

The Hindlimb Myology of *Milvago Chimango* (Polyborinae, Falconidae)

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ABSTRACT We describe the hindlimb myology of *Milvago chimango*. This member of the Falconidae: Polyborinae is a generalist and opportunist that can jump and run down prey on the ground, unlike Falconinae that hunt birds in flight and kill them by striking with its talons. Due to differences in the locomotion habits between the subfamilies, we hypothesized differences in their hindlimb myology. Gross dissections showed that the myology of *M. chimango* is concordant with that described of other falconids, except for the following differences: the *m. flexor cruris medialis* has one belly with a longitudinal division; the *m. iliotibialis lateralis* does not have a connection with the *m. iliofibularis*; the *m. fibularis longus* is strongly aponeurotic; the *m. tibialis cranialis* lacks an accessory tendons and the *m. flexor hallucis longus* has one place of origin, instead of two. The presence of the *m. flexor cruris lateralis* can be distinguished as it has been described absent for the Falconidae. We associated its presence with the predominant terrestrial habit of the *M. chimango*. Each muscle dissected was weighed and the relationship between flexors and extensors at each joint was assessed. The extensor muscles predominated in all joints in *M. chimango*. Among the flexors, the *m. flexor hallucis longus* was the heaviest, which could be related to the importance of the use of its talons to obtain food. *J. Morphol.* 274:1191–1201, 2013. © 2013 Wiley Periodicals, Inc.

KEY WORDS: muscle; bird of prey; terrestrial locomotion

INTRODUCTION

Falconidae are diurnal birds of prey well-known for their hunting skills in flight. However, foraging habits within the family are diverse (Griffiths, 1999). Two subfamilies can be recognized within the Falconidae: Falconinae (Leach, 1920) and Polyborinae Bonaparte 1837 (Friedmann, 1950; White et al., 1994; Griffiths, 1999). The former, consisting of the genus *Falco* among others, feed on other birds, which they hunt in flight and kill by striking with their talons and beak (Cade, and Digby, 1982; Sustaita, 2008; Sustaita and Hertel, 2010). In contrast to the rather uniform hunting strategies in Falconinae, the Polyborinae show diverse hunting strategies (Fuchs et al., 2012).

Some genera like *Daptrius* and *Ibicter* are omnivorous and arboreal, while others, for example, *Milvago*, *Caracara*, and *Phalcoboenus*, feed on a general diet (invertebrates, vertebrates, and carrion; Fuchs et al., 2012). These last three genera are largely terrestrial and ambulatorial with distinctive morphological features like relatively long legs and short toes (Friedmann, 1950; Griffiths, 1999). *Milvago chimango* (vernacular name: Chimango caracara) is a Polyborinae with a wide distribution in South America (Canevari et al., 1991; White et al., 1994). This species spends much time on the ground searching for food, where it tends to run and jump to pursue its prey (White et al., 1994; Biondi et al., 2005). While the hindlimb morphology in the Falconinae has been fairly well-studied, especially its myology, that of the Polyborinae has received relatively less attention. Garrod (1873) studied only *Caracara plancus* and other Falconinae. Hudson (1937, 1948) studied several species of the genus *Falco* and Berger (1956a) dissected a specimen of *Polihierax semitorquatus*. Jollie (1977a,b) studied, among other features, the myology of the hindlimb of *Milvago chimachima*, *Daptrius ater*, and *Polyborus cherway* (for a complete list of the specimens of Falconiformes and the body parts dissected by the different authors see Jollie, 1977a,b).

Current studies on the gross anatomy of the hindlimb muscles of birds are scarce (e.g., Verstappen et al., 1998; Gangl et al., 2004; Picasso, 2010) even though this information is necessary to carry out comparative myological studies, as well as morphofunctional and ecomorphological analyses (Bock, 1994; Liem et al., 2001). Among birds, feeding and locomotion are very

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diverse activities that are associated with the differences in the morphology of the body regions involved (Ericson, 2008). Given the differences in locomotor habits of the Polyborinae compared to the Falconidae, we expect differences in their myology. The objective of this work is to study the myology of the hindlimb of *M. chimango* to compare it with the available information of others Falconid birds.

MATERIALS AND METHODS

Eighteen specimens of *M. chimango* were dissected. In 11 specimens both limbs were used while in the others just one limb was dissected. The study was performed at the División Paleontología Vertebrados, Museo de La Plata from July 2011 to December 2012. The material was obtained as part of the project "Programa de Control de Aves en Rellenos Sanitarios y

Áreas Aledañas (ProCoA)" in the province of Buenos Aires, Argentina. This research complied with protocols approved by the animal care committee and adhered to the legal requirements of Argentina. Muscles were fixed by immersion in a 4% formaldehyde solution for 3 days and preserved in a 70% alcohol solution. Each muscle was identified and carefully removed from its origin and insertion site. Subsequently, the attachment areas were drawn into a figure of the bones. The anatomical nomenclature follows Baumel et al. (1993).

Photographs were taken with a Nikon D-40 digital camera. The descriptions follow the order of appearance from superficial to deep muscles. The mass of each muscle (one limb considered) was measured to the nearest 0.01 g with a digital scale and presented in Table 1 together with its percentage with respect to the body mass. The smallest muscles *iliofemoralis externus*, *iliofemoralis internus*, *obturatorius lateralis* were not considered. The main role of muscles during terrestrial locomotion follows the works of Jacobson and Hollyday (1982), Gatesy (1999), and Smith et al. (2006). We compared the flexors and extensors of *M. chimango* at the different joints (Table 2). Finally, we plotted the myological traits in the different groups commonly

TABLE 1. Table showing the list of muscles dissected, their abbreviation, the mean weight (g), and standard error, their percentage with respect to the average body mass (280 g) and their main muscle action according to Goslow (1967), Jacobson and Hollyday (1982) and Gatesy (1999)

Muscle	Abbreviation	Mean weight	Standard errors	%	Main muscle action
<i>M. iliotibialis cranialis</i>	IC	0.449	0.023	0.160	Hip flexion
<i>M. iliotibialis lateralis</i>	IL	0.548	0.037	0.196	Hip flexion and extension of TBT (weak)
<i>M. iliofibularis</i>	IF	0.809	0.044	0.289	Flexion of TBT
<i>M. flexor cruris lateralis</i>	FCL	0.477	0.026	0.170	Hip extension and flexion of the TBT (weak)
<i>M. flexor cruris medialis</i>	FCM	0.383	0.017	0.137	Hip extension and flexion of the TBT (weak)
<i>M. iliotrochantericus caudalis</i>	ITC	0.636	0.027	0.227	Hip flexion
<i>M. iliotrochantericus cranialis + medialis</i>	ITCR + M	0.139	0.008	0.050	Hip flexion
<i>M. obturatorius medialis</i>	OM	0.107	0.008	0.038	Uncertain
<i>M. ischiofemoralis</i>	ISF	0.208	0.027	0.074	Hip extension
<i>M. caudofemoralis</i>	CF	0.191	0.013	0.068	Hip extension
<i>M. ambiens</i>	A	0.044	0.007	0.016	Aid the MFPDII
<i>M. pubo-ischio-femoralis</i>	PIF	1.258	0.048	0.449	Hip extension
<i>M. femorotibialis lateralis + intermedius</i>	FTL + I	1.172	0.043	0.419	Extension of TBT
<i>M. femorotibialis medialis</i>	FTM	0.201	0.011	0.072	Extension of TBT
<i>M. fibularis longus</i>	FL	0.405	0.038	0.145	Weak flexion of digit III and extension of TMT
<i>M. fibularis brevis</i>	FB	0.218	0.102	0.078	Inward rotation of TMT
<i>M. tibialis cranialis</i>	TC	0.884	0.042	0.316	Flexion of TMT
<i>M. gastrocnemius</i>	G	1.555	0.076	0.555	Extension of TMT
<i>M. extensor digitorum longus</i>	EDL	0.252	0.023	0.090	Extension of digits II–IV
<i>M. popliteus</i>	PO	0.020	0.003	0.007	Uncertain
<i>M. plantaris</i>	PI	0.288	0.014	0.103	Extension of TMT
<i>M. flexor perforans et perforatus digiti II</i>	FPPDII	0.261	0.020	0.093	Flexion of digit II
<i>M. flexor perforans et perforatus digiti III</i>	FPPDIII	0.290	0.018	0.104	Flexion of digit III
<i>M. flexor perforatus digiti II</i>	FPDII	0.114	0.018	0.041	Flexion and adduction of digit II
<i>M. flexor perforatus digiti III</i>	FPDIII	0.262	0.021	0.094	Flexion of digit III
<i>M. flexor perforatus digiti IV</i>	FPDIV	0.285	0.020	0.102	Flexion of digit IV
<i>M. flexor digitorum longus</i>	FDL	0.359	0.021	0.128	Flexion of digit II–IV and aid flexion of digit I
<i>M. flexor hallucis longus</i>	FHL	1.130	0.051	0.404	Flexion of digits I–IV
<i>M. extensor hallucis longus</i>	EHL	0.069	0.013	0.025	Extension of digit I
<i>M. flexor hallucis brevis</i>	FHB	0.061	0.009	0.022	Flexion of digit I
<i>M. abductor digiti II</i>	AbDII	0.080	0.000	0.029	Abduction of digit II
<i>M. abductor digiti IV</i>	AbDIV	0.028	0.005	0.010	Abduction of digit IV
<i>M. adductor digiti IV</i>	AdDIV	0.010	0.000	0.004	Adduction of digit IV

The values correspond just to one limb. TBT: tibiotarsus, TMT: tarsometatarsus. The following muscles are not included in the table: iliofemoralis externus (IFE), iliofemoralis internus (IFI), obturatorius lateralis (OL), obturatorius medialis (OM).

TABLE 2. Percentage of the muscles of the hindlimb with respect to the bodymass grouped in extensors and flexors at the different joints

M. chimango	Extensors	Flexors
Pelvic girdle	1.40	0.66
Knee	0.40	0.28
Ankle	0.8	0.31
Digits	0.10	0.98
Total	2.70	2.23

known as “birds of prey” on a phylogenetic diagram. The cladogram was constructed with recent phylogenetic analyses for Falconidae (Fuchs et al., 2012), Accipitridae (Griffiths et al., 2007), and birds as a whole (Hackett et al., 2008).

RESULTS

A total of 37 muscles were found for each bird, of which 17 muscles belong to the *pelvis* and *femur* (thigh), 14 correspond to the *tibiotarsus* (shank) and six correspond to the *tarsometatarsus*.

Muscles on the Pelvis and Femur

M. iliotibialis cranialis (IC). Origin: fleshy in the antero-ventral end of the *fossa iliaca dorsalis* (Fig. 2). The origin of IC covers the anterior portion of the *m. iliotrochantericus cranialis*. It is strap-like and fleshy, located on the cranio-medial

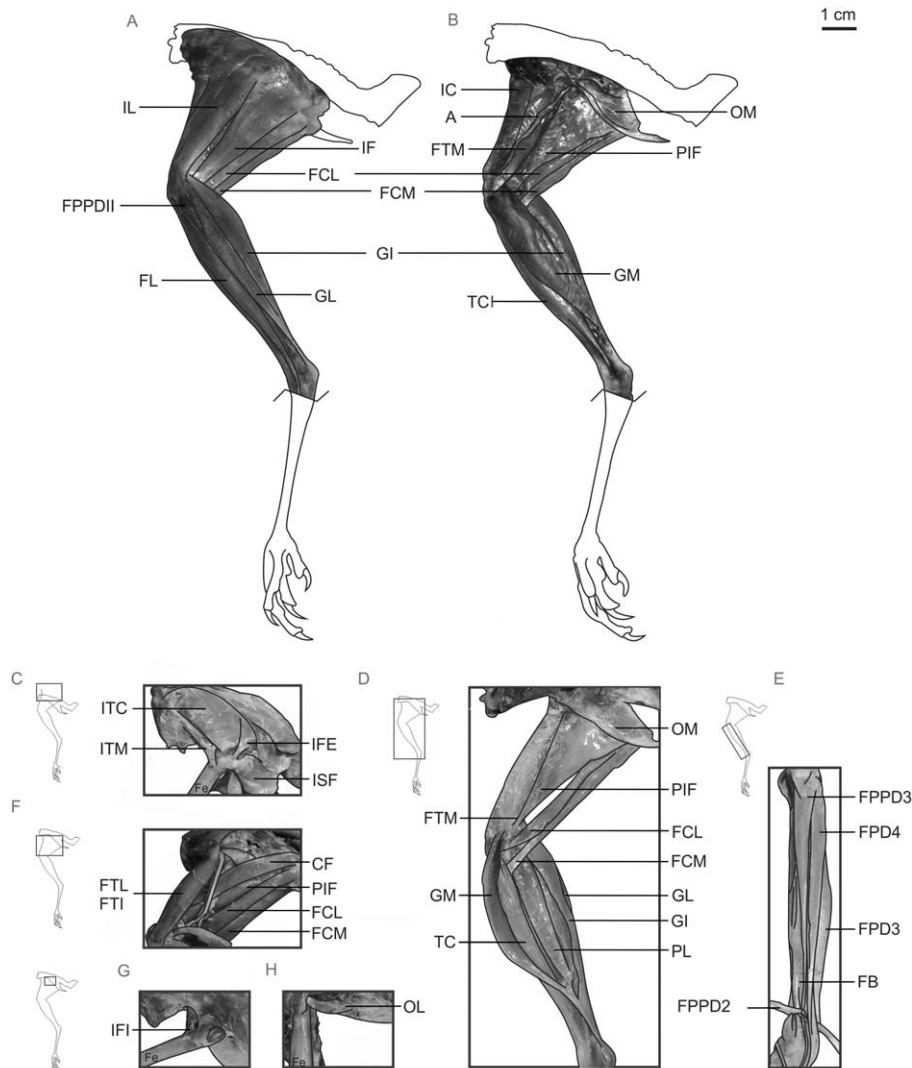


Fig. 1. Photographs with the outline of the muscles drawn of the hindlimb muscles of *M. chimango*. (A) Lateral view and (B) medial view showing superficial muscles. (C) lateral view of the pelvis; (D) medial view of the femur and tibiotarsus; (E) lateral view of the tibiotarsus; (F) lateral view of the femur; (G, H) lateroproximal view of the femur. (C–H) show deep muscles. A, ambiens; CF, caudofemoralis; Fe, femur; FB, fibularis brevis; FCL, flexor cruris lateralis; FCM, flexor cruris medialis; FL, fibularis longus; FPPDIII, flexor perforans digiti III; FPPDIV, flexor perforans digiti IV; FPPDII, flexor perforans et perforatus digiti II; FPPDIII, flexor perforans et perforatus digiti III; FTL + FTI, femorotibialis lateralis + femorotibialis intermedius; FTM, femorotibialis medialis; GI, gastrocnemius intermedius; GL, gastrocnemius lateralis; GM, gastrocnemius medialis; IC, iliotibialis cranialis; IF, iliofibularis; IFE, iliofemoralis externus; IFI, iliofemoralis internus; IL, iliotibialis lateralis; ISF, ischiofemoralis; ITC, iliotrochantericus caudalis; ITM, iliotrochantericus medialis; OL, obturatorius lateralis; OM, obturatorius medialis; PIF, pubo-ischio-femoralis; PL, plantaris; TC, tibialis cranialis.

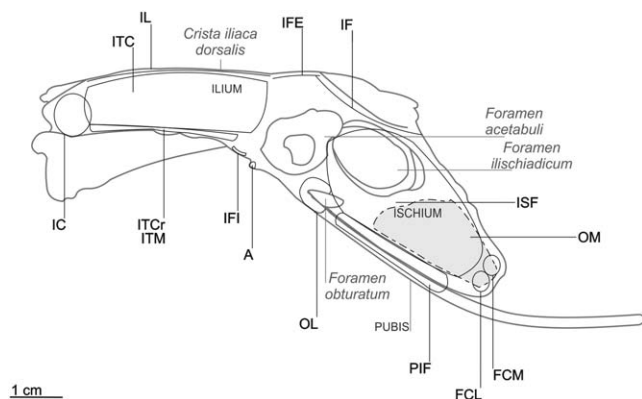


Fig. 2. Sketch of the lateral view of the pelvis of *M. chimango* with the origins of the muscles drawn. The dotted line (the origin of the OM) is located in the medial aspect of the pelvis. A, ambiens; FCL, flexor cruris lateralis; FCM, flexor cruris medialis; IC, iliotrochantericus cranialis; IF, iliofibularis; IFE, iliofemoralis externus; IFI, iliofemoralis internus; IL, iliotibialis lateralis; ISF, ischiofemoralis; ITC, iliotrochantericus caudalis; ITCr + ITM, iliotrochantericus cranialis + iliotrochantericus medialis; OL, obturatorius lateralis; OM, obturatorius medialis; PIF, pubo-ischio-femoralis.

edge of the *femur*, covering the cranial portion of the *m. iliotibialis lateralis* (Fig. 1A,B).

Insertion: fleshy on the ligamentum patellaris and the crista cnemialis cranilis.

M. iliotibialis lateralis (IL). It is mainly aponeurotic, the fleshy portion restricted to the middle region of the muscle. It presents the preacetabular and acetabular portion and lacks the postacetabular one (Fig. 1A).

Origin: aponeurotic, along the *crista iliaca dorsalis* (Fig. 2), from its cranial end to the vertex.

Insertion: aponeurotic on the patella. It also inserts by a tendon on the edge of the proximal end of the *tibiotarsus*, this tendon arises from the outer edge of the muscle (Fig. 3H).

M. iliofibularis (IF). It is a well-developed muscle with a wide fleshy portion of triangular shape (Fig. 1A).

Origin: fleshy, both preacetabular and acetabular along the *crista dorsolateralis ilii* (Fig. 2).

Insertion: by a tendon in the *tuberculum m. iliofibularis* of the *fibulae* (Fig. 3E,G) after crossing the *ansa iliofibularis*, located between the *pars lateralis* and *intermedia* of the *m. gastrocnemius*.

M. iliofemoralis externus (IFE). It is a small muscle compared to the rest of the other muscles (Fig. 1C).

Origin: fleshy, in the *sulcus antitrochantericus* of the *ilium*. (Fig. 2).

Insertion: by a wide tendon on the lateral surface of the *trochanter femoris*. (Fig. 3C).

M. iliofemoralis internus (IFI). It is one of the smallest muscles (Fig. 1G).

Origin: fleshy on the ventral edge of the *ischion* (Fig. 2), anterior to *tuberculum preacetabulare*.

Insertion: by a small tendon in the first proximal third of the *femur* (Fig. 3D) on the craniomedial edge.

M. iliotrochantericus caudalis (ITC). It is a large fleshy muscle that covers two thirds of the *m. iliotrochantericus cranialis* and *m. iliotrochantericus medius* and completely covers the *m. iliofemoralis externus* (Fig. 1C).

Origin: fleshy along the whole *crista iliaca dorsalis* until the *vertex* and the *ala iliaca* (Fig. 2).

Insertion: by a short tendon in the *trochanter femoris* (Fig. 3C). The *femur*, at this place, shows the impression of all the iliotrochantericus: *impressiones iliotrochanterici*.

M. iliotrochantericus cranialis (ITCr) and M. iliotrochantericus medius (ITM). These muscles are fused, however, in one specimen they were found to be independent (Fig. 1C).

Origin: fleshy, in the ventral edge of the *fossa iliaca dorsalis* (Fig. 2).

Insertion: by a short tendon in the proximal region of the *corpus femoralis*, below the *trochanter femoris* (Fig. 3C).

M. ambiens (A). Origin: by a short tendon on the *tuberculum preacetabulare* (Fig. 2). It has a fleshy fusiform belly and from the distal third of the *femur* has a tendon that crosses the patella towards the lateral surface of the *tibiotarsus* (Fig. 1B).

Insertion: on the *m. flexor perforatus digiti IV*.

M. flexor cruris lateralis (FCL). This muscle only presents the *pars pelvica*. It is a fleshy strap-shaped muscle, partially covered by the *m. flexor cruris medialis* and partially covering the *m. puboischiofemoralis* (Fig. 1A,B,D,F).

Origin: fleshy in the posterior limit of the *processus terminalis ischii* (Fig. 2).

Insertion: by a short tendon in the proximo-medial region of the *tibiotarsus* (Fig. 3F), posterior to the ligament *impressio ligamentum collaterale medialis* that joins the *femur* with the *tibiotarsus*.

M. flexor cruris medialis (FCM). It is a fleshy elongated muscle, tendinous in its final portion. Towards the middle of the belly a division can be observed although the two different portions cannot be distinguished (Fig. 1A,B,D,F).

Origin: fleshy on the posterior end of the *ischion* and *pubis* (Fig. 2). It partially covers the *m. flexor cruris lateralis*.

Insertion: by a small tendon in the proximal portion of the medial surface of the *tibiotarsus* (Fig. 3F), below the *impressio ligamentum collaterale medialis* and *m. flexor cruris lateralis*. This tendon inserts between the *m. gastrocnemius pars medialis* and *lateralis*.

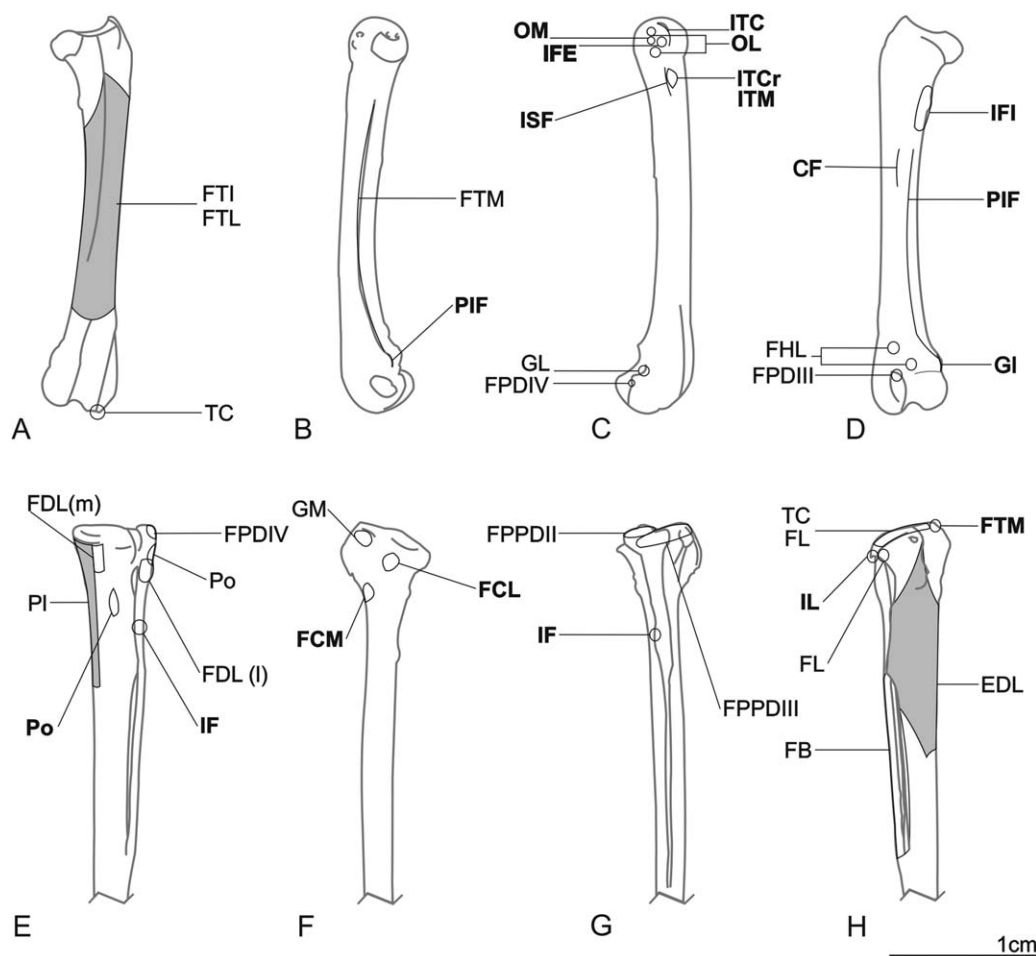


Fig. 3. Sketch of the femur (A–D) and tibiotarsus (E–H) of *M. chimango*; from left to right: anterior, medial, lateral and posterior view. Insertions are indicated by bolt print and the origins without bold. CF, caudofemoralis; EDL, extensor digitorum longus; FB, fibularis brevis; FCL, flexor cruris lateralis; FCM, flexor cruris medialis; FDL(l), flexor digitorum longus (lateralis); FDL(m), flexor digitorum longus (medialis); FHL, flexor hallucis longus; FL, fibularis longus; FPDIII, flexor perforatus digiti III; FPDIV, flexor perforatus digiti IV; FPPDII, flexor perforans et perforatus digiti II; FPPDIII, flexor perforans et perforatus digiti III; FTL + FTI, femorotibialis lateralis + femorotibialis intermedius; FTM, femorotibialis medialis; GI, gastrocnemius intermedius; GL, gastrocnemius lateralis; GM, gastrocnemius medialis; IF, iliofibularis; IFE, iliufemoralis externus; IFI, iliufemoralis internus IL, iliotibialis lateralis; ISF, ischiofemoralis; ITC, iliotrochantericus caudalis; MITCr + ITM, iliotrochantericus cranialis + iliotrochantericus medialis; OL, obturatorius lateralis; OM, obturatorius medialis; PIF, puboischio-femoralis; PI, plantaris; Po, popliteus; TC, tibialis cranialis.

M. ischiofemoralis (ISF). Origin: fleshy on the posterior edge of the *ischion* (Fig. 2) (where the *m. caudofemoralis* passes), below the *crista dorsolateralis illi*.

Insertion: by a tendon in the proximal portion of the lateral surface of the *femur* (Fig. 3C), in the *trochanter femoris*, near to the insertion of the *m. iliotrochantericus caudalis* (Fig. 1C).

M. puboischiofemoralis (PIF). It has the two typical *pars*: *lateralis* and *medialis* (Fig. 1B,D,F).

Origin: fleshy along the ventral edge of the *ala ischii* (Fig. 2), below the posterior half of the *foramen ilioschiadicum*.

Insertion: fleshy, common for both parts on the caudal aspect of the *corpus femoris* (Fig. 3B,D).

M. obturatorius lateralis (OL). It is a small muscle compared to the other muscles, entirely fleshy (Fig. 1H).

Origin: beneath the *foramen obturatorium* (Fig. 2).

Insertion: by a tendon in the lateral aspect of the proximal region of the *femur* (Fig. 3C), on the *impressiones obturatoriae*, below the tendon of the *m. obturatorius medialis* (H).

M. obturatorius medialis (OM). It is a fan-shaped muscle located in the medial side of the *pelvis* (Fig. 1B,D).

Origin: fleshy along the medial side of the *ala ischii* and the anterior half of the *pubis* (Fig. 2).

Insertion: by two tendons that go through the *foramen obturatorum*, both inserted on the *trochanter femoris* (Fig. 3C).

M. caudofemoralis (CF). The *pars caudalis* is the only *pars* present and is a strap-like fleshy muscle that covers the first half of the *m. ischiofemorialis* and *m. puboischiofemorialis* (Fig. 1F).

Origin: by a small tendon on the aponeurosis *cruciata* of the *m. depressor caudalis* at the base of the *pygostylus*, exceeding the posterior edge of the *crista dorsolateralis illi*.

Insertion: by a short and wide tendon, on the proximal third on the posterior surface of the *femur* (Fig. 3D).

M. femorotibialis lateralis and m. femorotibialis intermedius (FTL and FTI). Origin: these two muscles are fused along their contiguous borders, except proximally where the *femorotibialis lateralis* is originated by a small tendon on the shaft of the *femur*, immediately below the region of the trochanter, whereas the *femorotibialis intermedius* has a fleshy origin. Both occupy the whole cranial and lateral surface of the shaft of the *femur* (Figs. 1F and 3A).

Insertion: on the patella by a wide aponeurosis.

M. femorotibialis medialis (FTM). Origin: fleshy in the medial part of the two distal thirds of the shaft of the *femur* (Figs. 1B,D, and 3B).

Insertion: by a tendon on the *tibiotarsus*, on the limit between the articular surface and the *crista cnemialis cranialis* (Fig. 3H).

Muscles that Originate in the Distal Region of the Femur and the Proximal Region of the Tibiotarsus

M. fibularis longus (FL). It is the most superficial muscle of the cranial surface of the *tibiotarsus* (Fig. 1A).

Origin: fleshy along the shaft of the *tibiotarsus* by a wide aponeurosis between the *cristae cnemialis cranialis* and *lateralis* (Fig. 3H). In the distal end of the *tibiotarsus* the muscle runs towards the lateral surface of that bone where it bifurcates into two tendons.

Insertion: one of those tendons inserts in the tibial cartilage and the other one extends laterally and connects with the tendon of the *m. flexor perforatus digiti III*.

M. fibularis brevis (FB). This muscle is thin, fleshy, and strap-like and goes along the fibula (Fig. 1E).

Origin: fleshy from the *crista fibularis* (Fig. 3H) along the shaft of the fibula and part of the *tibiotarsus*.

Insertion: by a tendon to the *tuberculum m. fibularis brevis* of the *tarsometatarsus* (Fig. 4B).

M. tibialis cranialis (TC). Large muscle with two differentiated portions, the *caput tibiale*, is the largest and most superficial, and the *caput*

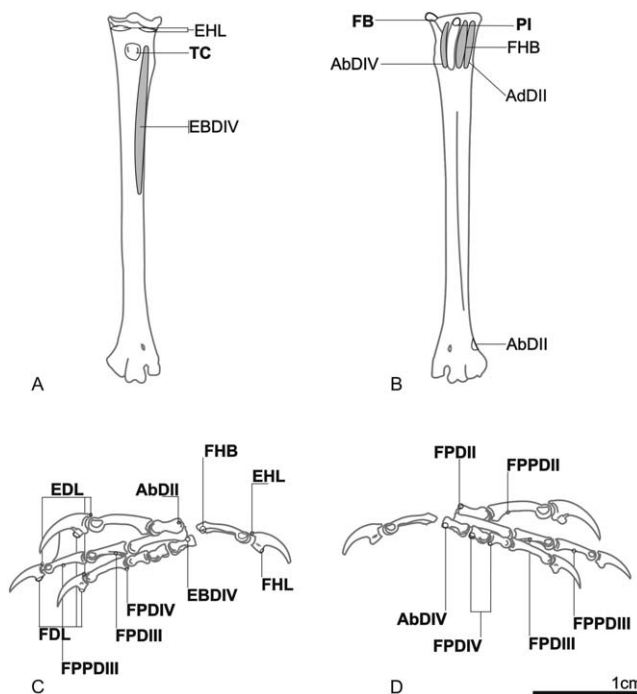


Fig. 4. Sketch of the tarsometatarsus in anterior (A) and posterior (B) view; and phalanges in medial (C) and lateral (D) view of *M. chimango*. AbDII, abductor digitii II; AbDIV, abductor digitii IV; AdDII, adductor digitii II; EBDIV, extensor brevis digitii IV; EHL, extensor hallucis longus; FB, fibularis brevis; FDL, flexor digitorum longus; FHB, flexor hallucis brevis; FHL, flexor hallucis longus; FPDII, flexor perforatus digiti II; FPPDIII, flexor perforatus digiti III; FPPDII, flexor perforans et perforatus digiti II; FPPDIII, flexor perforans et perforatus digiti III; PI, plantaris; TC, tibialis cranialis.

femorale, which is smaller and covered by the former (Fig. 1B,D).

Origin: the *caput tibiale* has a fleshy origin between the *cristae cnemialis cranialis* and *lateralis* (Fig. 4A), whereas the *caput femorale* originates by a small tendon in the *condylus lateralis* of the *femur*, in the *fovea tendineus m. tibialis cranialis* (Fig. 3A). Both *caput* fuse and originate a tendon that inserts into the proximal region of the *tarsometatarsus*, in the *tuberositas m. tibialis cranialis*, after passing under the *retinaculum extensorium tibiotarsi*.

M. extensor digitorum longus (EDL). It is a thin, strap-like muscle, and is the deepest one of the cranial surface of the *tibiotarsus*.

Origin: fleshy from the cranial proximal edge of the *tibiotarsus* extending to the beginning of the fibula and running along the cranial surface of the *corpus tibiotarsi* (Fig. 3H), where it is attached to the proximal half of that bone. As a tendon, this muscle goes beneath the *pons supratendineus* and along the anterior surface of the *tarsometatarsus*. It divides into two branches, lateral and medial; the lateral branch divides again into two smaller tendons which extend towards digits III and IV.

The medial branch also divides and sends one smaller tendon to digit II and the other to digit III. The tendon of digit II is the widest and both tendons of digit III fuses at the point of insertion.

Insertion: in the extensor tubercle of digits II, III, and IV (Fig. 4C).

M. gastrocnemius. It is a large muscle and the most superficial of the caudal surface of the *tibiotarsus*. It consists of three fleshy parts of fusiform shape: *pars lateralis*, *medialis*, and *intermedia* (Fig. 1A,B,D).

Origin: of *pars lateralis* (GL) (Fig. 3C) by a short tendon on the lateral condyle of the *femur*, in a small pit. The *pars intermedia* (GI) (Fig. 3D) is the smallest *pars* whose fleshy origin is in the *epicondylus medialis*. The *pars medialis* (GM) is the most developed *pars*, its origin is fleshy along the edge of the *crista cnemialis cranialis* and the *facies* of the *gastrocnemius* (Fig. 3F). It also extends along the medial edge of the proximal region of the *tibiotarsus*.

Insertion: the three portions converge in a common tendon that runs along the *tibiotarsus* to the cartilage tibialis.

M. plantaris (Pl). It is an elongated, well-developed muscle (Fig. 1D).

Origin: fleshy from the posterior edge of the *facies articularis medialis* of the *tibiotarsus* (Fig. 3E), running along the *tibiotarsus* attached to the shaft.

Insertion: by a tendon in the proximal end of the *hypotarsus* after passing the *cartilage tibialis* (Fig. 4B).

M. flexor perforans et perforatus digiti II (FPPDII). It is the most superficial muscle of the lateral surface of the *tibiotarsus* (Fig. 1A,E).

Origin: it has two places of origin, one aponeurotic on the *crista cnemialis lateralis*, which strongly attaches to the FPPDIII, and the other, fleshy on the proximo-posterior region of the *fibula* (Fig. 3G).

Insertion: by a tendon that crosses the *cartilago tibialis*, extends on the posterior surface of the *tarsometatarsus* and inserts into the lateral surface of the second phalanx of digit II (Fig. 4D).

M. flexor perforans et perforatus digiti III (FPPDIII). Origin: fleshy between the caput *fibulae* and the *crista cnemialis lateralis* of the *tibiotarsus* (Figs. 1E and 3G).

Insertion: by a tendon in the distal end of the third phalanx of digit III (Fig. 4C,D).

M. flexor perforatus digiti II (FPDII). It is the smallest and thinnest muscle of the *perforatus*.

Origin: fleshy on the intercondylar region of the *femur*, becomes a tendon at half of the *tibiotarsus* and runs through the *tibiotarsus-tarsometatarsus* joint.

Insertion: by this tendon on the first phalanx of digit II on its proximo-lateral end (Fig. 4D).

M. flexor perforatus digiti III (FPDIII). It is the largest *perforatus* muscle and has two portions of different size (Fig. 1E).

Origin: the largest belly originates by a short tendon on the *fossa poplitea* (Fig. 3D), the smallest one originated by a long tendon on the *condylus femoralis lateralis*. This long tendon has a small belly.

Insertion: each portion possesses a tendon that fuses and runs along the *tarsometatarsus* and splits into two onto the first phalanx of digit III, each smaller tendon inserts in the second phalanx (Fig. 4C,D). In two specimens, this muscle was originated from just one tendon instead of two.

M. flexor perforatus digiti IV (FPDIV). It is a thin, strap-like muscle (Fig. 1E).

Origin: fleshy from the intercondylar region of the *femur* and *caput fibulae* (Fig. 3C,E). In the distal third of the *tibiotarsus* this muscle becomes a tendon.

Insertion: the tendon goes to digit IV and trifurcates at the first phalanx; each smaller tendon inserts on the first, second and third phalanx (Fig. 4C,D).

M. flexor hallucis longus (FHL). It is a large muscle with a great fusiform belly.

Origin: on the *fossa poplitea*, in the intercondylar region of the *femur*. It has one origin whose most superficial portion is tendinous and its deepest portion is fleshy (Fig. 3D).

Insertion: by a tendon that is ossified along the shaft of the *tarsometatarsus*. This tendon inserts in the flexor tubercle of the ungual phalanx of digit I (Fig. 4C) and is connected to the *m. flexor digitorum longus* by a tendinous *vinculum*.

M. flexor digitorum longus (FDL). Origin: with two heads, a lateral head and a medial one. The lateral arises from the *caput fibulae* (Fig. 3E) covering part of the *m. popliteus*. The origin of the medial head arises below the edge of the *facies articularis medialis* (Fig. 3E), medial to the *tuberositas popliteus*. These two heads are joined in the first quarter of the *tarsometatarsus*.

Insertion: by a tendon that is ossified along the posterior surface of the *tarsometatarsus*; at the distal end of this bone it divides into three branches that run towards digit II, III, and IV and insert in the flexor tubercle of the ungual phalanx of each digit (Fig. 4C).

M. popliteus (Po). It is a small muscle located on the caudal surface of the *tibiotarsus*.

Origin: fleshy on the proximal end of the *tibiotarsus* (Fig. 3E).

Insertion: fleshy on the *tuberositas popliteus* of the *fibula* and barely extending distally to this feature on the *corpus fibulae* (Fig. 3E).

Short Muscles of the Tarsometatarsus

M. extensor hallucis longus (EHL). Origin: with two fleshy bellies (Fig. 4A), the first one

originates in the *fossa infracotylaris dorsalis*, below the edge of the articular facet, lateral to the *tuberositas m. tibialis cranialis*. The second belly, the smallest one, has its origin below the articular facet, although medial to the *tuberositas*. The tendon of the *m. tibialis cranialis* is between the two parts, which remain independent until the middle of the *tibiotarsus* where they fuse and originate as a single tendon.

Insertion: in the extensor tubercle of the ungual phalanx in the hallux (Fig. 4C).

M. flexor hallucis brevis (FHB). Origin: fleshy in the *fossa parahypotarsalis medialis* (Fig. 4B), the belly is short and the tendon begins in the *hypotarsus*, running through the lateral surface of the *tarsometatarsus*.

Insertion: in the most proximal portion of phalanx 1 of the hallux (Fig. 4C).

M. abductor digiti II (AbDII). Origin: fleshy, in the proximal portion of *trochlea metatarsi I* (Fig. 4B).

Insertion: by a short tendon in the medial surface of the phalanx 1 of digit II (Fig. 4C).

M. adductor digiti II (AddII). It is a very small muscle with a small fleshy portion and a long tendon.

Origin: fleshy on the proximal posterior surface of the *tarsometatarsus*, medial to the *hypotarsus* (Fig. 4E).

Insertion: the tendon runs along the bone and inserts on the medial surface of the first phalanx of digit II.

M. extensor brevis digiti IV (EBDIV). Origin: fleshy in the *sulcus extensorius* (Fig. 4A), the first quarter of the muscle is fleshy, then the tendon arises, travels distally along the *tarsometatarsus* and through the *foramen vasculare distale*.

Insertion: by a tendon in the first phalanx of digit IV, in the proximo-medial region (Fig. 4C).

M. abductor digiti IV (AbDIV). Origin: fleshy, on the lateral edge of the *fossa* lateral to the *hypotarsus* (Fig. 4B).

Insertion: by a tendon on the lateral surface of the first phalanx of digit IV (Fig. 4D).

Finally, the following muscles were not found in *M. chimango*: *m. lumbricalis*, *m. adductor digitii IV*, *m. extensor brevis digitii III*, and *m. extensor proprius digitii III*.

Muscular Mass

The average weight of the specimens was 280 g (Standard Error (SE): 12.65, $n = 6$) and the total muscle mass of the hindlimb (considering both limbs) represented 9.42% of the body mass (Table 1). Of the 33 weighed muscles, 26 had masses of up to 0.2% and only seven muscles exceeded this value, approaching or exceeding 0.4% of the body mass.

The *gastrocnemius* had the greatest mass, while among the flexors it was found that the *m. flexor hallucis longus* was the heaviest.

In general terms, the extension of the hip, the knee, and the ankle exceeded the flexion while in the digits this relationship is opposite in all the species analyzed (Table 2).

DISCUSSION

The hindlimb myology of the family Falconidae, according to Hudson (1948), is characterized by the fusion of the *mm. iliotrochantericus medialis* and *cranialis*, the *m. iliotibialis lateralis* without the *pars postacetabularis*, a well developed *m. plantaris* and the absence of the *m. flexor cruris lateralis*. Although the hindlimb myology of *M. chimango* is concordant with that described for other falconids, it showed some differences and distinctive features. The *m. iliotibialis lateralis* has no connection with the *m. iliofibularis*, unlike Hudson's (1937, 1948) descriptions in which *Falco* has a ventral tendinous connection between these two muscles. The *m. flexor cruris lateralis* is present in this species whereas it is absent in all the falconids studied by Hudson (1937, 1948) and Jollie (1977a,b). Regarding the *m. flexor cruris medialis*, in falconids, it typically has two separated bellies (Hudson, 1937, 1948), whereas in *M. chimango*, it is divided longitudinally along its only belly. In the species studied by Hudson (1937, 1948) and Jollie (1977a,b), the tendon of the *m. ambiens* passes laterally to the insertion of the *m. iliofibularis* (except in *Polihierax* where it passes medially; Jollie, 1977a,b). As for Chimango Caracara, this muscle is not close enough to the *m. iliofibularis*, so this classification could not be made.

The absence of the *m. flexor cruris lateralis* has been an established feature characteristic of the Falconidae (Hudson, 1937, 1948; George and Berger, 1966). However, its presence in the Chimango Caracara demonstrates the need to analyze the variation of the muscles among species to establish whether a particular trait is typical of a certain taxonomic level. The presence of this muscle can be related to the predominant terrestrial locomotion that characterizes this bird. In this locomotor habit this muscle is an important hip extensor during the stance phase (when the limb contacts the ground) and also prevents hyperextension of the knee (Jacobson and Hollyday, 1982; Gatesy, 1999). In birds the presence of this muscle is fairly constant although with variations (e.g., presence/absence of the *pars accesoria*; George and Berger, 1966). The *m. flexor cruris lateralis* is present and well developed in basal birds like palaeoganthous birds and galliforme birds (George and Berger, 1966). They are characterized by predominantly or exclusively terrestrial locomotion. In addition to the Falconidae, the absence of this muscle is known in Pandionidae, Accipitridae, Strigidae, and Fregata (Hudson, 1937; George and Berger, 1966), groups that do not usually make

use of terrestrial locomotion. In the Tyrannid family, Mckittrick (1986) observed that this muscle is present in those members with terrestrial habits, whereas it was absent in those with aerial habits, similar to the Falconidae.

Regarding the muscles of the *tibiotarsus*, the origin of the *m. fibularis longus* is strongly aponeurotic, located between both *cristae* of the *tibiotarsus* and closely attached to the *m. tibialis cranialis*, whereas in *Falco* the origin is tendinous on the *fibula* and adjacent muscles (Hudson, 1937, 1948). Jollie (1977a,b) mentioned that *Milvago chimachima* and other studied Polyborinae present the *m. fibularis longus* with muscular fibers covering part of this muscle. Unfortunately, the author does not give more detail in the descriptions or in the figures to allow a better understanding. The anatomy of the flexor muscles of the digits (*mm. flexores perforatii* II, III, and IV, *flexores perforans et perforatii* II and III) is similar to that studied in other falcons by Hudson (1937, 1948) and Jollie (1977a,b). Some variations were observed at an individual level in two specimens: the *m. flexor perforatus digiti* III showed two bellies, whereas in the others three bellies were found. Also, the *m. iliotrochanterichus cranialis* and *m. iliotrochanterichus medialis* were independent of each other in one specimen. Intraspecific variation is common in avian myology (Berger, 1956b; Berman et al., 1990), giving reason to study the myology using the largest number of individuals possible in order to avoid misleading interpretations (Berger, 1956b). The *mm. extensor brevis digiti* III, *lumbricalis* and *extensor proprius digiti* III were not found in the *M. chimango*. These were described by Hudson (1937, 1948) and Jollie (1977a,b) in other Falconidae, although the *m. extensor proprius digiti* III was rudimentary in *Falco* (Hudson, 1948).

In raptors in general, the *mm. tibialis cranialis*, *flexor digitorum longus* and *flexor hallucis longus* are the muscles primarily responsible for talon closure (Goslow, 1967; Ward et al., 2002; Sustaita, 2008). In *M. chimango* these muscles are present and show few differences from *Falco*. The *m. tibialis cranialis* does not have accessory tendons like in *Falco* (Hudson, 1948). The *m. flexor hallucis longus* only has one place of origin whereas *Falco* has two (Hudson, 1948); but in both *Falco* and *M. chimango*, the tendons of the *mm. flexor digitorum longus* and *flexor hallucis longus* are ossified to the same extent.

The relationship between the hindlimb muscular mass and the body mass provides information of their potential activity (Hartman, 1961). The percentage of hindlimb mass of *M. chimango* (9.42%) was similar to that found in other Polyborinae like *Milvago chimachima* (11–12%; one specimen used in this calculation), *Caracara cheriway* (12.9%) and also to the Falconinae *Falco peregrinus* 12% (Hartman, 1961).

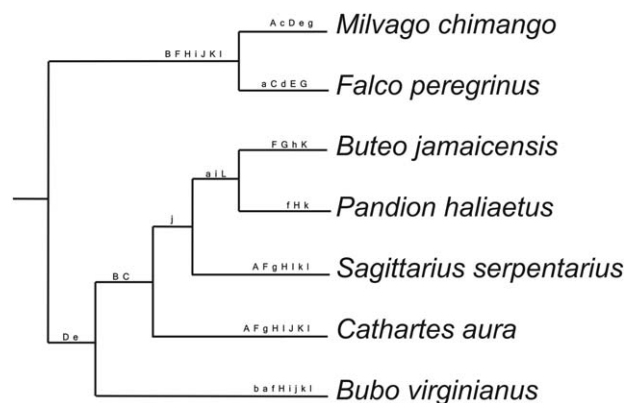


Fig. 5. Phylogenetic diagram plotting the status of myological features. 1. Presence (A) or absence (a) of the *m. flexor cruris lateralis*; 2. Presence (B) or absence (b) of the *m. ambiens*; 3. Tendon of insertion of *m. ambiens* adjacent (C) or distant (c) of tendon of the *m. iliofibularis*; 4. Bellies of *m. flexor cruris medialis*: one (D) or two (d); 5. With (E) or without (e) accessory tendons in the insertion of the *m. tibialis cranialis*; 6. Presence (F) or absence (f) of the *m. fibularis longus*; 7. The *m. fibularis longus* with fleshy (G) or aponeurotic (g) origin; 8. The *m. gastrocnemius* with one (H) or two (h) tendons of insertion; 9. The origin of the *m. gastrocnemius medialis* is extended (I) or not extended (i) towards the knee; 10. Presence (J) or absence (j) of the *m. plantaris*; 11. The *m. flexor perforatus digiti* IV with one (K) or two (k) heads of origin; 12. Origin of the *m. abductor digiti* II: on the proximal half (L) or distal half (l) of the tarsometatarsus.

Extension and flexion are the main movements of leg segments during locomotion in birds. Regarding the proportions of the muscles that produce them, it can be noted that extensor muscles predominate over flexors in the hip, the knee, and the ankle joints. This predominance may be due to its main role as an antigravity support and as stabilizers during locomotion; as it occurs in other birds with terrestrial habits (Verstappen et al., 1998; Smith et al., 2006). Instead, flexors prevail over extensors in the digits. These muscles are responsible for grasping movements which require more strength (Raikow, 1985).

The *m. flexor hallucis longus*, the only flexor with a percentage above the average, plays an important role in falcons and hawks because it is responsible for talon closure together with the *mm. tibialis cranialis* and *flexor digitorum longus* (Ward et al., 2002). Although *M. chimango* does not use the same hunting techniques as falcons, it would be interesting to study in detail the movements of the hallux in a comparative context to associate the degree of *m. flexor hallucis longus* development with a particular function.

As a result of plotting the morphological traits on the phylogenetic diagram (Fig. 5) it can be seen that *m. ambiens* is only absent in *B. virginianus* although its functional implications are uncertain (Gatesy, 1999). Also, there is no information on what implication the variation may have on the topographic relation with the tendon of insertion

of the *m. iliofibularis*. Only in Falconinae the *m. flexor cruris medialis* forms two bellies and the *m. tibialis cranialis* has some accessory insertion tendons. The *m. flexor cruris lateralis* is present in those groups with a predominant terrestrial locomotion (i.e., *Sagittarius*, *Milvago* and, to a lesser extent, *Cathartes*) unlike birds with a predominant aerial locomotion (i.e., *Buteo*, *Pandion*, and *Bubo*). According to Jollie (1977a,b), the reduction of the *m. fibularis longus* is associated to a greater capacity of clenching, so its presence and its high degree of development could also be associated with the terrestrial habit. The presence of the *m. plantaris* occurs in Falconidae and Cathartidae, whereas it is missing in the other species of the cladogram. This well-developed muscle characteristic of the Falconidae family (Hudson, 1937, 1948). There is a trend towards a more proximally extended origin of the *m. abductor digiti II* in the *tarsometatarsus* within the clade formed by Strigidae to Accipitridae. This muscle is a little extended in the former and more extended in *Cathartes* (Hudson, 1937). *Sagittarius* does not follow this trend because in this species the *m. abductor digiti II* is shorter in the previous species. Lastly, *Pandion* has the origin at half length of the *tarsometatarsus* and *Buteo* has the most proximal origin (Hudson, 1937, 1948). Two heads of origin of the *m. flexor perforatus digiti IV* increases the force to flex the digit IV. This occurs in those groups that rely on their toes to hunt: *Bubo*, a facultative zygodactyl bird of prey with all its toes of relative similar size (Fowler et al., 2009) and *Pandion*, which preys on fish. Meanwhile, Accipitridae with its hypertrophied digit I and II (Fowler et al., 2009) do not use digit IV with such importance and *Cathartes* does not use its toes for feeding. Finally, in Falconidae, the hunting style relies more on hitting the prey and using its beak (Sustaita, 2008; Sustaita and Hertel, 2010).

In conclusion, the hindlimb muscles of the Polyborinae *M. chimango* are very similar to those of the Falconinae. A peculiar feature is the presence of the *m. flexor cruris lateralis*, which is absent in *Falco* as well as in other birds of prey like the Accipitridae. These birds in general do not use terrestrial locomotion like the Chimango Caracara and the presence of this muscle, together with other features like long legs, may contribute to a more effective locomotion on the ground. Further studies focused on comparative muscle architecture and biomechanics (kinetics and kinematics of terrestrial locomotion) between *M. chimango*, other Polyborinae and Falconinae will extend and enrich the present findings.

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