossorial Mammals**

Many lineages of mammals are well-adapted diggers. This is to suggest that these animals display specialized limb morphology related to their mode of digging. Animals specialized for digging can be divided into groups based on their specific mode of digging behavior: humeral-rotation digging (e.g., moles), hook-and-pull digging (e.g., anteater), scratch digging (e.g., badger), chisel-tooth digging (e.g., gopher), and head-lift digging (e.g., golden mole) (Hildebrand & Goslow, 2001). Of these modes of digging, the limbs must be highly specialized for humeral-rotation, hook-and-pull, and scratch digging. During humeral-rotation digging, the teres major rotates the relatively short and

wide humerus about its long axis while the elbow is held superior the shoulder joint. This limb conformation does not require pronation and supination of the antebrachium for digging power, but instead serves only to correctly position the large, flat forefeet and allows the majority of power for digging to be generated by the teres major muscles via exaggerated rotation at the shoulder joint (Yalden, 1966; Hildebrand & Goslow, 2001). Much of the family of true moles (*Talpidae*: Nowak & Paradiso, 1983) are humeral-rotation diggers, moving as fast as 2 body lengths per minute (Hildebrand, 1985) underground. For these species, the insertion of the teres major on the teres tubercle of the humerus is contralateral to the joint's axis of rotation, therefore increasing its muscle moment arm (Hildebrand, 1985) and the capability of the teres major to generate high torque and power at the shoulder joint.

Hook-and-pull digging is exhibited by anteaters (Family *Myrmecophagidae*: Nowak & Paradiso, 1983). The giant anteater (*Myrmecophaga tridactyla*) for example, hooks one of its long, sharp claws into an ant or termite mound and forcefully retracts the forelimb to pull the mound apart. The giant anteater has massive digital flexor muscles and a long supinator muscle, the latter of which is highly specialized by being divided into separate muscle heads that perform supination and flexion, respectively, thus facilitating the action of digital flexors and overall augmenting their mechanical power output (Hildebrand & Goslow, 2001). Additionally, the long-fibered medial head of the triceps brachii is modified such that it does not insert on the olecranon process of the ulna, but joins with the tendon of the DDF (Hildebrand, 1985) to further increase power output of the digital flexors during digging. Interestingly, the giant anteater must walk on its knuckles (contacts the ground with the dorsum of the manus at the metacarpophalangeal joint) in order to protect its foreclaws, thus giving this species a rather slow and clumsy gait, especially when galloping to evade predation by large cats (Nowak & Paradiso, 1983).

Scratch digging behavior is widely exhibited in diverse mammalian lineages. Provided are numerous examples of familiar mammals that employ this mode of digging. 1) The monotreme platypus (*Ornithorhynchus anatinus*: Nowak & Paradiso, 1983) is specialized for both swimming and digging, and commonly folds the webbed part of its forefeet under the claws when digging (Hildebrand & Goslow, 2001). 2) The marsupial mole

(*Notoryctes typhlops*: Nowak & Paradiso, 1983) is a well-adapted scratch digger that can be described as “swimming through the earth” by use of its large foreclaws (Hildebrand & Goslow, 2001). 3) The insectivorous golden mole (*Chrysochloris asiatica*: Nowak & Paradiso, 1983) is a highly specialized scratch digger with a unique ‘extra’ bone that replaces part of the unipennate ulnar head of the DDF muscle, resulting in simultaneous and powerful flexion of both the foreclaws (digits) and elbow joint (Hildebrand, 1985). 4) The armadillo (*Dasypodidae*: Nowak & Paradiso, 1983) display rough, heavy bones and a long olecranon process (Hildebrand, 1985), which is important for insertion of the large triceps brachii muscle used to powerfully extend the elbow joint during digging. 5) Rodents including sciurids (*Sciuridae*), pocket gophers (*Geomyidae*), and mole-rats (*Bathyergidae*) collectively comprise the largest group of scratch diggers (Walker & Nowak, 1983; Hildebrand, 1985).

Among rodent families, the sciurids are an especially diverse group, and are among the most studied of scratch digging specialists, despite the paucity of forelimb muscle architectural data available for this class of diggers as a whole. One study (Lagaria & Youlatos, 2006) of muscle architecture in the European ground squirrel, *Spermophilus citellus*, predicted the long head of the triceps brachii to be the most powerful muscle in forelimb based on its large PCSA. Relating muscle architectural properties (e.g., PCSA) to their function (e.g., force production) in digging is important for determination of digging performance. An index of fossorial ability, defined as olecranon length divided by ulna length distal to the olecranon process (Lagaria & Youlatos, 2006) indicates the mechanical advantage of the elbow flexors. This index provides an estimate of joint torque and power output potential during elbow extension. Sciurid genera with the highest fossorial ability are the marmots, including the groundhog (*Marmota monax*) and prairie dogs (*Cynomys gunnisoni*) (Lagaria & Youlatos, 2006). Despite the high fossorial ability of marmots, scratch diggers with perhaps the highest fossorial ability are not rodents but involve several diverse genera of small-to-medium sized mammals including pangolins (*Manidae*: Nowak & Paradiso, 1983), aardvarks (*Orycteropus afer*: Nowak & Paradiso, 1983), and badgers (*Melinae, Mellivorinae, Taxidiinae*: Koepfli et al., 2008).

Because the scratch diggers are the largest group of digging mammals, two scratch diggers were chosen as subjects for study. The badger and groundhog, two animals that



are phylogenetically diverse, yet employ the same mode of scratch digging, will now be considered. Details of the phylogeny, habitat, social behavior, diet and morphological specializations of each species are given below.

### **The American Badger**

The American badger, *Taxidea taxus*, is a member of the family *Mustelidae* (Long, 1973). *Mustelidae* includes otters (*Lutrinae*), martens (*Martes*), and the wolverine (*Gulo gulo*). *Mustelidae* also includes a variety of animals of the genus *Mustela*, for example ferrets, minks, and weasels. The family *Mustelidae* is part of the larger superfamily, *Musteloidae*, consisting of raccoons (*Procyonidae*), skunks (*Mephitidae*), and the red panda (*Ailuridae*) (Flynn et al., 2005; Yonezawa et al., 2007; Sato et al., 2009). *T. taxus* can be divided into two subspecies: the Northern badger and Southern badger, or Mexican badger. The northern subspecies of *T. taxus* is distinguished by its larger body size and short white dorsal stripe extending to shoulders. The Mexican badger is typically smaller with a long dorsal stripe and reddish fur (Long, 1973).

American badgers are found in the grasslands North America ranging as far north as Alberta, Canada and extend south throughout the country of Mexico (Eads & Biggins, 2008). In the United States, badgers range east-to-west from Ohio to all states along the west coast (Lindzey, 2003). Spatial distribution of badgers varies with prey availability. On average the spatial distribution of the American badger is estimated at 1 badger for every 2.6 km<sup>2</sup> (Seton, 1929; Lindzey, 1978; Goodrich & Buskirk, 1998), with the home range of adults varying between a minimum of 1.6 km<sup>2</sup> (Messick & Hornocker, 1981) to a maximum of 17 km<sup>2</sup> (Lampe & Sovada, 1981). Males have larger home ranges than females, and during the breeding season, the home ranges of males expand more than those of females (Minta, 1993). Badger homes consist of a subterranean den that has a characteristic ellipsoid shape and are primarily used for periods of torpor during the winter and for rearing of young (Long, 1999). In general, American badgers are solitary animals with interactions between males and females being only brief associations for mating. Similarly, the interaction between a mother and her cubs is also brief, where a female badger will rear her young for 10-12 weeks, although cubs may have short-term associations after dispersal (Lindzey, 2003). The mating season for badgers reportedly occurs in late July and August. Badgers, like wolverines, delay implantation and

development of the blastocysts until early February (Wright, 1966) and young are born in late March or early April when food becomes more abundant.

The American badger is one of a few carnivorous mammals that hunt primarily by digging. *T. taxus* has a highly carnivorous diet and typically hunts and kills small rodents that share the fossorial habit and include pocket gophers, ground squirrels, mice and rats (Long, 1973). *T. taxus* will also eat invertebrates such as insects and grub worms, especially during times when food and other resources are limited. In addition, badgers supplement their primarily carnivorous diet by consuming some vegetative foods, namely oats and corn (Jense, 1968). Badgers hunt tunneling rodents (e.g., ground squirrels) by excavating their burrows and or plugging up openings into their tunnels. Badgers have even been observed to use tools such as wood blocks to plug openings into burrows in order to trap their prey (Michener, 2004). A particular easy prey for badgers are hibernating animals. Badgers primarily seek out the subterranean dwellings of hibernating animals and strike to kill by a single bite to the thorax (Michener & Iwaniuk, 2001).

The total body length of *T. taxus* is typically 60-73 cm, with the tail vertebrae accounting for 10.5-13.5 cm of total body length. An average male has a body mass of 8.4 kg while females have a body mass of 6.4 kg (Long, 1973), however, despite differences in body size, each sex displays key morphological specializations for their fossorial habit. First, badgers and other animals adapted for a subterranean lifestyle have a nictitating membrane (third eyelid) that protects the eyes from dirt and debris that might compromise their vision during digging. Second, *T. taxus* has large hindfeet (10.5 cm in length) that are shovel-shaped (Lindzey, 2003), and the toes on the hindfeet are partially webbed for shoveling and scooping dirt dislodged by the powerful digging actions of forelimbs. Third, *T. taxus* displays robust forelimbs with forefeet that have five large, sharp foreclaws up to 5 cm in length that are used to excavate dirt during scratch digging.

### **The Groundhog**

The groundhog or woodchuck, *Marmota monax*, is a rodent that belongs to the family *Sciuridae* (Steppan et al., 2004). *Sciuridae* includes many genera of squirrels (e.g., *Ratufa* (giant squirrels), *Sciurus* (grey squirrels), *Spermophilus* (ground squirrels): Nowak & Paradiso, 1983), prairie dogs (*Cynomys*: Nowak & Paradiso, 1983), chipmunks

(*Tamias*, *Eutamias*: Nowak & Paradiso, 1983), and marmots (*Marmota*: Steppan et al., 1999). *M. monax* is one of 14 marmot species, all of which are ground-dwelling rodents with the largest body sizes of any of the sciurids.

*M. monax* ranges throughout the United States and Canada. Groundhogs can be found as far east as Maine, as far west as the Eastern portion of Alaska, and as far south as the states of Mississippi and Georgia. One early study (Hamilton, 1934), estimated their spatial distribution at 50 groundhogs per square mile in New York state alone. More recent studies (Ferron & Ouellett, 1989; Meier, 1992; Swihart, 1992) indicate that their spatial distribution ranges between 25-855 groundhogs per square mile in areas extending from Quebec, Canada to Ohio. This represents a substantial increase in the numbers of groundhogs per unit of land despite heavy deforestation and modern urban development (Bezuidenhout & Evans, 2005). Home range sizes have been reported to be approximately 0.39 ha (hectares) in northern regions of the US (Merriam, 1971) and up to 1.99 ha in the southern regions (Hayes, 1977), suggesting home range size varies significantly with location. The groundhog makes its home by digging burrows in open pastures and at the edges of forests. Burrows may be simple, having no defined structure, or complex, containing several chambers or dens. Burrows have been observed to be up to 2 m deep and 1-13 m long (Kwiecinski, 1998). The burrows of groundhogs are primarily used for hibernation and the rearing of young much like other subterranean mammals. Adults breed and raise their young after emerging from hibernation, which commonly occurs in early February. Unlike badgers, groundhogs are true hibernators and may hibernate for 7 months out of the year, especially in northern regions where winter is long (Bezuidenhout & Evans, 2005). Like badgers, groundhogs are also solitary animals. In fact, groundhogs are the most solitary of the marmots and will rarely share a den even with a mate. Groundhogs give birth to litters of 2-9, and after weaning at six weeks, they are chased off by the aggressive behavior of both parents (Bezuidenhout & Evans, 2005). Interestingly, groundhogs also have several vocalization patterns, including a sharp whistle which serves as an alarm to other animals that a predator is near (Lloyd, 1972).

The groundhog is a subterranean herbivore that eats primarily the vegetative parts of plants. Alfalfa and clover are staples of the groundhog diet. However, groundhogs are opportunistic and will supplement their diet by consuming a variety of farm crops

including peas, corn, and oats (Bezuidenhout & Evans, 2005). Groundhogs are also known to eat certain invertebrates, namely snails and grasshoppers, in times of food shortages (Hamilton, 1934). Being an herbivore, groundhogs are often the prey of diverse groups of predators ranging from terrestrial non-avian reptiles (e.g., rattlesnakes), to avian reptiles (e.g., hawks and owls), and to carnivorous mammals such as canids (e.g., dog, foxes) and mustelids (e.g., minks and weasels) (Kwiecinski, 1998). The American badger, *T. taxus*, does prey on yellow-bellied marmots (Armitage, 2004), but does not prey on *M. monax* because these animals are not known to occupy a similar habitat.

Groundhogs have a short, stocky body with brown and gray fur. Average adult body length (excluding the tail) is 55.5 cm, while the tail length is 12.5 cm, and hindfoot length is 7.6 cm. Adult body mass typically ranges from 2.7 to 5.4 kg (Bezuidenhout & Evans, 2005), with an average body mass of 3.8 kg for males and 3.5 kg for females (Snyder et al., 1961). Body mass varies with hibernation behavior, with the peak body mass occurring immediately prior to hibernation. *M. monax* share common morphological features typical of fossorial habit. First, they have a nictitating membrane, although these structures are reduced (covers only the medial corners of the eye cornea: Bezuidenhout & Evans, 2005) in the groundhog compared to badgers. Second, *M. monax* also has relatively large hindfeet for shoveling and scooping dirt dislodged by the digging actions of forelimbs. The feet of groundhogs however, are less specialized than those of badgers because they lack webbing between the toes and a characteristic shovel-shape. Lastly, *M. monax* does display robust forelimbs (i.e. triceps brachii muscles) but, the forefeet have only four foreclaws to be used in excavation of dirt during scratch digging. Compared with the badger, the foreclaws of groundhogs are reduced (1.5 cm in length: Bezuidenhout & Evans, 2005) and overall, the forefeet appear less specialized.

### **Objectives and Hypotheses**

The musculoskeletal anatomy of several fossorial animals has been previously described (e.g., Parsons, 1901; Hall, 1926, 1927; Lehman, 1963; Lessa, 1990, 2008; Lagaria & Youlatos, 2006), although these studies focused on limited aspects of the cranial (skull bones and dentition: Howell, 1915; Pocock, 1920; Long, 1965; Caumul, 2005; Druzinsky, 2010) and postcranial (baculum and penis: Wade, 1940; Long & Frank, 1968; Long, 1969) anatomy. The badger and groundhog make interesting models of study in

this regard. Only one study (Hall, 1927) is known to have identified the skeletal muscles in the limbs of the American badger along with their bony origins and insertions. Similarly, only descriptive data on muscle names, origins, and insertions exist for the groundhog (Bezuidenhout & Evans, 2005). To date no studies have been done to describe muscle fiber architecture or evaluate architectural properties of the forelimb muscles and the functional significance of their design. This study aims to further investigate muscle specializations of the forelimbs in two fossorial animals, the American badger and groundhog.

The objective of this study is to quantify muscle architectural properties of the forelimbs of the American badger (*Taxidea taxus*) and groundhog (*Marmota monax*) as they relate to digging performance. An understanding of muscle architecture and fiber type in the forelimbs of highly specialized digging animals such as *T. Taxus* and *M. monax* will provide insight into the evolution and functional significance of their limb morphology. Architectural properties studied included: muscle mass, muscle length, muscle moment arm, muscle volume, physiological cross-sectional area (PCSA), muscle fiber length and fiber angle. These measurements were made on major forelimb flexor and extensor muscles involved with digging behavior. Maximum isometric force production and mechanical power generation were estimated for each muscle as an indicator of functional performance.

It is hypothesized that most forelimb muscles will have long fascicles in a parallel fiber architecture, allowing for fast shortening and force production over a large range of joint motion. This muscle architecture and functional capacity is expected to be optimized for digging and tunneling behaviors. The forelimbs will show the largest concentration of muscle mass in elbow flexors and extensors. Specifically, the *triceps brachii m.* is hypothesized to have the largest PCSA and muscle volume, and thus the highest force production and power generation capacity of all the forelimb musculature. Flexors of the wrist and digits are also hypothesized to show a high concentration of limb muscle mass, and have muscle architecture consistent with high work and power generation capacity. Inherent to these hypotheses is an evolutionary perspective that ecology and anatomy are closely linked; indicating that species evolved anatomical specializations to increase their chances of survival in their respective habitats. Thus, the

badger and groundhog have both evolved certain muscle architectural properties consistent with specializations for digging and high work and power performance for this adaptive behavior.

Table 1. Morphometric data for experimental animals and limb specimens.

Specimen	Sex	Limb	Body mass (kg)	Humerus length (cm)	Ulna length (cm)	Olecranon length (cm)	Metacarpal III length (cm)	Fossorial ability index	Triceps out-force index
<b>Badger</b>									
<i>Tt</i> 1031	F	R	6.5	10.0	11.0	3.0	2.6	0.38	0.28
<i>Tt</i> 1101	F	L	5.7	10.0	10.5	2.7	1.8	0.35	0.28
<i>Tt</i> 1112	F	R	7.2	9.0	10.2	2.5	2.4	0.33	0.25
<i>Tt</i> 1119	M	R	11.7	11.0	11.4	3.0	2.4	0.36	0.28
<i>Tt</i> 0119	M	L	6.5	10.4	11.0	3.1	2.2	0.39	0.31
<i>Tt</i> 0203	M	L	8.0	11.0	11.0	3.5	2.5	0.47	0.35
			<b>7.6±2.2</b>	<b>10.2±0.8</b>	<b>10.9±0.4</b>	<b>3.0±0.3</b>	<b>2.3±0.3</b>	<b>0.38±0.05</b>	<b>0.29±0.04</b>
<b>Opossum</b>									
<i>Dv</i> 0625	F	L	2.7	7.0	9.2	1.5	2.2	0.20	0.15
<i>Dv</i> 0305	M	L	2.0	6.9	8.1	1.4	2.4	0.21	0.15
<i>Dv</i> 1027	M	L	2.9	6.8	8.2	1.9	2.7	0.30	0.21
<i>Dv</i> 0302	F	L	1.6	6.5	7.6	1.4	2.2	0.23	0.17
<i>Dv</i> 0517	M	R	2.0	7.6	8.6	1.6	2.2	0.23	0.17
<i>Dv</i> 1119	M	R	1.1	5.6	7.1	1.0	1.9	0.16	0.13
			<b>2.0±0.7</b>	<b>6.7±0.7</b>	<b>8.1±0.7</b>	<b>1.5±0.3</b>	<b>2.3±0.3</b>	<b>0.22±0.05</b>	<b>0.16±0.03</b>

Values in bold are mean±SD

Indices are defined as in Lagaria & Youlatos (2006). Fossorial ability index, ratio of olecranon length to total ulna length minus olecranon length; Triceps out-force index, ratio of olecranon length to the sum of ulna and metacarpal length minus olecranon length

Table 2. Origins, insertions, actions and fibre architecture of major intrinsic forelimb musculature for American badger, *Taxidea taxus*.

<b>Muscle</b>	<b>Abbreviation</b>	<b>Origin</b>	<b>Insertion</b>	<b>Action</b>	<b>Fibre Architecture</b>
Supraspinatus	SUPRA	Supraspinous fossa	Greater tubercle of humerus	Humeral stabilizer, shoulder extension	Parallel
Infraspinatus	INFRA	Infraspinous fossa	Greater tubercle	Humeral stabilizer, shoulder flexion	Unipennate
Teres major	TEMA	Axillary border of scapula	Medial margin of pectoral ridge ( <i>in common with latissimus dorsi</i> )	Shoulder flexion, limb retraction	Parallel
Teres minor <sup>a</sup>	TEMI	Proximal flange of infraspinous fossa	Greater tubercle of humerus	Humeral stabilizer, shoulder flexion	Parallel
Subscapularis	SUB	Subscapular fossa	Lesser tuberosity of humerus	Humeral stabilizer, limb adduction	Multipennate
Epitrochlearis	EPI	Pectoralis, latissimus dorsi muscles	Medial aspect of olecranon process	Antebrachial fascia tensor	Parallel
Triceps brachii long	TBLO	Axillary border of scapula	Posteromedial aspect of olecranon	Shoulder flexion, elbow extension, limb retraction	Parallel
Triceps brachii medial	TBM	Mid-axillary border of scapula	Proximal aspect of olecranon	Shoulder flexion, elbow extension, limb retraction	Unipennate
Triceps brachii lateral	TBLA	Deltoid ridge, greater tubercle of humerus	Lateral, posterodorsal aspect of olecranon	Elbow extension	Unipennate
Anconeus	ANC	Lateral epicondyle, supracondyloid ridge of humerus	Dorsolateral olecranon, distal margin of semilunar notch	Elbow extension	Parallel
Brachialis	BCH	Posterolateral aspect of proximal humerus	Medial aspect of coronoid process	Elbow flexion	Parallel
Biceps brachii	BB	Supraglenoid tubercle	Bicipital tuberosity	Elbow flexion	Parallel
Brachioradialis	BR	Dorsal aspect of lateral epicondyle	Styloid process of radius	Elbow flexion	Parallel
Flexor carpi ulnaris	FCU	Ventromedial olecranon, medial epicondyle	Pisiform bone	Carpal flexion	Unipennate
Flexor carpi radialis	FCR	Medial epicondyle	Base of metacarpal 2	Carpal flexion	Unipennate
Pronator teres	PT	Medial epicondyle	Distal half of the medial side of radius	Pronation	Unipennate



Palmaris longus	PL	Medial epicondyle, in common with fibers of SDF	Proximal phalanges of digits 2-4, fibrous pad overlying the pisiform	Assists in carpal flexion	Unipennate, parallel
Flexor digitorum superficialis <sup>b</sup>	SDF	Medial epicondyle, fibers in common with DDFHA, DDFHB	Base of middle phalanx of digits 2-4	Digital flexion	Bipennate
Flexor digitorum profundus ulnar	DDFU	Posteromedial olecranon to styloid process of ulna			Unipennate
Flexor digitorum profundus radial	DDFR	Interosseous membrane, proximal radius, radial aspect of ulna			Parallel
Flexor digitorum profundus humeral A	DDFHA	Medial epicondyle	The palmar surface of the common tendon of the wrist that divides into five tendons which insert onto the distal phalanx of digits 1-5	Digital flexion	Unipennate
Flexor digitorum profundus humeral B	DDFHB	Medial epicondyle			Unipennate
Flexor digitorum profundus humeral C	DDFHC	Tendon from medial epicondyle			Parallel
Pronator quadratus	PQ	Distal third of flexor surface of ulna	Distal third of flexor surface of radius	Pronation	Parallel
Extensor carpi radialis	ECR	Lateral epicondyle	Bases of metacarpals 2 and 3	Carpal extension	Parallel
Extensor digitorum communis	EDC	Lateral epicondyle	Proximal phalanx of digit 2, middle and distal phalanges of digits 3 and 4, phalanges of digit 5	Digital extension	Parallel
Extensor digitorum lateralis	EDL	Lateral epicondyle	Phalanges of digits 3 and 5, proximal and middle phalanges of digit 4	Digital extension	Unipennate; parallel
Extensor carpi ulnaris	ECU	Lateral epicondyle	Base of 5 <sup>th</sup> metacarpal	Carpal extension	Parallel
Extensor indicis	EI	Dorsolateral surface of ulna distal to semilunar notch	Proximal phalanges of digits 1 and 2.	Digital extension	Parallel
Extensor pollicis brevis	EPB	Length of radius	Base of 1 <sup>st</sup> metacarpal	Digital extension	Parallel
Supinator	SUP	Lateral humeral condyle, lateral aspect of radial head	Length of the radius along the extensor surface	Supination	Parallel

Table 3. Muscle architectural properties data from badger forelimbs

<b>Muscle</b>	<b>n</b>	<b>Mass (g)</b>	<b>Belly length (cm)</b>	<b>Fascicle length (cm)†</b>	<b>Pennation angle (°)†</b>	<b>Volume (cm<sup>3</sup>)</b>	<b>PCSA (cm<sup>2</sup>)</b>	<b>Fmax (N)</b>	<b>Power (W)</b>
Supraspinatus	6	13.9±5.6	8.2±0.8	4.5±1.7	6±9	13.2	2.92	87.7	2.99
Infraspinatus	6	10.9±3.1	7.8±0.8	2.9±0.6	14±4	10.2	3.69	111	2.37
Teres minor	6	7.4±2.4	8.5±2.0	5.1±1.2	0	6.98	1.36	40.8	1.57
Teres major	6	4.9±1.5	7.7±0.5	5.7±0.8	0	4.64	0.81	24.3	1.05
Subscapularis	6	16.1±4.9	8.2±0.9	1.1±0.3	21±5	15.2	14.5	434	3.65
Epitrochlearis	6	1.4±0.5	5.3±0.6	4.5±0.7	0	1.36	0.31	9.17	0.31
Triceps brachii long head	6	17.9±6.2	10.5±0.9	9.3±1.3	0	16.9	1.81	54.2	3.80
Triceps brachii medial head	6	24.8±8.2	8.5±0.4	4.2±1.6	11±12	23.4	5.63	169	5.36
Triceps brachii lateral head	6	23.5±5.8	8.1±0.8	5.4±1.4	5±12	22.2	4.15	125	5.01
Anconeus	5	3.1±1.4	4.2±0.3	2.9±0.8	0	2.95	0.99	29.6	0.66
Brachialis	6	5.4±1.5	7.5±1.1	5.8±1.0	0	5.05	0.87	26.2	1.14
Biceps brachii	6	6.7±2.0	7.0±0.7	5.2±0.9	0	6.28	1.20	36.0	1.41
Brachioradialis	6	4.8±1.8	8.7±0.9	7.8±0.9	0	4.57	0.59	17.6	1.03
Flexor carpi ulnaris	6	2.0±0.3	6.8±0.8	1.9±0.5	13±8	1.90	1.05	31.4	0.44
Flexor carpi radialis	6	1.9±0.5	6.4±0.4	1.9±0.4	13±5	1.85	1.01	30.3	0.43
Pronator teres	6	5.5±1.2	7.5±0.7	3.3±0.8	11±8	5.23	1.63	48.8	1.20
Palmaris longus A	5	0.8±0.3	4.7±1.1	2.6±0.9	3±4	0.77	0.30	8.90	0.17
Palmaris longus B	6	2.1±0.5	6.0±0.9	1.9±0.4	14±8	1.94	1.08	32.4	0.45
Flexor digitorum superficialis	6	8.4±2.1	7.6±0.6	2.1±1.0	19±8	7.94	4.07	122	1.89
Flexor digitorum profundus ulnar head	6	7.5±1.9	8.9±0.6	2.8±0.4	21±6	7.06	2.73	81.8	1.70

Flexor digitorum profundus radial head	6	6.7±1.9	5.4±0.5	3.7±0.8	0	6.30	1.73	51.8	1.42
Flexor digitorum profundus humeral A	6	7.8±3.4	7.7±0.9	2.5±0.5	16±4	7.32	3.04	91.1	1.71
Flexor digitorum profundus humeral B	6	6.7±1.2	7.3±0.7	2.5±0.7	17±6	6.27	2.67	80.1	1.47
Flexor digitorum profundus humeral C	6	1.7±0.6	5.2±0.7	3.8±0.9	0	1.58	0.42	12.6	0.35
Pronator quadratus	6	0.7±0.1	2.5±0.4	1.6±0.4	0	0.64	0.40	12.0	0.14
Extensor carpi radialis	5	4.4±0.9	7.0±0.4	5.6±1.0	1±3	4.12	0.74	22.1	0.93
Extensor digitorum communis	5	5.7±1.4	7.6±0.8	3.4±1.0	5±6	5.40	1.60	48.0	1.22
Extensor digitorum lateralis A	5	3.9±1.5	7.2±1.8	2.5±1.0	9±7	3.69	1.51	45.2	0.84
Extensor digitorum lateralis B	2	1.6±0.4	6.5±0.7	4.2±1.3	0	1.54	0.37	11.1	0.35
Extensor carpi ulnaris	5	3.0±1.1	6.8±1.1	2.4±1.0	11±3	2.86	1.20	35.9	0.66
Extensor indicis	5	2.2±2.1	6.2±1.6	2.6±1.4	6±11	2.09	0.81	24.2	0.47
Extensor pollicis brevis	2	2.6±0.6	7.3±0.4	1.5±0.5	16±2	2.45	1.74	52.1	0.57
Supinator	5	1.5±0.6	5.4±0.9	3.7±1.1	0	1.43	0.39	11.7	0.32

† indicates value is a grand mean of 5-10 measurements per animal; all other measured properties are presented as mean±SD  
 Calculated and estimated properties are given as single values determined from mean properties across individual limbs

Table 4. Muscle architectural properties data from opossum forelimbs

<b>Muscle</b>	<b>n</b>	<b>Mass (g)</b>	<b>Belly length (cm)</b>	<b>Fascicle length (cm)†</b>	<b>Pennation angle (°)†</b>	<b>Volume (cm<sup>3</sup>)</b>	<b>PCSA (cm<sup>2</sup>)</b>	<b>Fmax (N)</b>	<b>Power (W)</b>
Supraspinatus	6	3.6±1.1	5.7±0.6	3.6±1.0	0	3.41	0.96	28.7	0.87
Infraspinatus	6	2.6±0.9	5.8±1.1	2.3±1.1	12±5	2.42	1.06	31.8	0.63
Teres minor	6	1.4±0.5	5.3±1.5	2.2±0.7	17±7	1.29	0.62	18.6	0.34
Teres major	6	2.5±0.9	5.9±1.0	4.7±1.3	0	2.38	0.51	15.2	0.61
Subscapularis	6	4.3±1.4	5.7±0.5	4.8±1.2	0	4.02	0.83	25.1	1.02
Epitrochlearis	6	1.0± 0.3	4.7±0.8	3.9±1.2	0	0.96	0.24	7.28	0.24
Triceps brachii long head	6	6.8±2.6	5.7±1.1	4.3±1.2	0	6.36	1.49	44.8	1.62
Triceps brachii medial head	6	2.3±0.8	4.6±0.6	3.2±0.8	0	2.19	0.68	20.3	0.56
Triceps brachii lateral head	6	3.6±1.8	5.1±1.0	3.8±1.3	0	3.43	0.90	27.1	0.88
Brachialis	6	1.5± 0.5	4.5±0.8	2.8±0.6	0	1.39	0.49	14.7	0.35
Biceps brachii	6	2.8±0.8	4.7±0.5	3.6±1.5	0	2.63	0.73	21.9	0.67
Brachioradialis	6	0.9±0.3	4.5±0.6	2.9±0.6	13±9	0.84	0.29	8.8	0.22
Flexor carpi ulnaris	6	1.9±0.6	5.5±1.2	1.7±0.5	12±6	1.81	1.12	33.7	0.47
Flexor carpi radialis	6	0.6±0.2	3.6±0.6	0.9±0.3	8±5	0.53	0.60	17.9	0.14
Pronator teres	6	1.2± 0.4	5.1±1.5	2.2±0.8	13±7	1.11	0.53	15.9	0.29
Palmaris longus	6	0.3±0.1	3.9±0.6	2.6±0.9	0	0.25	0.10	2.85	0.06
Flexor digitorum superficialis	6	1.0±0.5	5.5±1.6	2.5±0.8	12±7	0.96	0.39	11.8	0.25
Flexor digitorum profundus ulnar head	6	1.6± 0.5	6.6±1.2	1.8±0.7	16±12	1.48	0.85	25.6	0.39
Flexor digitorum profundus radial head	6	0.8± 0.4	4.6±1.0	2.0±0.7	14±7	0.74	0.38	11.4	0.19

Flexor digitorum profundus humeral head	6	0.7±0.3	5.4±1.4	2.2±0.6	13±5	0.68	0.31	9.37	0.18
Pronator quadratus	6	0.2±0.2	1.0±0.5	0.7±0.1	0	0.20	0.30	9.05	0.05
Extensor carpi radialis longus	3	0.6±0.1	4.5±1.0	2.9±1.5	0	0.56	0.20	5.87	0.14
Extensor carpi radialis brevis	3	0.8±0.1	4.1±0.3	2.4±1.1	0	0.76	0.32	9.67	0.19
Extensor digitorum communis	3	0.4± 0.2	4.0±1.0	2.4±0.8	0	0.41	0.17	4.99	0.10
Extensor digitorum lateralis	3	0.3±0.1	3.2±0.4	1.9±0.8	0	0.25	0.13	3.98	0.06
Extensor carpi ulnaris	3	0.5±0.1	3.4±0.8	0.8±0.3	9±5	0.42	0.55	16.6	0.11
Extensor indicis proprius	3	0.2±0.0	5.4±1.3	1.0±0.4	12±5	0.15	0.15	4.36	0.04
Supinator	3	0.2±0.1	2.4±0.5	1.5±0.6	0	0.17	0.12	3.58	0.04

† indicates value is a grand mean of 5-10 measurements per animal; all other measured properties are presented as mean±SD  
 Calculated and estimated properties are given as single values determined from mean properties across individual limbs

Table 5. Summary of statistical results from multivariate analysis of variance test

<b>Muscle</b>	<b>Muscle mass</b>	<b>I<sup>F</sup></b>	<b>θ</b>	<b>PCSA</b>
Teres major	oo			
Subscapularis		oo	xx	xx
Triceps brachii long head	xx	xx		
Triceps brachii medial head	xx			xx
Triceps brachii lateral head	xx			
Biceps brachii	o			
Flexor carpi ulnaris	oo			oo
Flexor digitorum superficialis	xx			xx
Flexor digitorum profundus ulnar	x			
Flexor digitorum profundus radial	x		oo	

x, indicates normalized value is greater in badger; o indicates normalized value is greater in opossum  
x or o, significantly different at  $P < 0.05$ ,  
xx or oo, significantly different  $P \leq 0.001$

Table 6. Muscle moment arms and forelimb joint torques

<b>Muscle</b>	<b>Joint</b>	<b>Joint angle</b>	<b>Mean <math>r_m</math> (cm)</b>	<b>Joint Torque (N.cm)</b>	<b><math>l^F: r_m</math></b>
Teres major	Shoulder	100°	<b>2.1±0.6</b>	50.0	2.79
Teres minor			<b>2.0±0.5</b>	83.4	2.51
Infraspinatus			<b>0.9±0.4</b>	101	3.14
Subscapularis			<b>0.9±0.2</b>	393	1.24
Triceps brachii long head			<b>6.2±0.4</b>	341	1.49
Triceps brachii medial head			<b>2.8±0.6</b>	477	1.50
Biceps brachii			<b>1.6±0.5</b>	57.1	3.30
Brachialis	Elbow	100°	<b>1.8±0.6</b>	45.9	3.30
Triceps brachii long head			<b>2.2±0.2</b>	118	4.29
Triceps brachii medial head			<b>2.1±0.2</b>	361	1.98
Triceps brachii lateral head			<b>2.0±0.3</b>	244	2.73
Flexor carpi ulnaris	Carpus	0°	<b>1.5±0.3</b>	42.2	1.26
Flexor digitorum superficialis			<b>1.7±0.2</b>	230	1.22
Flexor digitorum profundus			<b>1.2±0.4</b>	396 <sup>‡</sup>	2.56 <sup>‡</sup>

$l^F$  is mean fascicle length

$r_m$  is mean moment arm

<sup>‡</sup> force and fascicle length averaged for all heads of DDF

Fig. 1. Lateral view of the skeletal anatomy for badger forelimb, and measurement of muscle moment arms. Shoulder, elbow and carpal joint angles were calculated by the convention diagrammed. Flexion is indicated by arrow direction. Muscle moment arm ( $r_m$ ) was measured for select flexors and extensors about the shoulder, elbow, and carpus as the perpendicular distance from the joint center of rotation to line of action of muscle force. Measurements of  $r_m$  were taken with the proximal forelimb joints in a neutral position ( $100^\circ$ ) as illustrated for triceps brachii long head (TBLO: shoulder flexor, elbow extensor) and triceps brachii lateral head (TBLA: elbow extensor). Measurements of  $r_m$  for carpal/digital flexors were done with the carpus positioned at  $0^\circ$  neutral (not illustrated).



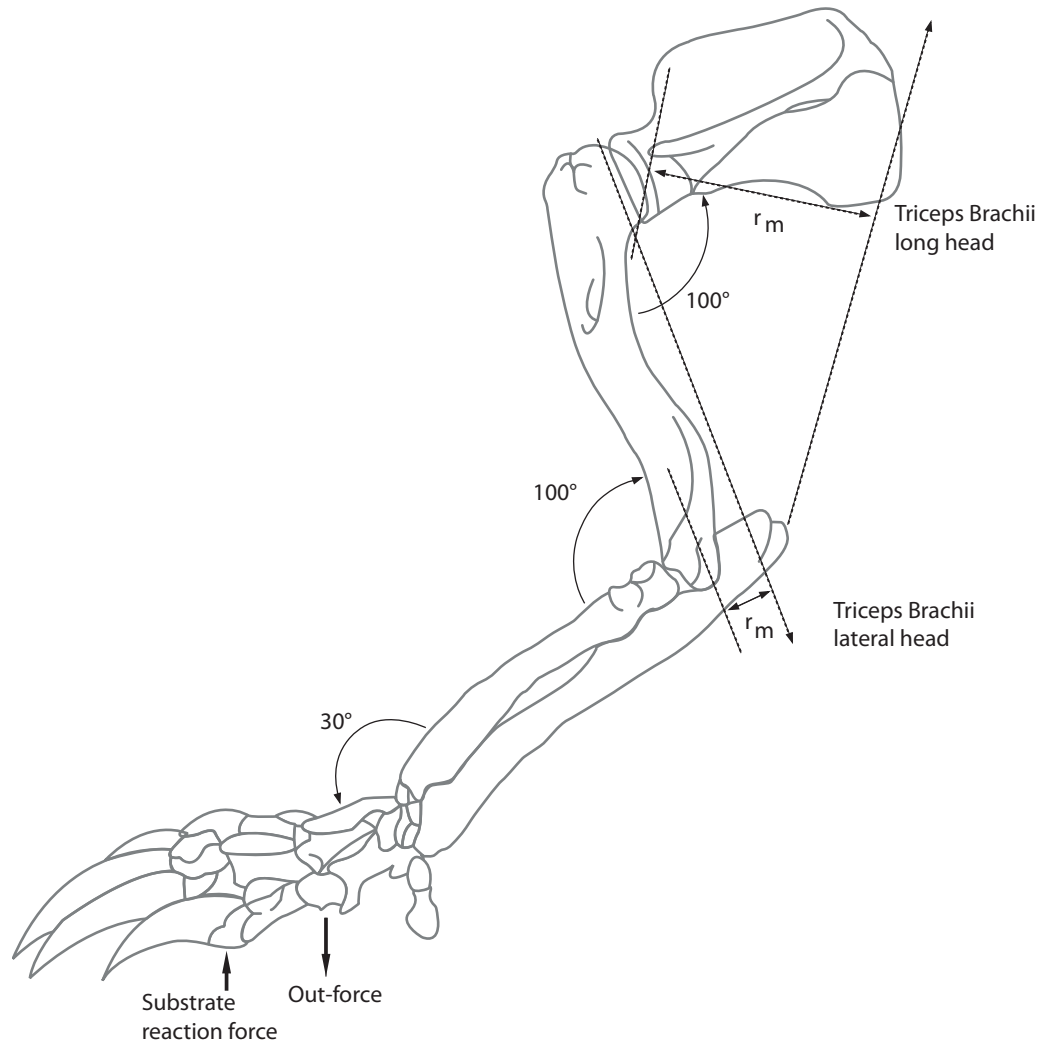


Fig. 2. Body size scaling relation for calculation of maximal shortening velocity ( $V_{\max}$ ) of muscle fibers for badger and opossum. Scaling relationship between  $V_{\max}$  and body mass for fast, MHC-2A isoform fibers across 7 species. All  $V_{\max}$  data (converted to FL  $s^{-1}$ ) are taken from Toniolo et al. (2007), and were measured by the slack test method at 12°C. The power relationship determined from these data ( $y=4.1632x^{-0.089}$ ;  $R^2 = 0.63$ ) was used to predict a relative shortening velocity of 1.87 FL  $s^{-1}$  for a 7.6 kg badger at 12°C, and 2.12 FL  $s^{-1}$  for a 2.1 kg opossum at 12°C. Arrows indicate the predicted  $V_{\max}$  for badger (upward arrow) and opossum (downward arrow) and their relative position on the relationship.

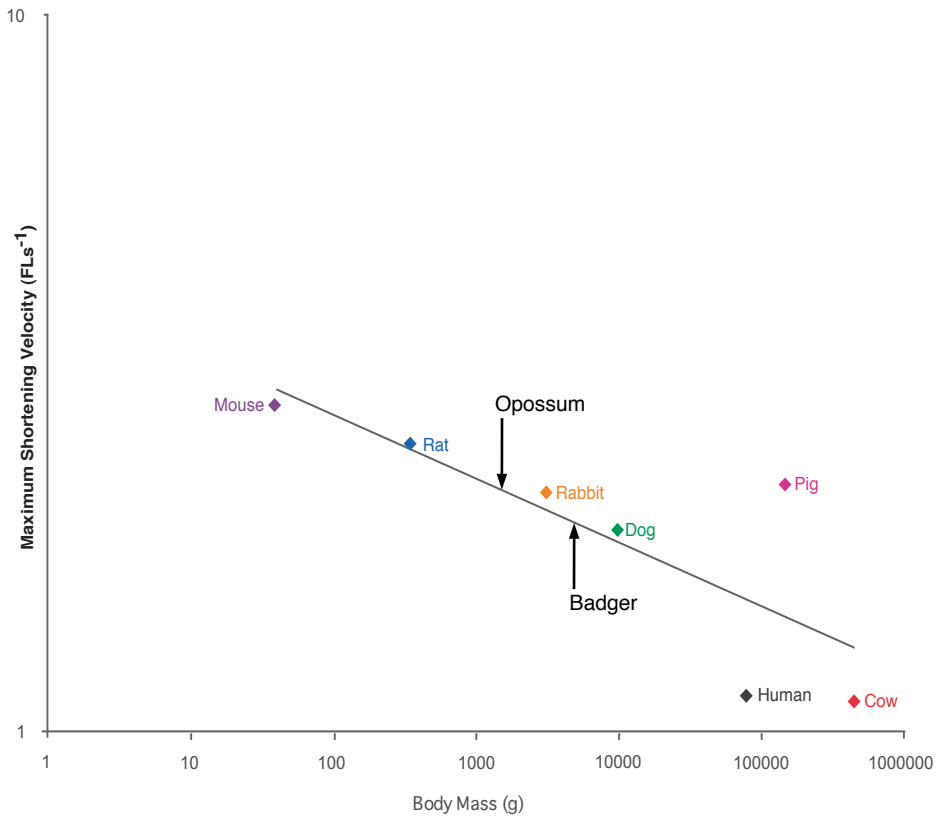


Fig. 3. Medial view of the intrinsic forelimb musculature for badger with functionally important muscles identified. Photograph of a left forelimb depicting the relative mass of major shoulder, elbow, carpal and digital flexor and extensor muscles. Scale bar is 5 cm.

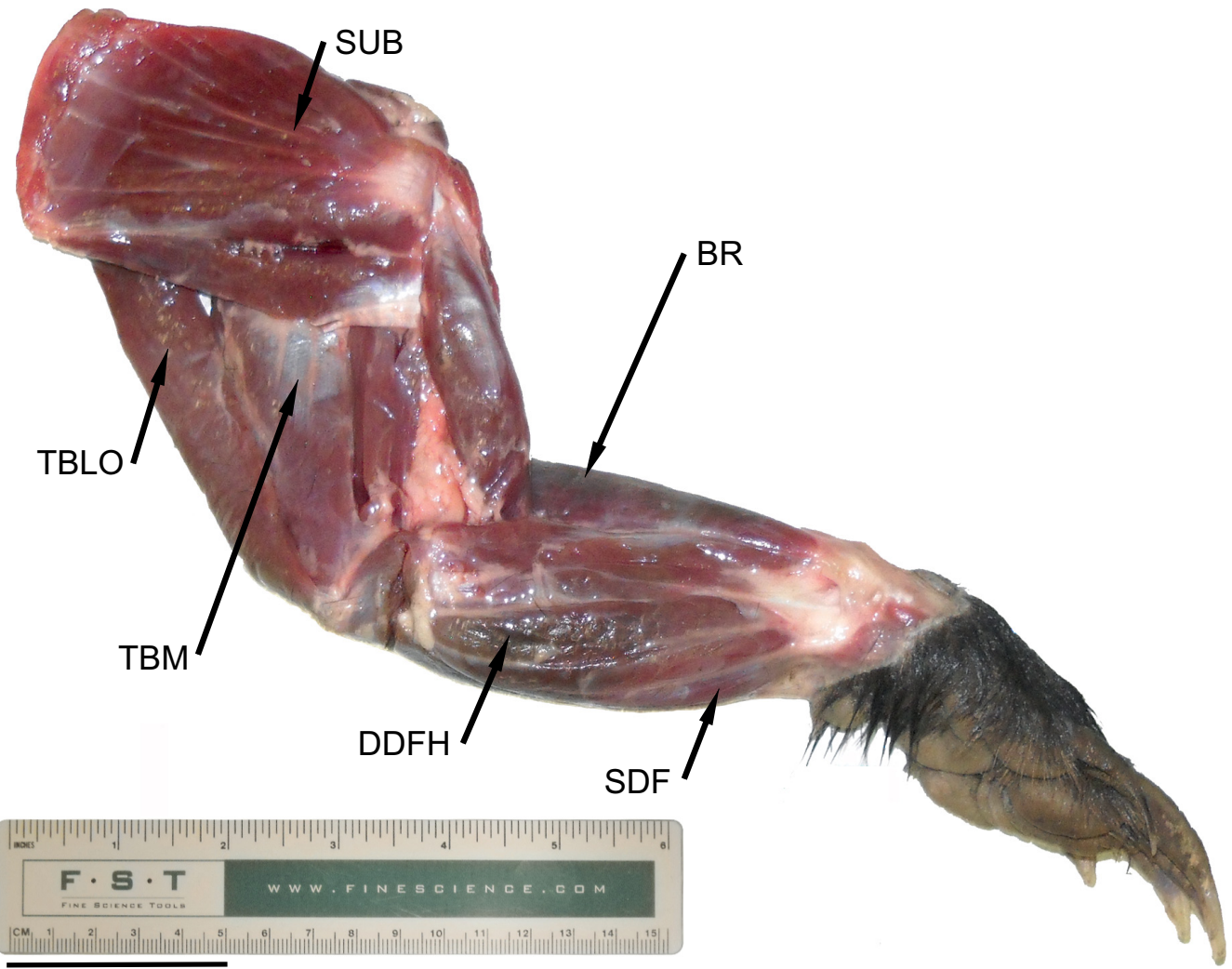


Fig. 4. Architectural index of the distribution of functional group muscle mass to total forelimb muscle mass for badger and opossum. Total forelimb muscle mass was calculated as the summed mass of all individual forelimb muscles. Proximal-to-distal muscle group mass is expressed as a percentage, with bars representing means for each functional group of muscles. Biarticular muscles were included in more than one functional group. Statistical differences between badger and opossum were tested by ANOVA, where \* is significantly different at  $P < 0.05$ , and \*\* is significantly different at  $P \leq 0.0001$ .

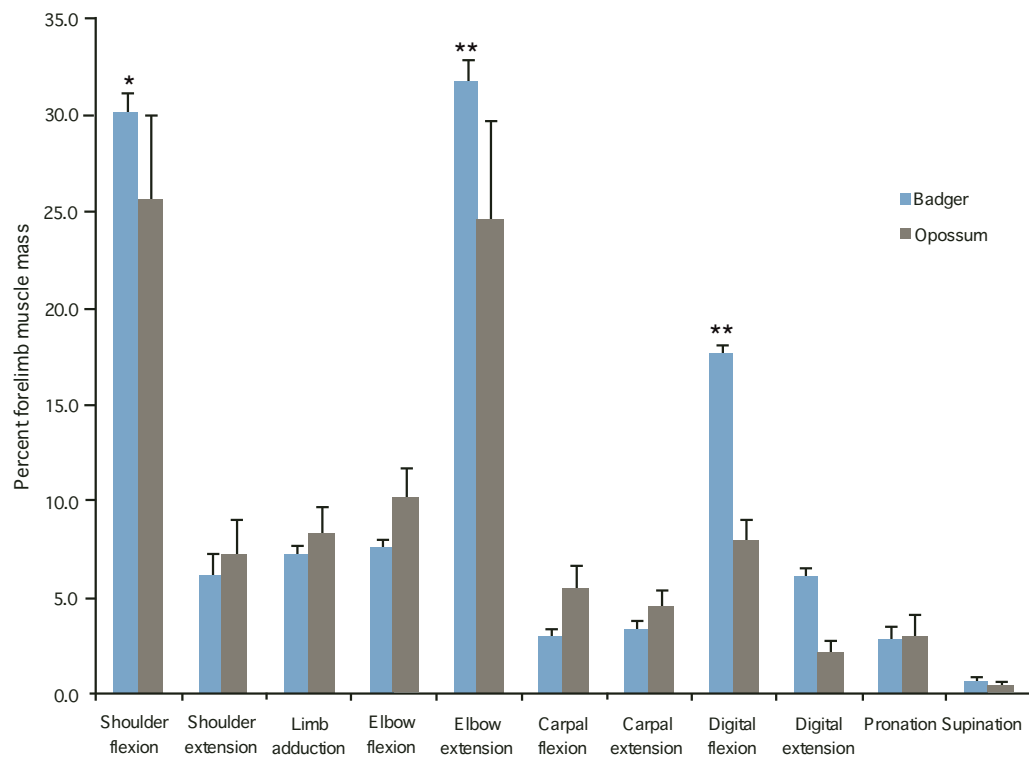


Fig. 5. **A** PCSA to muscle mass ratios for badger. High mean values indicate higher degrees of pennation and force production capability. **B** Fascicle length to muscle length ratios for badger. High mean values indicate greater range of contraction and shortening capability. The combination of both higher PCSA:muscle mass and fascicle length:muscle length ratios indicate a muscle capable of performing appreciable work (force x fiber length change) and generating high power (work ÷ time).



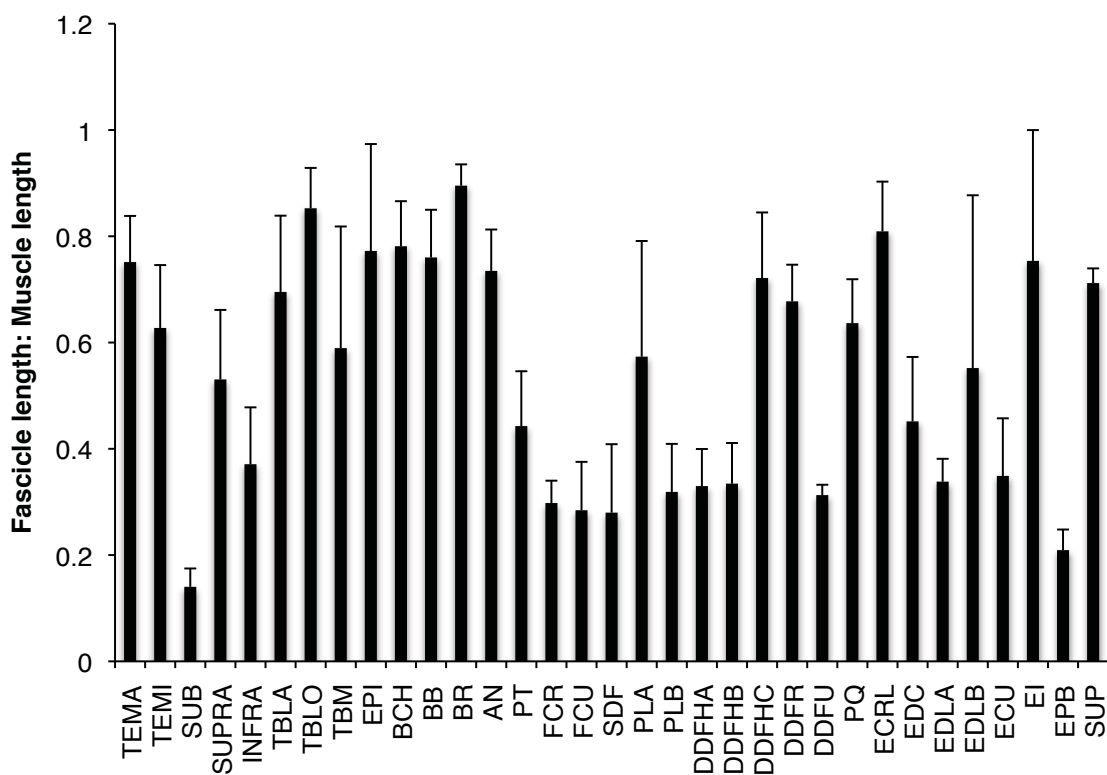
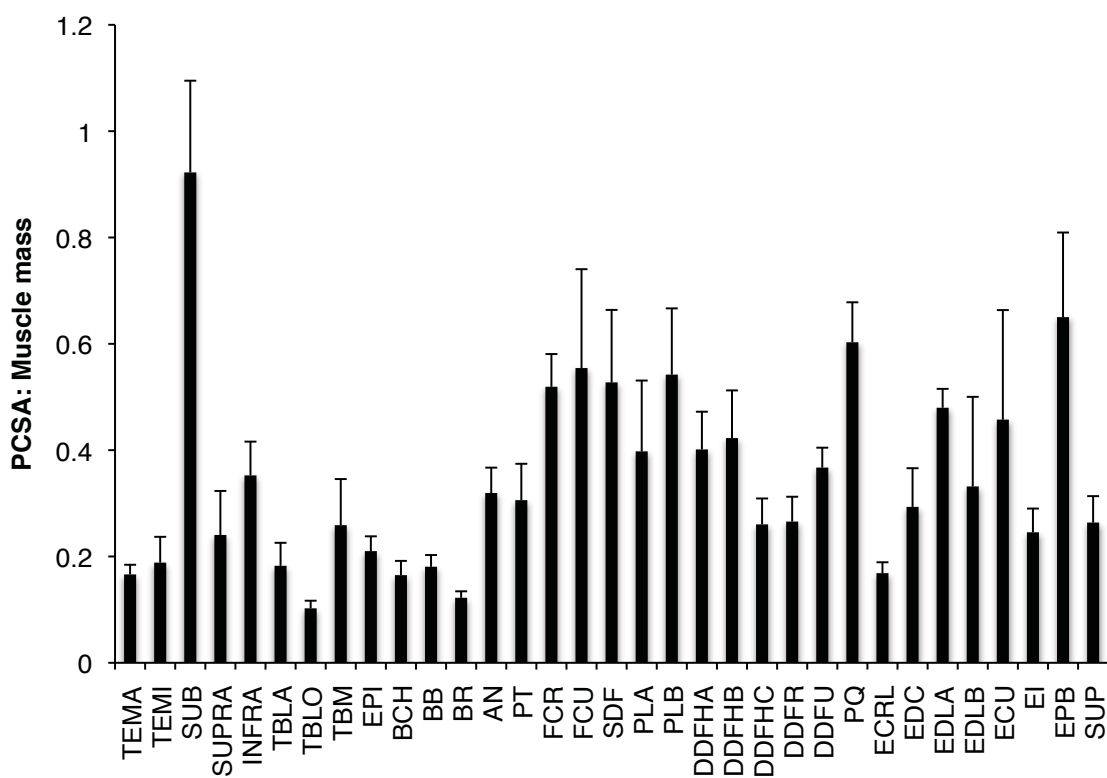
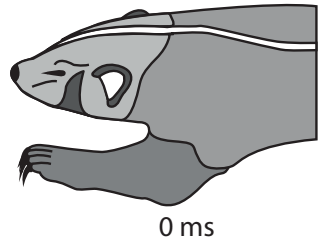
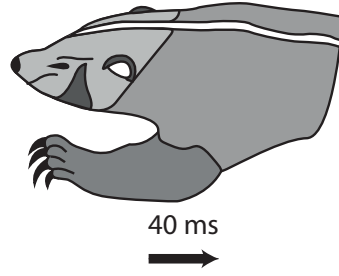


Fig. 6. Representative lateral sequence illustrations of power stroke phase of scratch-digging for badger. Arrow indicates the direction of limb travel. Relative time in milliseconds (ms) is shown on each illustration. **A** Initial contact of manus with the substrate. **B** Flexion of the digits brings the foreclaws in contact with the substrate as the forelimb begins retraction. **C-D** Foreclaws are further flexed and pushed into the substrate as the shoulder flexes and elbow begins extension. **E-F** The carpus is flexed concurrent with the shoulder while the limb is adducted. **G** The limb is further retracted and the manus is supinated, forming a shovel-like shape and bringing the manus posteroventral to the animal. The badger begins lateral flexion on the ipsilateral side, helping to deliver the power stroke. **H** The elbow is further extended as the shoulder nears maximal flexion, **I** Completion of power stroke. Images are adapted from original film tracings of Quaipe (1978).

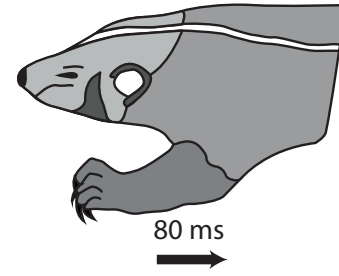
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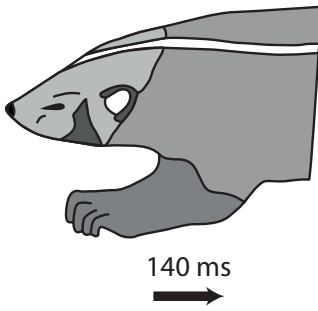
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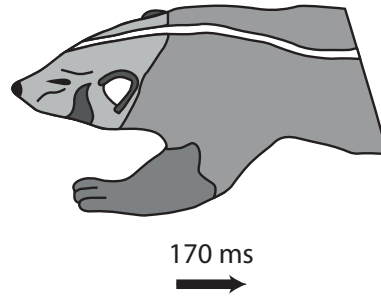
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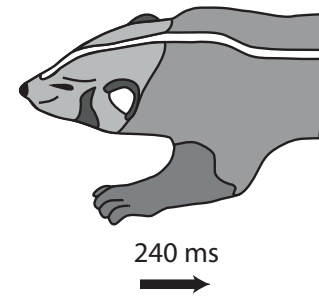
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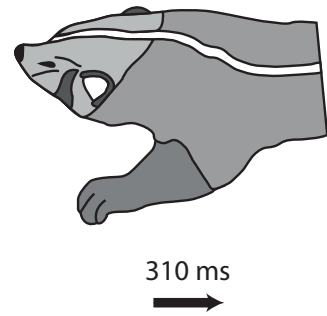
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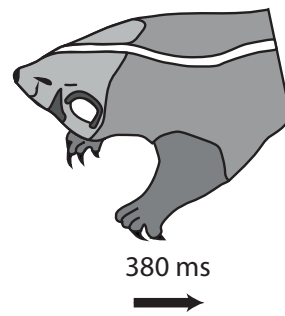
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I

