



Descriptive study of the intrinsic muscles of the shoulder and brachium in kinkajou (*Potos flavus*) and an evolutionary analysis within the suborder Caniformia

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Academic editors Clara Stefen | **Received** 24 February 2023 | **Accepted** 29 September 2023 | **Published** 13 October 2023

Citation: Vélez-García JF, Carrión Blanco DA, Moreno Gómez G, San Martín Cañas S (2023) Descriptive study of the intrinsic muscles of the shoulder and brachium in kinkajou (*Potos flavus*) and an evolutionary analysis within the suborder Caniformia. *Vertebrate Zoology* 73 957–980. <https://doi.org/10.3897/vz.73.e102645>

Abstract

The kinkajou (*Potos flavus*) is a carnivoran of the suborder Caniformia and the family *Procyonidae*, inhabiting regions throughout Central and South America. *Potos flavus* has arboreal preferences and exhibits unique anatomical adaptations that facilitate movement within trees. Its pelvic limbs enable hindfoot reversal, while its thoracic limbs possess remarkable prehensile capabilities. Previous anatomical studies in *Potos flavus* have presented discrepancies in the description of the intrinsic shoulder and brachial muscles. Therefore, this study aims to provide a comprehensive anatomical description of these muscles in five specimens. The findings are compared with descriptions reported for other caniforms. The application of the Density-Based Spatial Clustering of Application with Noise (DBSCAN) algorithm aids in identifying relationships among caniforms based on the presence or absence of specific muscles. Our analysis reveals several key differences, including the presence of a biceps brachii with two capita (longum and breve), two coracobrachiales muscles (longus and brevis), a tensor fasciae antebrachii with two distinct parts (cranialis and caudalis), and an anconeus medialis. The caput breve of the biceps brachii and coracobrachialis longus muscles are absent in some individuals, with prevalence rates of 10% and 20%, respectively. One specimen exhibited an accessory caput laterale of the m. triceps brachii bilaterally. The comparative analysis suggests that the shoulder and brachial muscles of *Potos flavus* share more similarities with those of *Ailurus fulgens* and ursids of the genera *Ursus* and *Tremarctos*. These findings suggest the retention of muscles that may have been present in the common ancestor of the infraorder Arctoidea.

Keywords

Anatomy, Arctoidea, attachments, Carnivora, myology, Procyonidae

Introduction

The kinkajou (*Potos flavus*) is a carnivorous species belonging to the family Procyonidae and suborder Caniformia (Nyakatura and Bininda-Emonds 2012; Hassanin et al. 2021). It has a broad geographic distribution from Mexico to Brazil and the center region of Bolivia (Nascimento et al. 2017). Within its ecosystem, *P. flavus* plays an important role in seed dispersal and plant pollination (Monterrubio-Rico et al. 2013). Despite not being yet classified as endangered by the International Union for Conservation of Nature (IUCN) (Helgen et al. 2016), the species is affected by high rates of deforestation, habitat degradation, illegal hunting, meat consumption, skin use, and, frequently, captivity as a pet (Monterrubio-Rico et al. 2013; Helgen et al. 2016). *Potos flavus* is characterized by solitary, territorial, nocturnal and arboreal behaviors. Its diet primarily consists of flowers, nectar, leaves, fruits, insects, small vertebrates and bird eggs (Monterrubio-Rico et al. 2013; Lambert et al. 2014). *Potos flavus* has unique anatomical adaptations that aid its arboreal lifestyle, such as a prehensile tail that functions as an additional limb for hanging from tree branches, maintaining balance, and facilitating communication. The species also possesses flexible knees and tarsal joints that enable 180° foot rotation, allowing it to descend from trees headfirst (Monterrubio-Rico et al. 2013). Adaptations in the bony and muscular structures of its pelvic limbs allow hindfoot reversal and suspension in trees (Marsh et al. 2021). Similarly, the thoracic limb muscles of *P. flavus* exhibit functional adaptations, mainly in the antebrachial muscles responsible for rotational hand movements (Taverne et al. 2018; Böhmer et al. 2019). These adaptations provide to the *P. flavus* with higher prehension and arboreal abilities compared to species in the genera *Nasua* and *Procyon* (McClearn 1992). Phylogenetically, *Potos* represents the earliest divergent branch among extant procyonids (*Bassaricyon*, *Bassariscus*, *Nasuella*, *Procyon*, and *Nasua*), which could have occurred approximately 17 million years ago (Nyakatura and Bininda-Emonds 2012). Another procyonid, *Bassaricyon alleni*, also shares similar arboreal abilities to *P. flavus*, although behavioral studies on this species are limited (Williams 2016).

While previous research has highlighted the importance of the anatomical adaptations of the antebrachial muscles of *P. flavus* for grasping tree branches and food (Taverne et al. 2018; Böhmer et al. 2019; Perdomo-Cárdenas et al. 2021; Vélez-García et al. 2022), the scapular and brachial muscles are essential for shoulder and elbow joint mobility and stability that allow more precise manus movements (Vélez-García and Miglino 2023). The shoulder joint's mobilization and stabilization are performed by two muscle groups: extrinsic and intrinsic. The elbow's similar actions primarily rely on intrinsic muscles in caniforms (Hermanson 2020; Liebich et al. 2020). The extrinsic muscles originate from the head, neck and trunk and insert into the scapular and brachial regions (Tarquini et al. 2023; Vélez-García and Miglino 2023). Notably, *P. flavus* stands apart from other procyonids mainly due to the presence of the m. atlantoscapularis, which evolved

from m. serratus ventralis cervicis to protract the scapula (Vélez-García and Miglino 2023).

On the other hand, intrinsic scapular and brachial muscles extend from the scapula to the brachial and antebrachial bones (Hermanson 2020; Liebich et al. 2020). Consequently, various studies have examined these muscles in different caniforms, providing insights into anatomical adaptations that vary among species to suit their habitat requirements (Vélez et al. 2018). While some gross anatomical studies of the shoulder and brachial muscles of *P. flavus* exist (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909; Böhmer et al. 2020), they are limited by their focus on single specimen, inconsistent terminology, and contrasting findings. Among these studies, only Julitz (1909) provided a detailed description of these muscles. These early investigations reported specific characteristics of these muscles in *P. flavus*, such as the fusion of m. teres minor with m. infraspinatus, two coracobrachialis muscles (m. coracobrachialis longus and m. coracobrachialis brevis), a m. biceps brachii with two heads (*Caput longum* and *Caput breve*), and a m. anconeus fused with the caput medialis of m. triceps brachii. Additionally, the m. tensor fasciae antebrachii was described as an inferior portion of m. latissimus dorsi (Beswick-Perrin 1871). The second study identified only one coracobrachialis muscle (brevis), and the m. tensor fasciae antebrachii was referred to as dorso-epitrochlearis (Windle and Parsons 1897). A third study did not name the m. anconeus epitrochlearis and described the heads of the m. triceps brachii as four anconeus heads (Julitz 1909). In the most recent study, the anconeus and teres minor were independent muscles, and the caput breve of the m. biceps brachii was described as a muscle belly from the m. articularis humeri (Böhmer et al. 2020). Additionally, a recent study on the brachial plexus in *P. flavus* described innervation to all thoracic limb muscles (Enciso-García and Vélez-García 2022), but did not detail the attachments and arterial supply to these muscles. Therefore, comprehensive examination and detailed description of the intrinsic shoulder and brachial muscles are necessary to clarify common anatomical patterns and possible variations in *P. flavus*. This knowledge provides information for recognizing evolutionary adaptations compared to other species within the suborder Caniformia and could be applicable in diagnostic and orthopedic procedures concerning the scapular, shoulder, and brachial regions. Consequently, this study aims to describe the origin, insertion, and arterial supply of the intrinsic shoulder and brachial muscles in *P. flavus* and compare the muscle configuration in *P. flavus* specimens with those of other caniforms to identify similarities and differences.

Materials and Methods

Dissection and documentation

Gross anatomical dissections in the scapular, humeral joint, and brachial regions were conducted on five *P.*

Table 1. Thoracic limbs dissected in *Potos flavus*.

Specimen	Sex	Age	Limb	ID
PfS1	M	J	R	M1R
			L	M1L
PfS2	M	A	R	M2R
			L	M2L
PfS3	F	A	R	F3L
			L	F3R
PfS4	F	A	R	F4L
			L	F4R
PfS5	F	A	R	F5L
			L	F5R

A, adult; F, female; I, infant; ID, Identification of the limb; J, juvenile; L, left; M, male; R, right.

flavus specimens, which were previously employed in a study of the extrinsic thoracic limb muscles (Vélez-García and Miglino 2023). Both thoracic limbs were dissected and meticulously identified (Table 1). The anatomical characteristics were described following the terminology of the Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature 2017). However, additional terms were incorporated due to the presence of other muscles and heads, such as the caput breve and caput longum of the m. biceps brachii, m. coracobrachialis brevis, m. coracobrachialis longus (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909), m. anconeus lateralis, and m. anconeus medialis (Barone 2020; Enciso-García and Vélez-García 2022). Photographs of the dissections were captured using a Canon T5i camera paired with a 60 mm macro lens and an EOS 6D camera paired with a 100 mm macro lens. This investigation received ethical approval from the bioethics committee of the Universidad del Tolima (2.3-059).

Statistical Analysis

The comparative analysis of the intrinsic shoulder and brachial muscles of caniforms can be framed as a classification problem of categorical variables or a clustering problem. Clustering represents an unsupervised machine learning technique utilized to identify and segregate natural groups based on the inherited properties within a dataset (Müller and Guido 2017; Kotu and Deshpande 2019). The DBSCAN (Density-Based Spatial Clustering of Application with Noise) algorithm, following a nearest neighbor distance approach, was designed to identify clusters with varying shapes and outliers (noise) (Ester et al. 1996). Considering the literature review (Table 2; see the discussion section), the muscles exhibiting the most variability among caniforms are the teres minor, coracobrachialis brevis, coracobrachialis longus, biceps brachii, triceps brachii, tensor fasciae antebrachii, and anconeus medialis. Consequently, these muscles were designated as the main categorical variables (i.e., Tmin, CBb, CBl, BB, TB, TFA, AM, respectively). The study engaged DBSCAN to cluster the studied species

based on these seven variables, and its predictive performance was measured using the silhouette coefficient (Rousseeuw 1987). The DBSCAN was applied using Scikit-learn 1.2.2 in Jupyter Notebook 6.5.2 (Kluyver et al. 2016). The final cluster visualization was generated using Tableau 2021.4.

For each specimen, the seven categorical variables underwent an encoding process to assign an integer value class corresponding to the muscle variants. Teres minor (Tmin), coracobrachialis brevis (CBb), coracobrachialis longus (CBl) and anconeus medialis (AM) variables were encoded into two classes, denoted as absent (0) or present (1). “Absent” was indicated when the muscle was either not described or reported as vestigial or fused with other muscle (e.g., m. teres minor was considered absent when reported as fused with m. infraspinatus in *P. flavus* as described by Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909). In some cases, the muscle was classified as “present” (1) when an author did not explicitly mention it, but other authors had reported its presence, and it was consistent with the family’s tendency to possess it. For example, m. anconeus medialis is considered present in the *P. lotor* specimens of Feeney (1999), since other authors had reported its presence in this species (Allen 1882; Windle and Parsons 1897). In addition, this muscle aligns with the typical characteristics of the Procyonidae family.

The variables triceps brachii (TB) and biceps brachii (BB) were numerically encoded into four classes based on the number of heads (capita). Therefore, values ranging from two (2) to five (5) were considered for each muscle. The reported caput angulare of the m. triceps brachii in mustelids was regarded as the caudal part of the m. tensor fasciae antebrachii (see the discussion section).

Finally, the tensor fasciae antebrachii (TFA) variable was encoded into five classes. “Absent” (0) was designated only when the author explicitly reported its complete absence (e.g., Böhmer et al. 2020 reported the absence of this muscle in *Vulpes vulpes* and *Cuon alpinus*). The presence of the cranial portion (1) was indicated when the muscle was solely reported to originate from the common tendon of the latissimus dorsi and teres major muscles (e.g., most canids). The presence of the caudal portion (2) was indicated when it originated from the m. teres major, caudal angle, or caudal margin of the scapula. The presence of both the cranial and caudal portions (3) was recorded (e.g., *P. flavus*). The presence of three portions (4) was considered in *Ursus americanus* based on Shepherd’s (1883) descriptions. This last characteristic was also extended to *Ursus maritimus*, as Kelley (1888) compared his findings with those of Shepherd (1883) in *U. americanus*.

It is important to note that some specimens were excluded from the statistical analysis because only one of the two anatomical regions was studied by the authors, either the shoulder or the brachium (e.g., Davis 1949; Pereira et al. 2010). However, anatomical description from *U. americanus* were considered because a subsequent publication concerning *Ailuropoda melanoleuca* highlighted differences between *U. americanus* and *Tremarctos ornatus* (Davis 1964).

Table 2. Reviewed species within the suborder Caniformia. N = number of dissected specimens.

Family	Species	N (sex)	Authors
Procyonidae	<i>Potos flavus</i>	1 (unknown sex)	Beswick-Perrin (1871)
		1 (unknown sex)	Windle and Parsons (1897)
		1 (unknown sex)	Julitz (1909)
		1 (unknown sex)	Davis (1964)
		1 (unknown sex)	Böhmer et al. (2020)
		5 (2 males and 3 females)	Present study
	<i>Bassaricyon alleni</i>	1 (unknown sex)	Beddard (1900)
	<i>Procyon cancrivorus</i>	1 (unknown sex)	Windle (1888)
		2 (males)	Santos et al. (2010b)
		5 (unknown sex)	Pereira et al. (2010)
		3 (two females and one unknown)	Tarquini et al. (2023)
	<i>Procyon lotor</i>	2 (females)	Allen (1882)
		1 (unknown sex)	Windle and Parsons (1897)
		1 (unknown sex)	Davis (1949)
		2 (1 female and 1 male)	Feeney (1999)
	<i>Nasua nasua</i>	1 (unknown sex)	Mackintosh (1875)
		3 (1 male and 2 females)	Santos et al. (2010a)
		1 (unknown sex)	Böhmer et al. (2020)
		3 (males)	Tarquini et al. (2023)
	<i>Nasua narica</i>	1 (unknown sex)	Mackintosh (1875)
1 (unknown sex)		Davis (1949)	
<i>Bassariscus astutus</i>	1 (unknown sex)	Davis (1949)	
Mustelidae	<i>Eira barbara</i>	1 (unknown sex)	Macalister (1873b)
	<i>Galictis cuja</i>	3 (1 female and 1 male)	Ercoli et al. (2015)
	<i>Taxidea taxus</i>	6 (unknown sex)	Moore et al. (2013)
	<i>Martes americana</i>	25 (19 males and 6 females)	Leach (1977)
	<i>Martes martes</i>	1 (1 male)	Yousefi et al. (2018)
		3 (unknown sex)	Böhmer et al. (2018)
	<i>Martes foina</i>	4 (unknown sex)	Böhmer et al. (2018)
		1 (unknown sex)	Böhmer et al. (2020)
	<i>Martes caurina</i>	1 (1 male)	Hall (1926)
	<i>Pekania pennanti</i>	25 (7 males and 18 females)	Leach (1977)
		4 (1 female and 3 males)	Feeney (1999)
	<i>Meles meles</i>	1 (unknown sex)	Böhmer et al. (2020)
		2 (1 female and 1 male)	Haughton (1864a)
	<i>Lutra lutra</i>	1 (male)	Haughton (1864b)
		1 (unknown sex)	Windle and Parsons (1897)
	<i>Enhydra lutris</i>	1 (unknown sex)	Howard (1973)
<i>Aonyx</i> sp.	1 (unknown sex)	Macalister (1873a)	
Mephitidae	<i>Mephitis mephitis occidentalis</i>	1 (male)	Hall (1926)
	<i>Spilogale gracilis phenax</i>	1 (female)	Hall (1926)
Ailuridae	<i>Ailurus fulgens</i>	1 (male)	Carlsson (1925)
		4 (3 females and 1 male)	Fisher et al. (2009)
		1 (unknown sex)	Davis (1964)
Ursidae	<i>Ursus americanus</i>	1 (male)	Shepherd (1883)
		1 (male)	Davis (1949)
		1 (unknown sex)	Windle and Parsons (1897)
	<i>Ursus maritimus</i>	1 (female)	Kelley (1888)
	<i>Ailuropoda melanoleuca</i>	2 (males)	Davis (1964)
	<i>Tremarctos ornatus</i>	1 (female)	Davis (1949)
<i>Melursus ursinus</i>	3 (unknown sex)	Annie et al. (2017, 2019)	

Family	Species	N (sex)	Authors
Canidae	<i>Canis lupus familiaris</i>	Non specified	Hermanson (2020)
	<i>Canis lupus dingo</i>	1 (unknown sex)	Haughton (1866)
	<i>Canis latrans</i>	1 (female) 1 limb	Feeney (1999)
	<i>Cuon alpinus</i>	1 (unknown sex)	Böhmer et al. (2020)
	<i>Cerdocyon thous</i>	6 (1 males and 5 females)	Vélez et al. (2018), Vélez-García et al. (2018)
	<i>Chrysocyon brachyurus</i>	3 (unknown sex)	Pereira et al. (2016)
	<i>Lycalopex gymnocercus</i>	22 (10 females and 12 males)	Souza-Junior et al. (2018)
	<i>Lycaon pictus</i>	1 (male)	Smith et al. (2020)
	<i>Vulpes vulpes</i>	5 (4 males and 1 female)	Feeney (1999)
		1 (unknown sex)	Böhmer et al. (2020)
		<i>Urocyon cinereoargenteus</i>	4 (2 females and 2 males)

Results

Lateral intrinsic muscles of the shoulder

M. deltoideus

The m. deltoideus comprises two parts: a cranial part referred to as the acromial part (pars acromialis) and a caudal part known as the scapular part (pars scapularis). The acromial part originates via a tendon and fleshy fibers from the ventral margin of the hamulus process of the acromion, while the scapular part originates from an aponeurosis along the scapular spine (Figs 1, 2). The scapular part merges with the acromial part, inserting onto the distal half of the lateral surface of the crest of the greater tubercle

and the deltoid tuberosity (Fig. 3). Both parts are supplied by the caudal circumflex artery, and the scapular part also receives supply from the subscapular artery (Fig. 4).

M. supraspinatus

The m. supraspinatus has a fleshy origin from the supraspinatus fossa and the cranial surface of the scapular spine (Figs 1, 2). It inserts via a tendon onto the proximal margin of the greater tubercle (Fig. 3). There is fibrous tissue connecting the supraspinatus tendon to the tendon of the cranial belly of the m. pectoralis profundus. Blood supply to this muscle is provided by the suprascapular artery, the superficial branch of the subscapular artery, and branches from the cervical superficial artery (Fig. 4). In one specimen (M1), the caudal humeral circumflex artery also supplied the m. supraspinatus bilaterally.

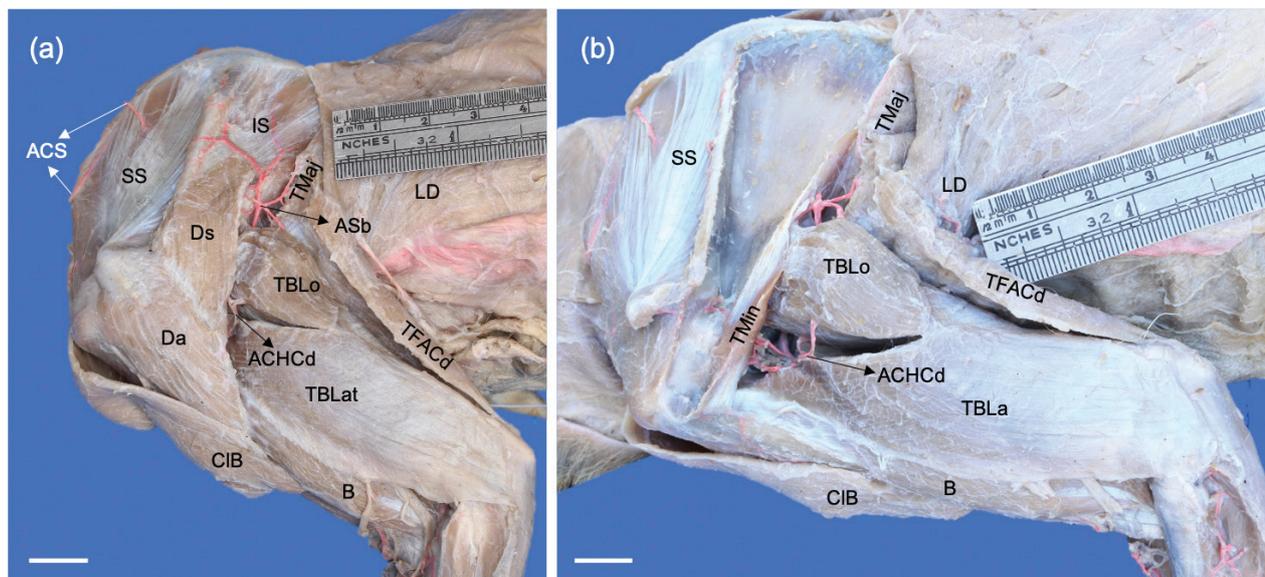


Figure 1. Lateral photographic views of the intrinsic shoulder and brachium muscles of *Potos flavus*. Superficial (a) and deep views (b) of a left thoracic limb. ACS, a. cervicalis superficialis; ACHCd, a. circumflexa humeri caudalis; ASb, a. subscapularis; ATD, a. thoracodorsalis; AL, m. anconeus lateralis; B, m. brachialis; CIB, m. cleidobrachialis; Da, m. deltoideus pars acromialis; Ds, m. deltoideus pars scapularis; IS, m. infraspinatus; LD, m. latissimus dorsi; SS, m. supraspinatus; TB, m. triceps brachii; TBLa, caput laterale; TBLo, caput longum; TFACd, m. tensor fasciae antebrachii pars caudalis; TMaj, m. teres major; TMin, m. teres minor. White bars: 10 mm.

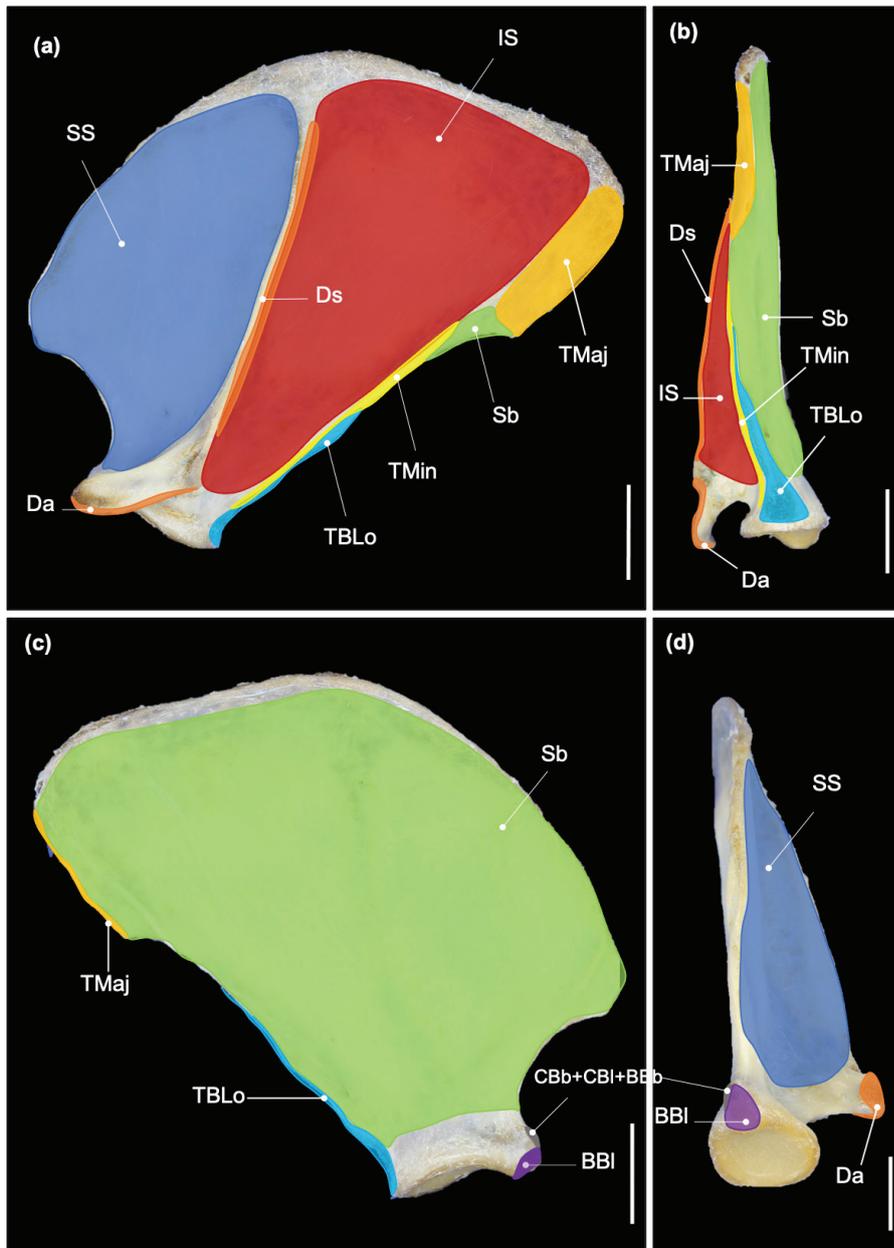


Figure 2. Muscle maps of the intrinsic shoulder and brachial muscles in a left scapula of *Potos flavus*. (a) Lateral view, (b) caudal view, (c) medial view, (d) cranial view. AL, m. anconeus lateralis; B, m. brachialis; BB, m. biceps brachii; BBb, caput breve; BBl, caput longum; CBb, m. coracobrachialis brevis; CBl, m. coracobrachialis longus; Da, m. deltoideus pars acromialis; Ds, m. deltoideus pars scapularis; IS, m. infraspinatus; Sb, m. subscapularis, SS, m. supraspinatus; TBLo, m. triceps brachii caput longum; TMaj, m. teres major; TMin, m. teres minor.

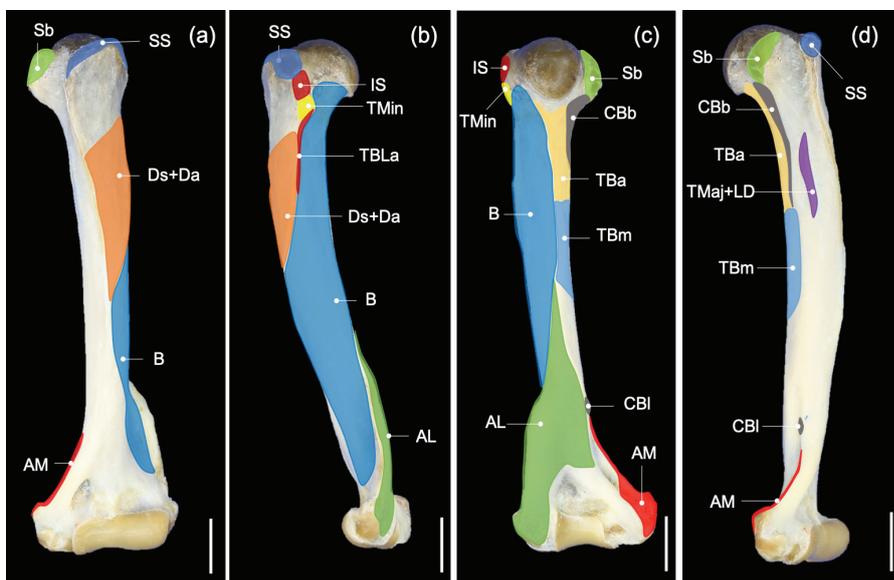


Figure 3. Muscle maps of the intrinsic shoulder and brachial muscles in a left humerus of *Potos flavus*. (a) Cranial view, (b) lateral view, (c) caudal view, (d) medial view. AL, m. anconeus lateralis; AM, m. anconeus medialis; B, m. brachialis; CBb, m. coracobrachialis brevis; CBl, m. coracobrachialis longus; Da, m. deltoideus pars acromialis; Ds, m. deltoideus pars scapularis; IS, m. infraspinatus; LD, m. latissimus dorsi; Sb, m. subscapularis, SS, m. supraspinatus; TBLa, m. triceps brachii caput laterale; TBm, m. teres major; TBa, caput accessorium; TMaj, m. teres major; TMin, m. teres minor.

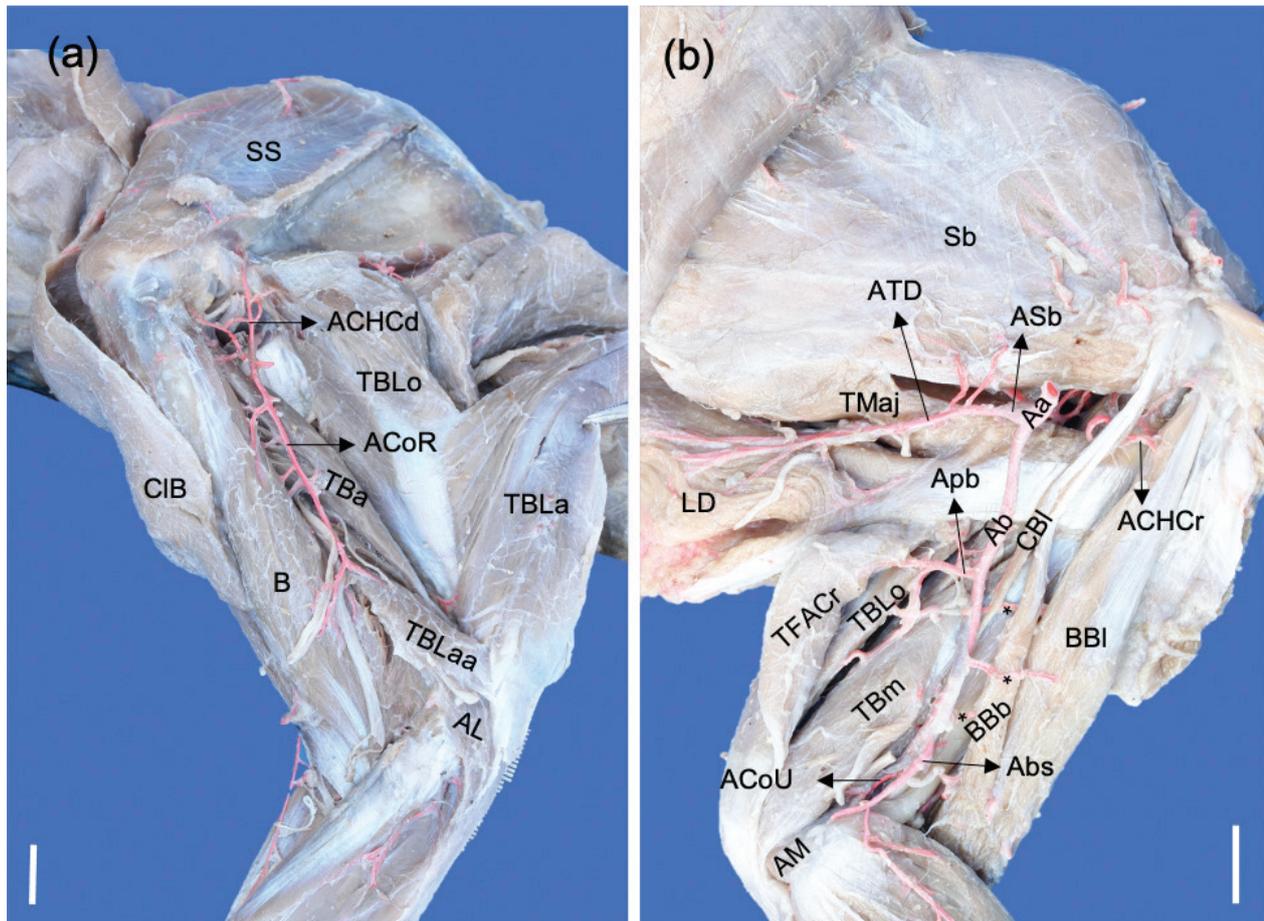


Figure 4. Lateral (a) and medial (b) photographic views of the intrinsic shoulder and brachial muscles with the arterial distribution in the left thoracic limbs of *Potos flavus*. Aa, a. axillaris; Ab, a. brachialis; Abi, a. brachialis superficiales; ACHCd, a. circumflexa humeri caudalis; ACHCr, a. circumflexa humeri cranialis; ACoR, a. collateralis radialis; ASb, a. subscapularis; ACoU, a. collateralis ulnaris; Apb, a. profunda brachii; AL, m. anconeus lateralis; AM, m. anconeus medialis; B, m. brachialis; BB, m. biceps brachii; BBb, caput breve; BBl, caput longum; CBb, m. coracobrachialis brevis; CBl, m. coracobrachialis longus; CIB, m. cleidobrachialis; LD, m. latissimus dorsi; Sb, m. subscapularis; SS, m. supraspinatus; TB, m. triceps brachii; TBa, caput accessorium; TBLa, caput laterale; TBLaa, caput laterale accessorium; TBLo, caput longum; TBm, caput mediale; TFACr, m. tensor fasciae antebrachii pars cranialis; TMaj, m. teres major; *, branches of the brachial artery to the m. biceps brachii. White bars: 10 mm.

M. infraspinatus

The m. infraspinatus originates via fleshy fibers from the infraspinatus fossa, the caudal surface of the scapular spine, and the origin aponeurosis of the m. teres minor (Figs 1, 2). It inserts via a tendon onto the greater tubercle on the facies m. infraspinatus (Fig. 3). A synovial bursa was observed proximal to the insertion, beneath the infraspinatus tendon. Blood supply to this muscle is provided by the suprascapular, subscapular, caudal humeral circumflex and scapular circumflex arteries (Fig. 4).

M. teres minor

The m. teres minor originates via an aponeurosis from the two ventral thirds of the caudal scapular margin and inserts tendinously onto the teres minor tuberosity distal to the infraspinatus insertion (Figs 1–3). Blood supply to this muscle is primarily through the caudal circumflex artery (Fig. 4).

Medial intrinsic shoulder muscles

M. subscapularis

The m. subscapularis is multipennate with eight bellies originating from fleshy fibers within the subscapular fossa, along the caudal margin of the scapula, and intermuscular septum adjacent to the m. teres major (Figs 1, 2). It inserts onto the lesser tubercle and the medial aspect of the articular capsule of the shoulder joint (Fig. 3). Blood supply to this muscle is provided by the suprascapular and subscapular arteries (Fig. 4). Additionally, the thoracodorsal artery supplied this muscle in four limbs (F1R, M1R, M1L, M2R), and the cranial humeral circumflex artery supplied it in one specimen (M1) bilaterally.

M. teres major

The m. teres major originates from the dorsal third of the caudal scapular margin, the lateral and medial surfaces

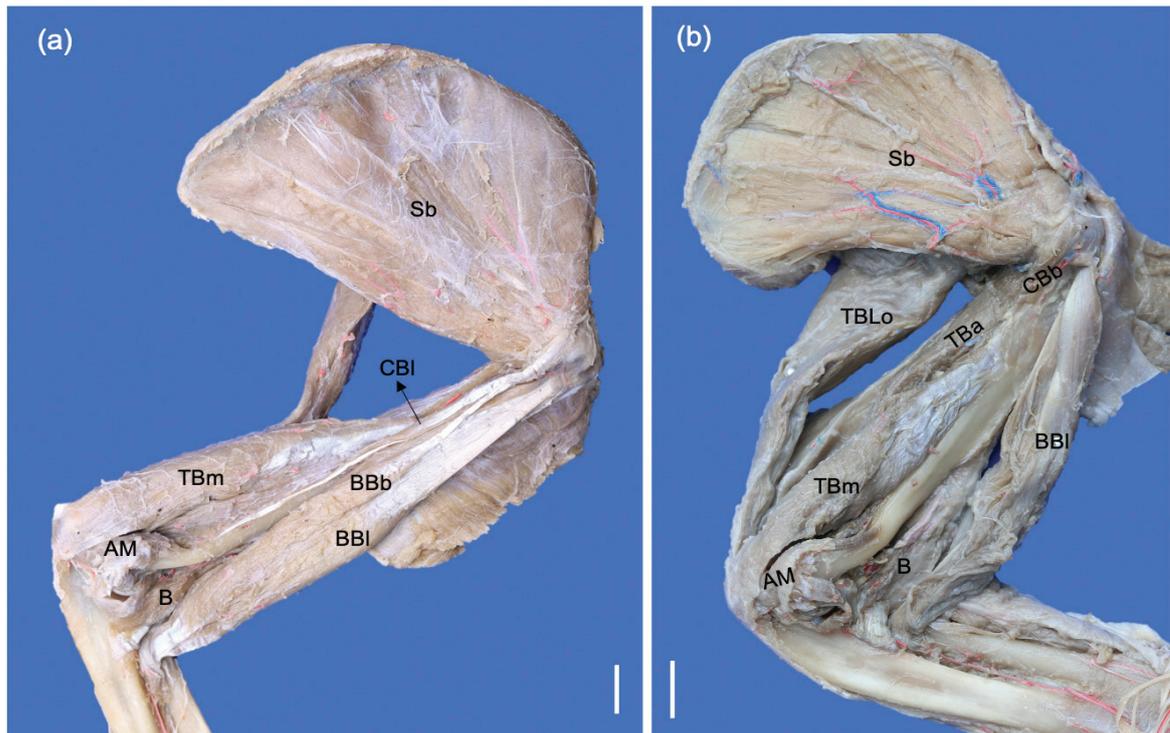


Figure 5. Medial deep photographic views of the intrinsic shoulder and brachial muscles of the left thoracic limbs of *Potos flavus*. (a) The caput accessorium of the m. triceps brachii was displaced caudally; (b) absence of m. coracobrachialis longus. AL, m. anconeus lateralis; AM, m. anconeus medialis; B, m. brachialis; BB, m. biceps brachii; BBb, caput breve; BBI, caput longum; CBB, m. coracobrachialis brevis; CBI, m. coracobrachialis longus; CLB, m. cleidobrachialis; Sb, m. subscapularis; TB, m. triceps brachii; TBa, caput accessorium; TBLo, caput longum; TBm, caput mediale. White bars: 10 mm.

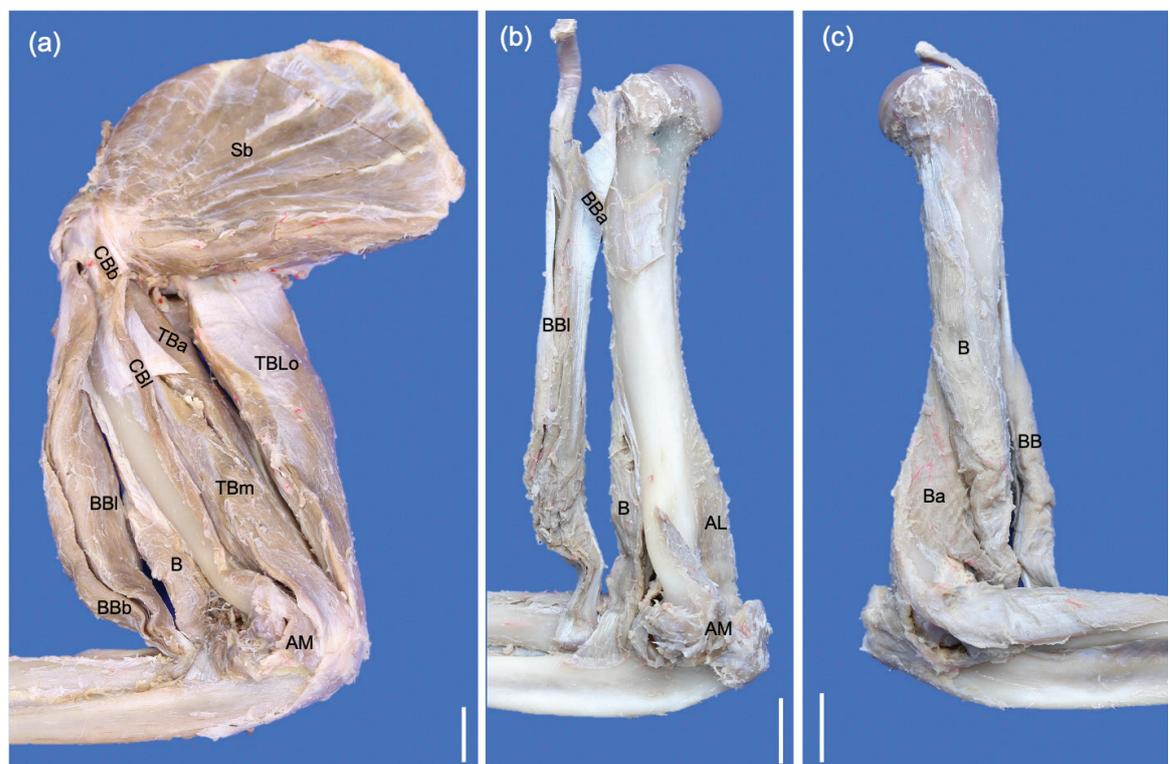


Figure 6. Variants of the m. biceps brachii in *Potos flavus*. (a) Medial view of a right thoracic limb where the caput breve was fused to the caput longa of the m. biceps brachii; (b) medial view of a right thoracic limb with an accessory caput of the m. biceps brachii; (c) lateral deep view of a right thoracic limb. B, m. brachialis; Ba, caput accessorium of the m. brachialis (anatomical variant); BB, m. biceps brachii; BBA, caput accessorium; BBb, caput breve; BBI, caput longum; CBB, m. coracobrachialis brevis; CBI, m. coracobrachialis longus; Sb, m. subscapularis; TB, m. triceps brachii; TBa, caput accessorium; TBLo, caput longum; TBm, caput mediale. White bars: 10 mm.

of the caudal scapular angle, and the intermuscular septum shared with the *m. subscapularis* (Figs 1, 2). It fuses with the *m. latissimus dorsi* to insert via a common tendon onto the intertubercular groove at the level of the crests of the greater and lesser tubercles (Figs 3, 4). Blood supply to this muscle is provided by the subscapular and thoracodorsal arteries (Fig. 4).

Mm. coracobrachiales (*m. coracobrachialis longus* and *m. coracobrachialis brevis*)

There are two coracobrachiales muscles, namely *m. coracobrachialis brevis* and *m. coracobrachialis longus*, which originate from the coracoid process of the scapula via a common tendon shared with the *caput breve* of the *m. biceps brachii* (Figs 4–6). Respectively, they insert via fleshy fibers onto the caudal surface to the crest of the lesser tubercle and via a tendon onto the proximal extreme to the supracondylar foramen (Fig. 3). The *m. coracobrachialis longus* was bilaterally absent in one specimen (M2) (Fig. 5). Both muscles receive blood supply from the cranial circumflex artery, and the *m. coracobrachialis longus* is also supplied by the brachial artery (Fig. 4).

Cranial brachial muscles

M. biceps brachii

The *m. biceps brachii* consists of two heads (*capita*), namely the *caput longum* and *caput breve*. The *caput*

longum originates from the supraglenoid tubercle of the scapula via a tendon that passes inside the articular capsule of the shoulder. The *caput breve* originates from the coracoid process via a common tendon shared with the *coracobrachiales longus* and *brevis* muscles (Figs 4, 5). Both *capita* fuse at the midpoint of the brachium and insert via a tendon onto the radial tuberosity (Fig. 7). Blood supply to both heads is provided by the cranial humeral circumflex, brachial, superficial antebrachial, and transverse cubital arteries. The brachial artery bifurcates into three branches at the midpoint of the brachium to both heads (Fig. 4). Notably, the *caput breve* was absent in the right brachia of two specimens (F2R and M2R). However, in one of these specimens (F2R), the *caput breve* was fused to the *caput longum* in one limb (Fig. 6). In the right brachium of another specimen (M2R), an accessory head (*caput accessorium*) originated via a tendinous fascicle from the medial aspect of the crest of the greater tubercle and fused distally to the *caput longum* (Fig. 6). Additionally, in two limbs (F1R and M1L), the musculocutaneous nerve perforated the *caput longum*, forming an accessory belly in one of them (F1R) (Fig. S1).

M. brachialis

The *m. brachialis* is a large muscle originating fleshy from the humeral neck, caudo-lateral surface of the humerus, sulcus of *m. brachialis*, and the medial aspect of the lateral supracondylar crest (Figs 1, 3, 6, 8). It inserts via a tendon onto the distal surface to the medial coronoid process (Figs 6, 7). Blood supply to this muscle is provid-

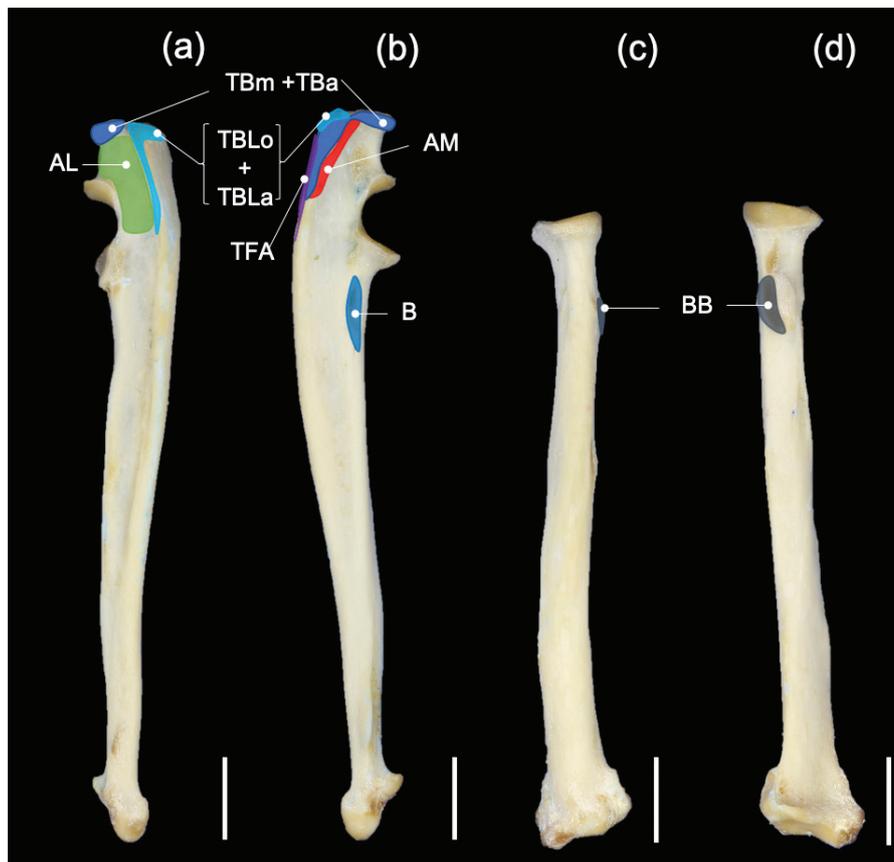


Figure 7. Muscle maps of the intrinsic shoulder and brachial muscles in a left ulna (a-b) and a left radius (c-d) of *Potos flavus*. (a) lateral view, (b) medial view, (c) cranial view, (d) caudal view. AL, *m. anconeus lateralis*; AM, *m. anconeus medialis*; B, *m. brachialis*; BB, *m. biceps brachii*; TBLa, *m. triceps brachii caput laterale*; TBLo, *caput longum*; TBM, *caput mediale*; TBA, *caput accessorium*; TFA, *m. tensor fasciae antebrachii*.

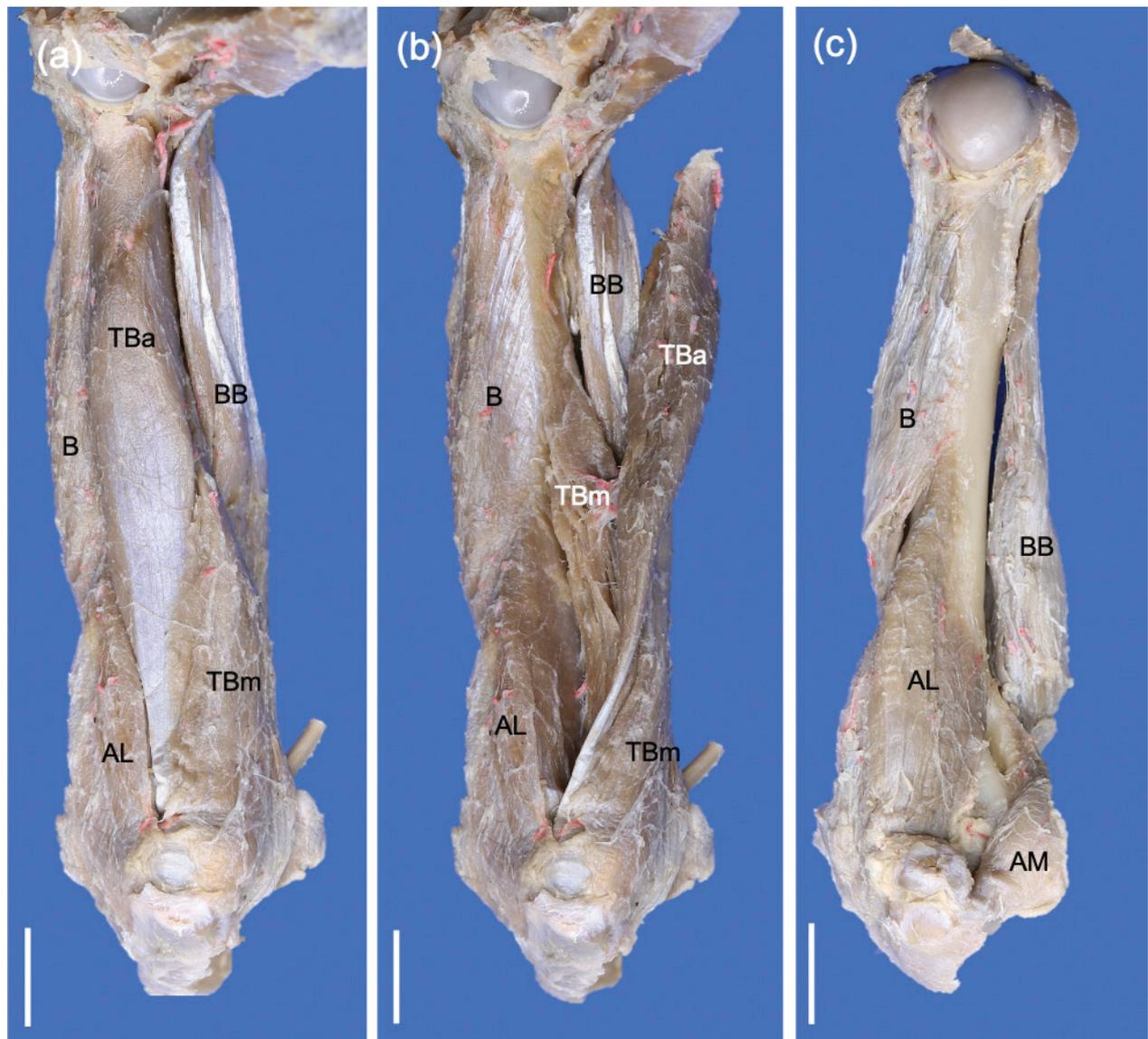


Figure 8. Caudal photographic views of the intrinsic brachial muscles of the left brachia of *Potos flavus*. (a) Caudal view without the capita longum and laterale of the m. triceps brachii, (b) caudal view after medially displacing the caput accessorium of the m. triceps brachii, (c) caudal view after eliminating all capita of the m. triceps brachii; AL, m. anconeus lateralis; AM, m. anconeus medialis; B, m. brachialis; BB, m. biceps brachii; TB, m. triceps brachii; TBa, caput accessorium; TBm, caput mediale. White bars: 10 mm.

ed by the radial collateral, transverse cubital, and superficial brachial arteries. The latter artery supplies it via a recurrent branch that passes between it and the m. biceps brachii (Fig. 4). In one limb (M2R), the belly divided into a proximal part originating from the humeral shaft and a distal part originating from the lateral supracondylar crest (caput accessorium) (Fig. 6).

Caudal brachial muscles

M. triceps brachii

The m. triceps brachii consists of four heads (capita longum, mediale, accessorium and laterale). The caput longum originates via a tendon from the ventral half of the caudal scapular margin (medial to the teres minor aponeurosis) and infraglenoid tubercle (Figs 1, 2). The caput laterale

originates from the brachial fascia and tricipital line via an aponeurosis. The caput laterale and caput longum fuse at the middle of the brachium and insert tendinously onto the caudal surface of the olecranon tuberosity (Fig. 7). The caput longum is supplied by the subscapular, caudal circumflex, radial collateral and deep brachial arteries. The caput laterale is supplied by the last three arteries (Figs 1, 4). On the left thoracic limbs of two specimens (M1 and M2), the caput longum originated from the ventral third of the caudal scapular margin. In one specimen (M1), another caput was found bilaterally, which originated from the proximal extreme of the caudal surface of the lateral supracondylar crest. This caput is joined to the caput laterale and is supplied by the radial collateral artery (Fig. 4). On the right thoracic limb, this accessory head was more developed than on the left thoracic limb.

The caput mediale originates via fleshy fibers widely from the second and third proximal fifth of the caudome-

dial surface of the humerus until the caudal surface of the proximal extreme to the supracondylar foramen. The caput accessorium also originates via fleshy fibers from the humeral neck and the first proximal fifth of the caudal surface of the humerus, where it is fused to the caput mediale (Figs 3, 8). Both capita insert via a common tendon onto the cranial surface of the olecranon tuberosity (Figs 7, 8). A synovial bursa (*B. subtendinea m. tricipitis brachii*) is present between the common tendon of the caput laterale and caput longum and the common tendon of the caput accessorium and caput mediale. The caput mediale is supplied by the brachial, deep brachial and ulnar collateral arteries. The caput accessorium is supplied by the radial collateral and deep brachial arteries (Fig. 4). The caudal humeral circumflex artery also supplied the caput accessorium in one specimen (M2) bilaterally.

M. anconeus lateralis (m. anconeus)

The m. anconeus lateralis (m. anconeus or m. anconeus lateralis) originates via fleshy fibers from the distal half of the caudolateral surface of the humeral shaft, lateral supracondylar crest, and lateral epicondyle of the humerus. It inserts via fleshy fibers onto the joint capsule of the elbow and the lateral surface of the olecranon (Figs 3, 8). Blood supply to this muscle is provided by the deep brachial, collateral radial, and collateral ulnar

arteries. In the right thoracic limb of a specimen (M2R), the muscle originated from the distal third of the humeral shaft.

M. anconeus medialis (m. anconeus epitrochlearis)

The m. anconeus medialis originates via fleshy fibers from the cranioproximal margin of the supracondylar foramen and medial epicondyle of the humerus (Figs 3, 5, 6). It inserts via fleshy fibers onto the medial aspect of the olecranon (Fig. 7). Blood supply to this muscle is provided by the ulnar collateral artery (Fig. 4).

M. tensor fasciae antebrachii

The m. tensor fasciae antebrachii comprises two parts: a cranial part (pars cranialis) and a caudal part (pars caudalis). The caudal part originates from the latissimus dorsi and teres major muscles. The cranial part originates from the latissimus dorsi, pectoralis profundus, and cutaneus trunci muscles. The muscle forms an aponeurosis to insert onto the medial caudal margin of the olecranon and antebrachial fascia (Figs 7–9). Blood supply to this muscle is provided by the deep brachial and thoracodorsal arteries. In one specimen (M1), the subscapular artery supplied it bilaterally (Fig. 4).

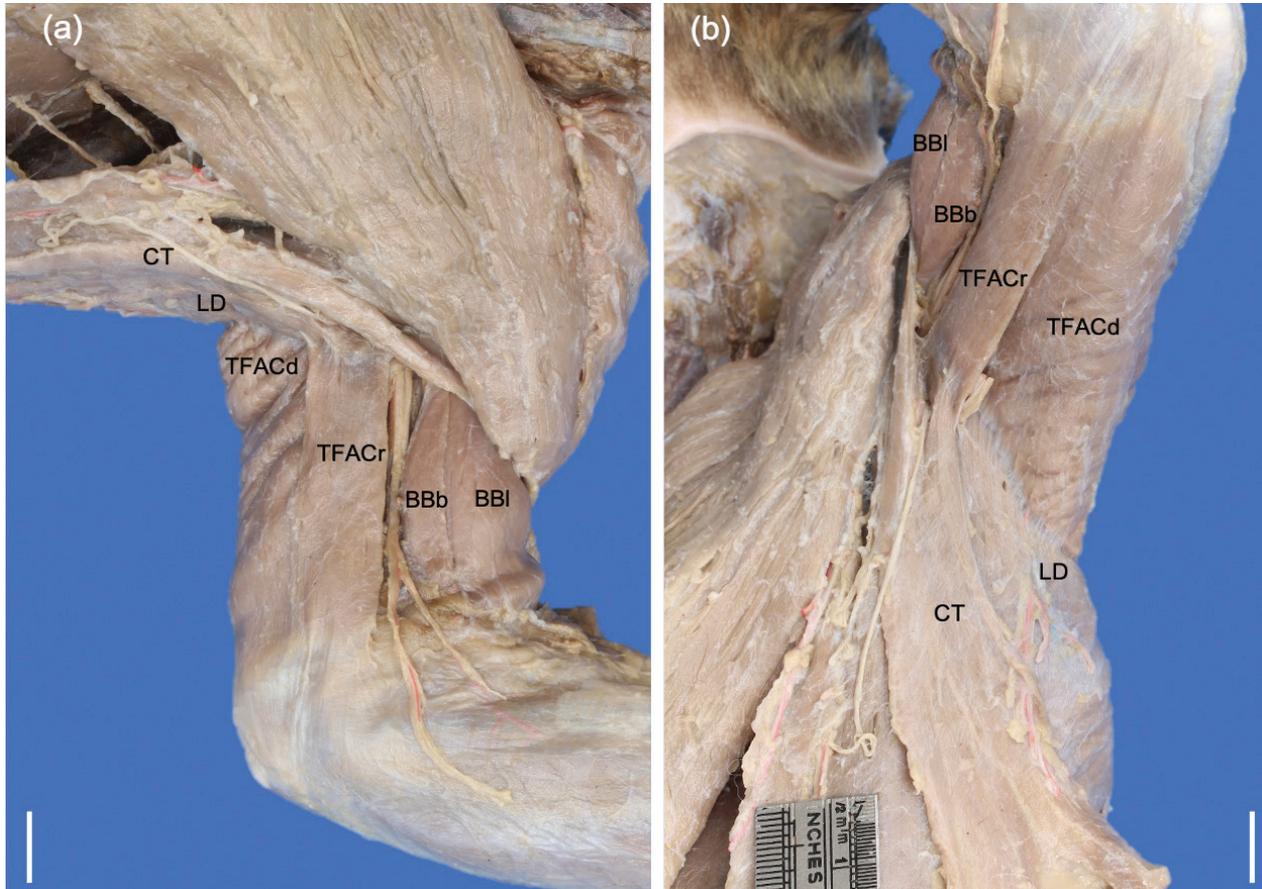


Figure 9. Superficial medial photographic views of the intrinsic brachial muscles of a left thoracic limb of *Potos flavus*. (a) Medial view, (b) caudomedial view; BB, m. biceps brachii; BBb, caput breve; BBI, caput longum; CT, m. cutaneus trunci; LD, m. latissimus dorsi; TFACr, m. tensor fasciae antebrachii pars cranialis; TFACd, m. tensor fasciae antebrachii pars caudalis. White bars: 10 mm.

rin 1871; Mackintosh 1875; Allen 1882; Windle 1888; Windle and Parsons 1897; Beddard 1900). However, it is worth noting that some procyonids, including *P. lotor* (Allen 1882), *P. cancrivorus* (Santos et al. 2010b) and *N. nasua* (Santos et al. 2010a; Tarquini et al. 2023) may exhibit origins from an intermuscular septum cranially to the cranial margin of the scapula. In *P. cancrivorus*, the supraspinatus insertion extends to the transverse humeral retinaculum (Tarquini et al. 2019) and may exhibit variations with two bellies in *P. cancrivorus* (Tarquini et al. 2023; Vélez García et al. 2023), and *P. lotor* (Allen 1882). This is distinct from most non-procyonid caniforms, which typically possess one belly as seen in *P. flavus*, while it normally has two bellies in canids (Feeney 1999; Vélez-García et al. 2018b) and three bellies in the mustelid *G. cuja* (Ercoli et al. 2015).

In the present study, the m. teres minor was completely separated from the m. infraspinatus in all *P. flavus* specimens, consistent with reports in the same species (Böhmer et al. 2020) and other procyonids (Davis 1949; Feeney 1999; Böhmer et al. 2020; Tarquini et al. 2023). However, it differs from previous descriptions, where fusion with the m. infraspinatus was documented in *P. flavus* (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909) and occasionally in *P. lotor* (Allen 1882). Origins from the infraglenoid tubercle, as found in *P. cancrivorus* (Santos et al. 2010b) and *N. nasua* (Santos et al. 2010a), were not observed in *P. flavus*. Among most non-procyonid caniforms, the m. teres minor is typically separated from the m. infraspinatus. However, fusion with the m. infraspinatus has been reported in the mustelid *Enhydra lutris* (Howard 1973), the mephitid *Mephitis mephitis* (Hall 1926), and the ursid *Ursus americanus* (Shepherd 1883). In some species, the muscle may be vestigial or entirely absent, as seen in the mephitid *Spilogale gracilis* (Hall 1926), the mustelids *Aonyx* sp. (Macalister 1873a) and *Lutra lutra* (Haughton 1864c), and occasional cases in *G. cuja* (Ercoli et al. 2015).

While examining the m. subscapularis, it was found that its attachments do not differ among procyonids, corroborating previous descriptions (Beswick-Perrin 1871; Allen 1882; Windle 1888; Julitz 1909; Santos et al. 2010a, 2010b). Nevertheless, the number of bellies varies across species, with *P. lotor* showing two to four bellies (Allen 1882; Windle and Parsons 1897; Davis 1949; Feeney 1999), *N. narica* exhibiting three, *N. nasua* presenting six (Mackintosh 1875), and *P. flavus* displaying up to eight. Additionally, the muscle may insert via two tendons onto the lesser tubercle in species as *Bassariscus astutus*, *P. lotor*, *N. narica* (Davis 1949), and *N. nasua* (Tarquini et al. 2023). In non-procyonid caniforms, the muscle has been reported to have a maximum of six bellies in *G. cuja* (Ercoli et al. 2015), *Martes martes* (Yousefi et al. 2018), *Canis lupus familiaris* (Hermanson 2020), and *Cerdocyon thous* (Vélez-García et al. 2018b). The insertion via two tendons has only been reported in *U. americanus* (Davis 1949) and *M. ursinus* (Annie et al. 2017).

The m. deltoideus of *P. flavus* closely resembled descriptions provided by other authors (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909; Böhmer

et al. 2020) and other procyonids (Windle 1888; Windle and Parsons 1897; Santos et al. 2010a, 2010b; Tarquini et al. 2023). However, the scapular part of the muscle may also originate from the infraspinatus fascia in *N. nasua* (Mackintosh 1875; Tarquini et al. 2023) and as a variation in *P. lotor* (Allen 1882). Additionally, the tendon has contact with the caput laterale of the m. triceps brachii in *P. lotor* (Allen 1882), while in *N. narica*, the insertion extends distally onto the humerus (Mackintosh 1875). The acromial part of the m. deltoideus may have some continuous fibers with the m. brachialis or inserts onto this muscle in *N. nasua* and *N. narica* (Mackintosh 1875; Tarquini et al. 2023). The division of the m. deltoideus into two parts is generally present in all caniforms, with each part inserting separately onto the deltoid tuberosity in *G. cuja* (Ercoli et al. 2015), *Aonyx* sp. (Macalister 1873a), *A. fulgens* (Fisher et al. 2009), and *M. ursinus* (Annie et al. 2017). It is important to highlight that the clavicular part (pars clavicularis) of the m. deltoideus, mentioned in previous studies (Beswick-Perrin 1871; Mackintosh 1875; Allen 1882; Windle 1888; Windle and Parsons 1897; Julitz 1909), is designated as the m. cleidobrachialis (International Committee on Veterinary Gross Anatomical Nomenclature 2017), since it originates from the clavicular intersection. Therefore, it is an extrinsic thoracic limb muscle because the clavicle is an absent or vestigial bone in procyonids (Souza Junior et al. 2020; Vélez-García and Miglino 2023). Nonetheless, in procyonids, this muscle has evolved from the m. deltoideus and retains innervation by the axillary nerve (Enciso-García and Vélez-García 2022; Vélez García et al. 2023; Vélez-García and Miglino 2023).

The m. teres major in *P. flavus* originates from the proximal third of the caudal margin of the scapula, consistent with previous descriptions (Windle and Parsons 1897; Julitz 1909). However, this muscle also originates from the caudal angle and the m. subscapularis, a characteristic not reported by other authors (Beswick-Perrin 1871; Windle and Parsons 1897). A similar origin is also found in *P. lotor* (Allen 1882; Feeney 1999), *P. cancrivorus*, and *N. nasua* (Santos et al. 2010a, 2010b; Tarquini et al. 2023). Additionally, an origin from the m. infraspinatus has been observed in *N. nasua* (Tarquini et al. 2023) and as a variation in *P. lotor* (Allen 1882). Among non-procyonid caniforms, the m. teres major exhibits considerable variation in its origin, while the insertion consistently occurs via a common tendon with the m. latissimus dorsi.

The arrangement of the coracobrachialis brevis and longus muscles in *P. flavus* are consistent with previous descriptions (Beswick-Perrin 1871; Julitz 1909; Davis 1964). The m. coracobrachialis longus may be absent in *P. flavus* (Windle and Parsons 1897), as similarly observed in one specimen of the present study. Böhmer et al. (2020) only described one muscle for *P. flavus*, although both muscles can be observed in the figures of their study. Therefore, based on the total limbs reported by several authors for *P. flavus* (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909; Davis 1964; Böhmer et al. 2020; present study), the prevalence of the absence of the m. coracobrachialis brevis would be 20% (4/20 limbs).

Table 3. Comparative terminology to the coracobrachialis, triceps, anconeus and tensor fasciae antebrachii muscles in caniforms.

Muscle name*	Homologous names used by other authors in Caniforms
M. coracobrachialis brevis*	M. coraco-brachialis brevis (Beswick-Perrin 1871; Macalister 1873b; Shepherd 1883; Kelley 1888)
	Short belly of the m. coracobrachialis (Leach 1977)
	M. articularis humeri (Ercoli et al. 2015; Böhmer et al. 2020; Tarquini et al. 2023)
M. coracobrachialis longus*	M. coraco-brachialis longus (Beswick-Perrin 1871; Macalister 1873b; Shepherd 1883; Kelley 1888)
	M. coracobrachialis accessorius (Haughton 1864)
	Main belly of the m. coracobrachialis (Leach 1977)
	M. coracobrachialis (Yousefi et al. 2018; Tarquini et al. 2023)
M. triceps brachii caput longum	M. anconeus longus (Julitz 1909); First or scapular head of the triceps (Allen 1882)
	Scapular head of the triceps (Shepherd 1883)
	Posterior division of the outer head (Beddard 1900)
	Anterior part or anterior head of the m. triceps longum (Davis 1949)
	Medial head of the m. triceps longum (Davis 1964).
	Triceps brachii – medial head (Moore et al. 2013)
	Anterior part of the caput longum of m. triceps brachii (Davis 1949; Annie et al. 2019)
M. triceps brachii caput longum accessorium*	Posterior part or posterior head of the caput longum of m. triceps brachii (Davis 1949; Annie et al. 2019)
	Lateral head of the m. triceps longum (Davis 1964)
	Caput magnum of the m. triceps brachii (Smith et al. 2020)
M. triceps brachii caput laterale	M. anconeus lateralis (Julitz 1909) Second or lateral humeral portion (Allen 1882)
	Outer head of the triceps (Shepherd 1883)
	M. triceps lateralis (Davis 1964)
	Anterior division of the outer head (Beddard 1900)
M. triceps brachii caput laterale accessorium*	Fourth head of the triceps (Shepherd 1883)
M. triceps brachii caput mediale	M. anconeus medialis (Julitz 1909) Third portion of the triceps (Allen 1882),
	internal head of the triceps (Shepherd 1883)
	Intermediate head of the m. triceps medialis (Davis 1964)
	Deep portion of the m. triceps brachii, which originates from the proximal part of the humerus (Beddard 1900)
	M. triceps medialis longus (Annie et al. 2017)
M. triceps brachii caput accessorium	M. anconeus posterior (Julitz 1909)
	Accessory muscular fibers of the second portion of m. triceps brachii (Allen 1882)
	Long head of the m. triceps medialis (Davis 1964)
	Deep portion of the m. triceps brachii, which originates from the under the lateral head (Beddard 1900)
	M. triceps medialis brevis or intermediate head of the caput mediale of the m. triceps brachii (Annie et al. 2017)
M. tensor fasciae antebrachii	Latissimus dorsi head (Haughton 1864)
	M. dorsi-epitrochlearis (Macalister 1873b; Mackintosh 1875; Shepherd 1883; Windle 1888)
	Dorso-epitrochlear slip (Allen 1882)
	Epitrochlearis (Davis 1964; Böhmer et al. 2018, 2020)
M. tensor fasciae antebrachii pars cranialis*	Inferior portion of the m. latissimus dorsi (Beswick-Perrin 1871)
	Part B of the m. epitrochlearis (Hall 1926)
	Medial head of the m. epitrochlearis (Davis 1964)
	Cranial portion of the m. tensor fasciae antebrachii (Feeney 1999)
	Epitrochlearis (Moore et al. 2013)
	Second part of the m. tensor fasciae antebrachii (Yousefi et al. 2018)

Muscle name*	Homologous names used by other authors in Caniforms
M. tensor fasciae antebrachii pars caudalis*	“Large slip from dorsal portion of the panniculus” (Beswick-Perrin 1871)
	Fourth or latissimus dorsi head of the triceps (Haughton 1864)
	Second dorso-epitrochlear (Beddard 1900)
	Caput anguli of the m. triceps brachii (Hall 1926)
	Part A of the m. epitrochlearis (Hall 1926)
	Main mass of the m. epitrochlearis (Davis 1964)
	Caudal portion of the m. tensor fasciae antebrachii (Feeney 1999)
	Triceps brachii – long head (Moore et al. 2013)
	M. triceps brachii caput angulare (Ercoli et al. 2015)
	First part of the m. tensor fasciae antebrachii (Yousefi et al. 2018)
Caudal belly to the m. tensor fasciae antebrachii (Tarquini et al. 2023)	
M. anconeus lateralis*	M. anconeus externus (Macalister 1873b)
M. anconeus medialis*	M. anconeus epitrochlearis (Beswick-Perrin 1871; Shepherd 1883; Windle and Parsons 1897; Davis 1964; Smith et al. 2021)
	M. anconeus internus (Macalister 1873a; Mackintosh 1875)
	Second slip of the third portion of the triceps (Allen 1882)
	“Part of the internal head which rose from the bridge of bone over the supracondylar foramen” (Windle and Parsons 1897)
	Medial portion of the m. triceps brachii (Howard 1973)
	Short portion of the medial head of the m. triceps brachii (Leach 1977)
	Triceps brachii caput mediale accessorium (Fisher et al. 2009; Ercoli et al. 2015; Tarquini et al. 2023)
M. triceps brachii caput accessorium (Böhmer et al. 2018; 2020)	
*Names not based on the NAV (International Committee on Veterinary Gross Anatomical Nomenclature 2017).	

In contrast, other procyonids typically have only one m. coracobrachialis (Mackintosh 1875; Allen 1882; Beddard 1900; Davis 1949; Santos et al. 2010a, 2010b; Böhmer et al. 2020; Tarquini et al. 2023), which, based on its insertion, corresponds to the m. coracobrachialis brevis. However, both muscles have been assigned with different names in the literature (Table 3). The insertion of the m. coracobrachialis brevis onto the intertubercular groove, as reported by Julitz (1909), was not observed in our study. The insertion of the m. coracobrachialis longus proximal to the supracondylar foramen was also reported in one study (Beswick-Perrin 1871), while another study reported it onto the medial supracondylar crest (Julitz 1909). In non-procyonid caniforms, both muscles may be present only in the ailurid *A. fulgens* (Carlsson 1925; Fisher et al. 2009), all ursids (Shepherd 1883; Kelley 1888; Windle and Parsons 1897; Davis 1949, 1964; Annie et al. 2017), and some mustelids, with a variant configuration. Both muscles are present in *Pekania pennanti* (Leach 1977; Feeney 1999), *Martes americana* (Leach 1977), *M. foina* (Mackintosh 1875), *M. martes* (Yousefi et al. 2018), and *Martes caurina* (Hall 1926). The m. coracobrachialis longus is uniquely present in *E. barbara* (Macalister 1873b), *M. martes* (Böhmer et al. 2018), and *M. foina* (Böhmer et al. 2018). Böhmer et al. (2018) initially described the insertion of this muscle (“m. epitrochlearis”) onto the olecranon. However, in a subsequent study, the insertion was described as occurring on the middle third of the humerus (Böhmer et al. 2020), which is consistent with other authors reporting in *M. caurina* (Hall 1926)

and *M. martes* (Yousefi et al. 2018). In other mustelids, the m. coracobrachialis longus inserts proximal to the supracondylar foramen, similar to *P. flavus* (Macalister 1873b; Mackintosh 1875; Leach 1977; Feeney 1999). In *G. cuja*, only the m. coracobrachialis brevis is typically present, although it might be absent (Ercoli et al. 2015). In other mustelids, both coracobrachialis muscles are entirely absent, as observed in *Aonyx* (Macalister 1873a), *L. lutra* (Haughton 1864), *E. lutris* (Howard 1973), and *T. taxus* (Moore et al. 2013). In mephitids, both coracobrachiales muscles are also totally absent in *M. mephitis* and *S. gracilis* (Hall 1926). In the ailurid *A. fulgens* and all ursids, the m. coracobrachialis longus reaches the medial epicondyle region (Shepherd 1883; Kelley 1888; Windle and Parsons 1897; Carlsson 1925; Davis 1949, 1964; Fisher et al. 2009; Annie et al. 2017).

Comparative anatomy of the brachial muscles in caniforms

In this study, we found that the m. biceps brachii in *P. flavus* exhibited two heads, as that reported previously (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909; Davis 1964; Böhmer et al. 2020). However, it is important to note that none of these prior studies reported the absence of the caput breve as an anatomical variant. In contrast, other procyonids typically have only one caput, corresponding to the caput longum, which inserts onto the radius (Allen 1882; Windle 1888; Windle and Parsons

1897; Beddard 1900; Davis 1949; Böhmer et al. 2020; Tarquini et al. 2023). Notably, the caput breve exhibited a feebly shape in *P. lotor* (Windle and Parsons 1897), and additional insertions onto the ulna were reported in *P. lotor* (Feeney 1999), *P. cancrivorus* (Pereira et al. 2010; Santos et al. 2010b) and *N. nasua* (Santos et al. 2010a). In non-procyonid caniforms, the presence of the caput breve was only found in the ailurid *A. fulgens* (Carlsson 1925; Davis 1964; Fisher et al. 2009) and ursids of the genera *Ursus* and *Tremarctos* (Shepherd 1883; Kelley 1888; Windle and Parsons 1897; Davis 1949, 1964). However, it was absent in the ursids *A. melanoleuca* (Davis 1964) and *M. ursinus* (Annie et al. 2019), and occasionally in *A. fulgens* (Fisher et al. 2009). Based on the reports from several studies, in *A. fulgens* (Carlsson 1925; Davis 1964; Fisher et al. 2009) and *P. flavus* (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909; Davis 1964; Böhmer et al. 2020; present study), the prevalence of the absence of the caput breve was 33% (4/12 limbs) and 10% (2/20), respectively. In other caniforms, the absence of the caput breve of m. biceps brachii is the common pattern.

Our findings suggest variations regarding the origin of the m. brachialis, particularly in *P. flavus*. While previous authors (Beswick-Perrin 1871; Windle and Parsons 1897; Julitz 1909) did not report the lateral supracondylar crest as an origin in *P. flavus*, our study identified this as an additional origin. Other origins have been reported from the proximal half of the humerus (Beswick-Perrin 1871), and along the lateral surface of the humerus and humeral crest (Julitz 1909). In other procyonids, the origin and insertion patterns are similar to *P. flavus* (Mackintosh 1875; Allen 1882; Feeney 1999; Tarquini et al. 2023). However, in *P. cancrivorus* and *N. nasua* (Pereira et al. 2010; Santos et al. 2010a, 2010b), the muscle may only originate from the proximal part of the lateral surface of the humerus. Further, it may even insert onto the radial and ulnar tuberosities in both species (Santos et al. 2010a, 2010b), or only onto the radial tuberosity in *P. cancrivorus* (Pereira et al. 2010). In non-procyonid caniforms, the proximal origin was normal, while the inclusion of the lateral supracondylar crest as an origin was only reported in *Aonyx* sp. (Macalister 1873a), *G. cuja* (Ercoli et al. 2015), *E. lutris* (Howard 1973), *P. pennanti* (Feeney 1999), *A. fulgens* (Fisher et al. 2009), *M. ursinus* (Annie et al. 2019), and *A. melanoleuca* (Davis 1964). In *A. melanoleuca*, the origin from the lateral supracondylar crest was attributed to a second head (Davis 1964), similar to our observations in one specimen of *P. flavus*.

We identified discrepancies in the nomenclature used in previous studies concerning the m. triceps brachii in *P. flavus*. Beswick-Perrin (1871) did not describe all capita of the m. triceps brachii and reported that the m. anconeus is not segmented from the medial portion of the m. triceps brachii. In contrast, Julitz (1909) described four heads (capita) as anconeus muscles, corresponding to those we have identified. However, the muscle that we have designated as m. anconeus medialis was not described by Julitz (1909). Furthermore, the muscle could not be segmented from the caput mediale of the m. triceps brachii,

as described by Beswick-Perrin (1871). Additionally, another recent study found that m. anconeus lateralis was completely independent in *P. flavus* (Böhmer et al. 2020), consistent with our findings. Previous studies did not describe the caput accessorium or a homologous portion in *P. cancrivorus*, *N. nasua* and *N. narica* (Mackintosh 1875; Windle 1888). However, a recent study (Tarquini et al. 2023) described it in the former two species. In one *P. lotor* (Allen 1882), the caput accessorium was described as accessory fibers from the humeral neck, and the “fourth head” actually corresponded to m. anconeus medialis (Table 3). Böhmer et al. (2020) described the m. anconeus medialis as the caput accessorium of the m. triceps brachii, and the caput accessorium was included on the caput mediale in caniforms. However, based on their figures, the caput accessorium is separated from the caput mediale as found in all procyonids (Allen 1882; Windle and Parsons 1897; Beddard 1900; Davis 1949; Feeney 1999; Tarquini et al. 2023). Therefore, in procyonids, the m. triceps brachii typically has four capita, similar to most caniforms. Additionally, other authors found an extra caput laterale originating from the lateral supracondylar crest in *P. lotor* (Windle and Parsons 1897), corresponding to the observations from one of our *P. flavus* specimens (M1). In other caniforms, additional heads have been reported. A total of five capita were reported due to the presence of another long head, such as the “posterior caput longum” in some ursids (Davis 1949, 1964; Annie et al. 2019), the “caput magnum” in the canid *Lycan pictus* (Smith et al. 2020), and the “caput anguli” in some mustelids (Windle and Parsons 1897; Hall 1926; Ercoli et al. 2015). Other authors also reported in mustelids this additional caput as the m. tensor fasciae antebrachii, the m. epitrochlearis (Table 3), or as one part of it (Macalister 1873b; Leach 1977; Feeney 1999; Böhmer et al. 2018, 2020; Yousefi et al. 2018). In the mustelid *T. taxus*, this caput was designated as “triceps brachii-long head”, while the caput longum was termed as “triceps brachii – medial head” (Moore et al. 2013) (Table 3). Considering that these authors described the humeral capita as a single caput (“Triceps brachii – lateral head” Moore et al. 2013), which may indicate an incorrect description of the m. triceps brachii in *T. taxus*.

Concerning the m. tensor fasciae antebrachii, our study identified variations in its configuration among the examined caniforms. The muscle was found to be divided into two parts, with diverse origins for both the caudal and cranial parts. Previous descriptions did not describe this division and offered different configurations for its origins. Only in the case of *P. lotor*, the muscle was also reported as divided into two parts (Feeney 1999). In the case of *P. flavus*, the caudal part was described as a slip originating from the m. cutaneus trunci (Beswick-Perrin 1871) or the m. teres major (Julitz 1909). The cranial part was reported as originating from the m. latissimus dorsi (Beswick-Perrin 1871; Julitz 1909), corresponding with our descriptions. Moreover, in *P. flavus*, the muscle was described as only originating from the m. latissimus dorsi (Mackintosh 1875; Allen 1882; Santos et al. 2010a, 2010b; Böhmer et al. 2020), as similarly reported for other

procyonids. In *N. nasua*, the muscle also originated from the m. cutaneus trunci, while in *P. cancrivorus*, it originated from two parts of the m. latissimus dorsi (Tarquini et al. 2023). In *B. alleni*, the m. tensor fasciae antebrachii was only reported as a slender and strap-shaped muscle with no descriptions for its attachments (Beddard 1900). Typically, a unique insertion onto the olecranon was described in most procyonids (Mackintosh 1875; Allen 1882; Santos et al. 2010a; Böhmer et al. 2020), while insertions onto the olecranon and antebrachial fascia were also reported in several procyonids, including *P. flavus* (Beswick-Perrin 1871; Julitz 1909), *N. nasua* (Tarquini et al. 2023), and *P. cancrivorus* (Pereira et al. 2010; Tarquini et al. 2023). In the case of *B. alleni*, an additional muscle was found originating from the tendinous junction of the latissimus dorsi and teres major muscles, and inserting nearer to the elbow joint than to the m. tensor fasciae antebrachii (Beddard 1900). In *P. cancrivorus*, a belly was found caudal to the m. tensor fasciae antebrachii originating from m. cutaneus trunci (Tarquini et al. 2023). It was not considered a part of the m. tensor fasciae antebrachii due to the separation of both parts by fascia (Tarquini et al. 2023). However, based on the belly topology and previous dissections performed on the distribution of the radial nerve in *P. cancrivorus* specimens (Vélez García et al. 2023), this part was also innervated by the branch to the m. tensor fasciae antebrachii (Fig. S2). Therefore, the other bellies of *P. cancrivorus* and *B. alleni* could be considered homologous to the caudal part of the m. tensor fasciae antebrachii of *P. flavus* (Table 3).

In non-procyonid caniforms, the m. tensor fasciae antebrachii has also been reported as consisting of two parts in the ursid *A. melanoleuca* (Davis 1964), as well as in several mustelids, including *E. barbara* (Macalister 1873b), *M. caurina* (Hall 1926), *M. martes* (Yousefi et al. 2018), and *P. pennanti* (Feeney 1999). Notably, one part originates from m. cutaneus trunci in *E. barbara* (Macalister 1873b) and *A. melanoleuca* (Davis 1964). However, the muscle may have three portions in *U. americanus*, which originate from the m. teres major, the m. cutaneus trunci, and the caudal margin of the scapula (Shepherd 1883). In contrast, the muscles or a homologous portion were not reported in *U. maritimus* (Kelley 1888). Among mephitids, the muscle is represented by muscle fibers of the caput longum of the m. triceps brachii, which originate from the medial belly of the m. latissimus dorsi (Hall 1926). The caudal part of this muscle is only present in certain mustelids, such as *M. foina* (Böhmer et al. 2018), *M. martes* (Böhmer et al. 2018), *M. americana* (Leach 1977), *P. pennanti* (Leach 1977), and *E. lutris* (Howard 1973). This portion was considered the caput anguli of the m. triceps brachii because it originates from the caudal angle of the scapula and inserts directly onto the olecranon in some mustelids (Windle and Parsons 1897; Hall 1926; Ercoli et al. 2015) and mephitids (Hall 1926). In the mustelid *T. taxus*, this portion was designated as the caput longum of the m. triceps brachii, and the cranial part as the “epitrochlearis” originating from the latissimus dorsi and pectoralis muscles (Moore et al. 2013). Our own dissection of a *Lontra longicaudis* specimen re-

vealed that the muscle presented a similar arrangement to that described in *E. lutris* (Howard 1973) and *G. cuja* (Ercoli et al. 2015). Additionally, the muscle was innervated by the first branch of the radial nerve (Fig. S2), similar to the innervation found in procyonids (Enciso-García and Vélez-García 2022; Vélez García et al. 2023). Consequently, it is possible that the caput angulare of the m. triceps brachii, as designated by the aforementioned authors in mustelids and mephitids (Windle and Parsons 1897; Hall 1926; Ercoli et al. 2015), may indeed be the m. tensor fasciae antebrachii, or a portion thereof (Ercoli et al. 2015). In the ailurid *A. fulgens*, the muscle may exhibit two parts, with the cranial part originating from the m. latissimus dorsi and the caudal part from the m. teres major, as reported by Carlsson (1925). It may also exhibit an indivisible muscle that originates from a raphe situated between the latissimus dorsi and teres major muscles, and fuses with the m. cutaneus trunci (Fisher et al. 2009). Among canids, only the cranial part appears to be present (Feeney 1999; Vélez-García et al. 2018b; Hermanson 2020; Smith et al. 2020), with the muscle being entirely absent in *Cuon alpinus* and *Vulpes vulpes* (Böhmer et al. 2020).

In other studies of *P. flavus*, the m. anconeus medialis was referred to as anconeus epitrochlearis (Beswick-Perrin 1871; Windle and Parsons 1897). However, our study did not corroborate certain described characteristics, such as insertion onto the anconeus process and the presence of continuous fibers connecting to the m. flexor carpi ulnaris (Beswick-Perrin 1871). In previous studies about *P. flavus*, this muscle was either left unnamed (Julitz 1909) or erroneously labeled as the caput accessorium mediale of the m. triceps brachii (Böhmer et al. 2020). In *N. narica*, the anconeus muscles are united to the biceps, while the m. anconeus medialis originates from the supracondylar foramen in *N. nasua* (Mackintosh 1875; Tarquini et al. 2023). In *B. alleni*, only the muscle itself was reported (Beddard 1900). In other studies, the m. anconeus medialis or a homologous portion was not described in *P. cancrivorus* (Windle 1888; Pereira et al. 2010; Santos et al. 2010b) and *N. nasua* (Santos et al. 2010a). However, recent findings in both species (Tarquini et al. 2023; Vélez García et al. 2023) indicate similar attachments to those observed in *P. flavus*. Furthermore, this muscle is innervated by the ulnar nerve (Vélez García et al. 2023), corresponding to innervation patterns observed in *P. flavus* (Windle and Parsons 1897; Enciso-García and Vélez-García 2022) and *P. lotor* (Windle and Parsons 1897). This corroborates that the muscle is derived from the m. flexor carpi ulnaris rather than the m. triceps brachii (Diogo and Abdala 2010; Vélez García et al. 2023). It is important to highlight that the muscle is constantly present in most caniform families, with exceptions observed in the Canidae and Ursidae families. Nevertheless, it may be fused to the caput mediale of the m. triceps brachii in the ursid *A. melanoleuca* (Davis 1964), or it may be vestigial in *U. maritimus* (Kelley 1888) and the canid *C. thous* (Vélez-García et al. 2018a) (Table 4). Additionally, although in the canid *C. alpinus*, Böhmer et al. (2020) reported this muscle, their figures may indicate a vestigial

Table 4. Tendency of presence and absence of the most variant muscles in the shoulder and brachial regions in caniform families.

Muscle	Canidae	Procyonidae	Mustelidae	Mephitidae	Ailuridae	Ursidae
Teres minor	Present	Present	Variable	Absent or vestigial	Present	Present
Coracobrachialis brevis	Present	Present	Variable	Absent	Present	Present
Coracobrachialis longus	Present	Absent except <i>P. flavus</i>	Variable	Absent	Present	Present
Biceps brachii caput breve	Absent	Absent except <i>P. flavus</i>	Absent	Absent	Variable	Present in <i>Ursus</i> and <i>Tremarctus</i> Absent in <i>Ailuropoda</i> and <i>Melursus</i>
Triceps brachii caput longum accessorium	Absent	Absent	Absent	Absent	Absent	Present
Tensor fasciae antebrachii pars cranialis	Present	Present	Variable	Present	Variable	Present
Tensor fasciae antebrachii pars caudalis	Absent	Present except <i>Nasua</i>	Present	Present	Present	Present except <i>Melursus</i>
Anconeus medialis	Absent	Present	Present	Present	Present	Absent or vestigial

behavior as similarly found in *C. thous* (Vélez-García et al. 2018a).

Functional and evolutionary analysis of the intrinsic shoulder and brachial muscles within the suborder Caniformia

The shoulder movements play a pivotal role in the arboreal and prehensile habits of *P. flavus*, requiring high abilities and precise control to move among the tree branches. Although the extrinsic muscles contribute to shoulder support, the intrinsic muscles execute more precise shoulder joint movements. Further, the scapular muscles are responsible for the lateral and medial rotation of the humerus when the limb is free. These muscles also stabilize the shoulder joint when the limb is in contact with a substrate. These functions are not unique to *P. flavus* but are also observed in other caniforms (Fisher et al. 2009; Moore et al. 2013; Souza-Junior et al. 2018; Vélez-García et al. 2018b; Smith et al. 2020). The m. teres major in *P. flavus* plays a critical role in flexing the shoulder, working synergistically with the m. latissimus dorsi (Vélez-García and Miglino 2023). It should facilitate the medial rotation of the humerus when the limb is not resting on a substrate. These actions are essential for *P. flavus* to propel its body trunk cranially during vertical tree climbing or when is navigating between branches. Additionally, the presence of a m. coracobrachialis longus with a more distal insertion onto the humerus increases adduction strength in the shoulder (Kardong 2012; Monroy-Cendales et al. 2020). This capability allows *P. flavus* to keep vertical suspension on tree trunks while climbing. Therefore, the m. coracobrachialis longus provides greater support when medially pulling the thoracic limb with more strength, while contracting the digital flexor muscles to grip the branches. In this case, taxa with this muscle (*P. flavus*, some mustelids, *A. fulgens*, and ursids) must have advantages over other specimens when climbing trees.

The m. biceps brachii in *P. flavus* delivers similar functions to those of other caniforms, including elbow flexion, shoulder extension, and cranial and medial stabilization of the shoulder joint (Moore et al. 2013; Souza-Junior et al. 2018; Vélez et al. 2018; Smith et al. 2020). Furthermore, the larger origin of the m. brachialis that reaches the lateral supracondylar crest, as observed in most arctoids, enhances elbow flexion. Elbow flexion is also supported by the brachioradialis and extensor carpi radialis muscles, mainly when the limb already exhibits some degree of flexion (Vélez-García et al. 2022; Vélez-García et al. 2022). The m. biceps brachii was previously considered a supinator in functional studies of the thoracic limb muscles and bones in carnivorans without caput breve (Taylor 1982; Feeney 1999), recent studies have not described this function (Fisher et al. 2009; Ercoli et al. 2015; Taverner et al. 2018; Böhmer et al. 2019; Tarquini et al. 2023). In mammals where the m. biceps brachii has the caput breve, the muscle indeed contributes to supination (Taylor 1978; Monroy-Cendales et al. 2020, 2023; Standing 2020; Richards et al. 2023). Thus, the caput breve likely supports supination alongside the brachioradialis and supinator muscles in *P. flavus* and other species, such as *A. fulgens* and ursids of the genera *Ursus* and *Tremarctos*. Even the greater development of the m. biceps brachii may also account for the larger size of the radial tuberosity in *P. flavus* compared to other procyonids (Tarquini et al. 2019). In addition, *P. flavus* exhibits more branches from the brachial artery supplying this muscle than cursorial caniforms as *C. thous* (Vélez et al. 2018) and *C. lupus familiaris* (Hermanson et al. 2020). Therefore, this suggests increased activity of the m. biceps brachii in *P. flavus*.

The presence of m. coracobrachialis longus and the caput breve of m. biceps brachii in arctoid species may be phylogenetically associated with a common ancestor with proficient arboreal and prehensile abilities. Among procyonids, both muscle bellies are preserved in *P. flavus*, whereas the muscle probably disappeared in the common ancestor of other procyonid genera. Notably, the genus *Bassaricyon*, which shares similar locomotor

skills with *P. flavus*, is the only genus showing such abilities. Therefore, although the presence of both muscle bellies is not essential for arboreal and prehensile abilities, its absence may represent an intra- and interspecific disadvantage. Moreover, the presence of both muscles likely contribute to better anatomical adaptations in most *P. flavus* specimens. However, the *B. alleni* and *P. flavus* specimens lacking these bellies may exhibit reduced supination and elbow flexion forces compared to other specimens, implying decreased abilities. Thus, further myological studies in *B. alleni* are required, as only one specimen has been studied to date (Beddard 1900), and their absence may represent an anatomical variant, similar to that observed in one *P. flavus* specimen (M2).

Elbow extension in caniforms is primarily performed by the caudal group of brachium muscles, including the m. triceps brachii with its four heads, m. tensor fasciae antebrachii, and m. anconeus lateralis (Souza-Junior et al. 2018; Vélez et al. 2018). Depending on the species, elbow extension may also involve an additional caput longum of the m. triceps brachii, a duplicated m. tensor fasciae antebrachii, and a m. anconeus medialis. In *P. flavus*, this extension is primarily achieved by the latter two muscular features. The caudal part of the m. tensor fasciae antebrachii is consistently present and well-developed in mustelids and mephitids, where it supports both shoulder and elbow flexion due to its direct origin from the scapula. In contrast, it contributes to shoulder flexion with less force in other arctoids due to its origin from soft tissues. Conversely, the cranial part of the m. tensor fasciae antebrachii only supports elbow extension and is invariably present in canids, procyonids and ursids. Therefore, the caudal part of the m. tensor fasciae antebrachii has phylogenetic significance within the infraorder Arctoidea, while the cranial part is characteristic of the suborder Caniformia.

The presence of m. anconeus medialis appears consistent in species within the infraorder Arctoidea, with the exception of ursids, where the muscle may appear in a vestigial shape or fused with the caput mediale of the m. triceps brachii (Kelley 1888; Davis 1964). This variation may be associated with the reduction (*Ailuropoda* and *Tremarctos*) or total absence (*Ursus*) of the supracondylar foramen in ursids (Davis 1964; Meloro and de Oliveira 2019; Jiangzuo and Flynn 2020). In canids, which lack this foramen entirely, the muscle is also completely absent or occasionally appearing in a vestigial manner (Vélez-García et al. 2018a). Consequently, in non-ursid arctoids, this muscle not only extends the elbow joint but also serves to medially stabilize it. This adaptation is particularly advantageous for smaller species that perform faster movements, requiring enhanced elbow stabilization. Meanwhile, the m. anconeus lateralis is responsible for extension and lateral stabilization of the elbow joint, with variations in force due to a more proximal origin. Consequently, in *P. flavus*, both anconeus muscles appear to have evolved to increase elbow joint stabilization when the antebrachial muscles are working on arboreal and prehensile activities.

Functional and phylogenetic implications of the clusters based on the presence and absence of the intrinsic shoulder and brachial muscles in Caniforms

The presence of the caput breve of m. biceps brachii, m. coracobrachialis longus and m. anconeus medialis is not exclusive to caniforms but extends to other mammalian taxa, including monotremes (Gambaryan et al. 2015), marsupials (Diogo et al. 2016; Richards et al. 2023), anteaters (Taylor 1978; Vélez-García et al. 2020; Vélez-García et al. 2021), rodents (Böhmer et al. 2020), and non-human primates (Diogo and Wood 2012; Monroy-Cendales et al. 2020, 2023). However, the presence or absence of these muscles also varies within species of the same clade. For instance, marsupials like *Vombatus* (common wombat) and *Didelphis* (opossum), with fossorial and arboreal habits, respectively, do not have m. coracobrachialis longus (Diogo et al. 2016; Richards et al. 2023), while the arboreal marsupial *Phascolarctos cinereus* (koala) has it (Richards et al. 2023). In the case of semiarboreal anteaters, the genus *Tamandua* and the terrestrial genus *Myrmecophaga* feature only m. coracobrachialis longus, while the arboreal *Cyclopes* lacks any coracobrachialis muscle (Taylor 1978; Vélez-García et al. 2020). Similarly, saltatorial and arboreal rodents like *Meriones unguiculatus* and *Sciurus vulgaris*, respectively, preserve the caput breve of the m. biceps brachii, while the terrestrial rodent *Rattus norvegicus* does not possess it (Böhmer et al. 2020). Therefore, the presence or absence of these intrinsic shoulder and brachial muscles can suggest a phylogenetic significance in mammals (Diogo and Abdala 2010).

In carnivorans within the suborder Caniformia, the presence or absence of intrinsic shoulder and brachial muscles holds both phylogenetic and functional implications. Notably, canids form a distinct group independent of arctoids, indicating the divergence of these species with fewer muscle bellies to provide medial support to the shoulder and elbow. This divergence may be attributed to the fact that canids predominantly require shoulder and elbow movements in a sagittal plane (Feeney 1999; Souza-Junior et al. 2018), setting them apart from arctoids (Davis 1964). An exception is found in *C. alpinus*, which is located outside the canid cluster. However, if the m. anconeus medialis is considered absent due to its vestigial shape, this species would fit within the canid cluster. This vestigial presence of the muscle in canids might be traced back to a shared phylogenetic link with the common ancestor of caniforms, suggesting that medial muscular support for the elbow through the m. anconeus medialis is dispensable in canids.

Another cluster featuring fewer muscles is the fifth cluster, including mephitids, the mustelid *T. taxus* and mustelids of the subfamily Lutrinae. These species lack the coracobrachialis muscles and, in some cases, even the m. teres minor in mephitids and lutrines. Notably, one limb of *Aonyx* sp. is grouped in the fourth cluster due

to the presence of *m. coracobrachialis brevis*. Therefore, if the tendency of lutrines had been taken into account, this limb would have been classified into the fifth cluster. This indicates that these species require less intrinsic muscular support for the shoulder. Thus, the coracobrachiales muscles may appear in a vestigial shape or fuse with another muscle. The absence of these muscles in mephitids could be a feature that emerged during their divergence from the common ancestor of ailurids and mustelids, while in lutrines, it might have occurred during their subsequent divergence within the family Mustelidae. The consistent presence of the *m. teres minor* in *T. taxus* indicates a phylogenetic connection with non-lutrine mustelids.

In the case of *P. flavus*, the intrinsic shoulder and brachial muscles consistently maintain a phylogenetic association within the infraorder Arctoidea, primarily with the ailurid *A. fulgens* and the ursids of the genera *Ursus* and *Tremarctos* (Cluster 3). This implies that these species have the highest level of muscular support for shoulder and elbow movements, including enhanced supination compared to other specimens and species. In the first and fourth clusters, support for elbow flexion and supination is diminished due to the absence of the *caput breve* of the *m. biceps brachii*. Within the first group, the enhanced medial support for the shoulder results from the presence of *m. coracobrachialis longus*. Consequently, some *P. flavus* specimens have reduced intrinsic muscle support for the shoulder and elbow, similar to other procyonids, mustelids, and the ursids *A. melanoleuca* and *M. ursinus*. Nevertheless, as previously discussed, this may indicate functional disadvantages for specimens preserving all these muscles. Additionally, individual specimens may exhibit dominance of one thoracic limb, as observed in Pfs4, where the right limb belongs to the first cluster, while the left limb is grouped within the third cluster.

In summary, *P. flavus* stands as the sole extant musteloid species potentially preserving the intrinsic shoulder and brachial muscles traced back to the common ancestor of arctoids. Furthermore, the presence of all these muscles in caniforms appears to provide both intra- and interspecific functional advantages. Consequently, *P. flavus* specimens equipped with all intrinsic shoulder and brachial muscles may exhibit greater strength and enhanced abilities in the shoulder and elbow when compared to other specimens or different species.

Despite our findings, it is important to acknowledge certain limitations in this study. Many authors did not provide detailed anatomical descriptions and often analyzed few specimens. Additionally, some characteristics were assigned based on family tendencies introducing potential biases into the statistical analysis. Therefore, to improve future investigations, it is imperative to conduct detailed anatomical studies including a broader range of arctoid species, using a larger sample size. Finally, although this study focused on a specific group of muscles in caniforms, future comparative analyses applying similar statistical methods can extend to diverse muscle groups and species.

Acknowledgements

We extend our deepest appreciation to Michael A. Kaminski (King Fahd University of Petroleum and Minerals, Editor-in-Chief, Micropaleontology) for his prompt and diligent review of our manuscript, which played a pivotal role in publishing our research. We are also grateful to the anonymous reviewers for their constructive feedback. Their meticulous assessment to maintain the high standards of this journal helped us to improve the quality of our research. This research was funded by the Research and Scientific Development Office (Oficina de investigaciones y desarrollo científico) of the Universidad del Tolima with the award number 160130517.

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Supplementary Material 1

Figure S1

Authors: Vélez-García JF, Carrión Blanco DA, Moreno Gómez G, San Martín Cañas S (2023)

Data type: .jpg

Explanation note: Medial view of a right thoracic limb of *Potos flavus*. B, m. brachialis; BB, m. biceps brachii; BBa, accessory belly; BBb, caput breve; BBl, caput longum; Mc, musculocutaneous nerve.

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Link: <https://doi.org/vz.73.e102645.suppl1>

Supplementary Material 2

Figure S2

Authors: Vélez-García JF, Carrión Blanco DA, Moreno Gómez G, San Martín Cañas S (2023)

Data type: .jpg

Explanation note: Branch of the radial nerve to the tensor fascia antebrachii in *Procyon cancrivorus* and *Lontra longicaudis*. Medial views of a right thoracic limb of *P. cancrivorus* (**a**, **b**); medial view of a left thoracic limb of *L. longicaudis* (**c**). R, radial nerve; R') branch to the m. tensor fasciae antebrachii, TFA) m. tensor fasciae antebrachii; TFACd, pars caudalis. TFACr, pars cranialis.

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Link: <https://doi.org/vz.73.e102645.suppl2>

Supplementary Material 3

Figure S3

Authors: Vélez-García JF, Carrión Blanco DA, Moreno Gómez G, San Martín Cañas S (2023)

Data type: .pdf

Explanation note: Complete figure 10 with all specimens.

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