

Long-legged caracaras: terrestrial habitat and hindlimb morphology

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Abstract

The hindlimb of the Polyborinae has always been characterized as long when it was compared with other diurnal raptors; however, no empirical work has been done to support such a traditional well-known fact. The objective of this work is to analyze the femur, tibiotarsus and tarsometatarsus of this group to corroborate whether this assumption has a significant statistical support. The proportions of these bones were analyzed with a one-way Kruskal–Wallis test and Dunn's test as *post hoc* comparisons. The allometric relationships between the long bones and body mass or the total length of the hindlimb were carried out with the reduced major axis method. In addition, the osteological study is complemented with a myological dissection of the hindlimb of *Milvago chimachima* and *Caracara plancus*. The three long bones of the limb of Polyborinae show significant differences with those from Falconinae. The presence of a long tarsometatarsus is a typical feature of terrestrial birds, it produces an increase in length stride allowing an effective locomotion on land. Among the myological differences, the most prominent are the presence of the *musculus flexor cruris lateralis* (absent in other Falconidae) and a well-developed *musculus fibularis longus*. These osseous and myological features are related to the terrestrial locomotion present in this subfamily.

Introduction

Avian hindlimb morphology shows great variability regarding bone length and muscle development, which has been related to habitat use and ecology (Engels, 1938; Berger, 1952; Ryländer, 1980; Niemi, 1985; Moreno & Carrascal, 1993a,b; Gatesy & Middleton, 1997; Barbosa & Moreno, 1999; Zeffer, Johansson & Marmebro, 2003; Kaboli *et al.*, 2007; Stoessel, Kilbourne & Fischer, 2013). For instance, a short tarsometatarsus is found in species that exploit vertical surfaces (Carrascal, Moreno & Tellería, 1990 and literature cited therein), whereas a long tarsometatarsus is commonly associated with birds that walk or run (Alexander, 1983; Kirkwood *et al.*, 1989; Bennett, 1996; Picasso, 2012). The hindlimb muscles also show variation related to different life styles, for example in waders (Order Charadriiformes) changes in stride frequency are correlated with changes in the origin and extension of muscles and cross-sectional physiological area of certain muscles (Barbosa & Moreno, 1999).

Hindlimb morphological diversity has been studied within and between different groups of birds (e.g. Engels, 1938; Norberg, 1979; Carrascal *et al.*, 1990; Gatesy & Middleton, 1997; Barbosa & Moreno, 1999; Zeffer *et al.*, 2003).

Notwithstanding, this issue has not been comparatively investigated among the subfamilies of Falconidae, an interesting family due to its high diversity of trophic habits and hunting techniques.

Three subfamilies are recognized within Falconidae (Fuchs, Johnson & Mindell, 2012), Herpetherinae (Laughing and Forest falcons), Falconinae (Falcons) and Polyborinae (Caracaras). Two main features make Falcons, genus *Falco*, the most recognized species within the Falconidae: their striking hunting technique and their cosmopolitan distribution, which make them more accessible to study. They hunt in flight by a strike with their talons and kill aided by their beaks (Cade, 1982; Sustaita, 2008; Sustaita & Hertel, 2010). The laughing and forest falcons (*Herpetheres* and *Micrastur*) are two genera endemic of the Neotropic. *Herpetheres cachinnans* has a peculiar mode of killing their prey hitting its foot against their prey on the ground, making a distinctive sound – GRIN (Global Raptor Information Network), 2015. The *Micrastur* genus comprises seven species whose general biology is little known. *Micrastur semitorquatus* and *Mic. ruficollis* are the two species with the most information available. For example, it is known that both hunt from perches and *Mic. ruficollis* also runs after small prey flushed by army ants

(White, Olsen & Kiff, 1994; GRIN, 2015). The third subfamily is Polyborinae, also with a Neotropical distribution and represented by 11 species of the genera *Caracara*, *Milvago*, *Phalcooboenus*, *Daptrius*, *Ibicter* and *Spizapteryx* (International Ornithological Committee 2011). In contrast to the other subfamilies, they are generalists and opportunists that include in their diet a high diversity of vertebrates and, invertebrates, fruits and also carrion (Biondi, Bó & Favero, 2005; Bó, Baladrón & Biondi, 2007; Sazima, 2007), though they scavenge carrion less than originally thought (see Friedmann, 1950; Brown & Amadon, 1968). The Polyborinae also have diverse feeding strategies (White *et al.*, 1994; Biondi *et al.*, 2005; Bó *et al.*, 2007; Fuchs *et al.*, 2012) that include tick picking, social foraging, eating garbage, searching for prey on trees or walking on the ground (Brown & Amadon, 1968; White *et al.*, 1994; Ferguson-Lees & Christie, 2001; Sazima, 2007). *Caracara plancus*, *Milvago chimachima*, *Mil. chimango* and *Phalcooboenus* spp. spend most of their time walking on the ground searching for food (Brown & Amadon, 1968; Vuilleumier, 1970; White *et al.*, 1994; Ferguson-Lees & Christie, 2001; GRIN, 2015). Instead, *Daptrius ater* and *Ibicter americanus* are more arboreal, the former with a generalist diet (invertebrates, vertebrates, fruits and carrion) and the latter with a specialized diet that consists of wasp grubs (Brown & Amadon, 1968).

In the more terrestrial species of the Falconidae, several morphological features like the presence of long hindlimbs have been noted (Friedmann, 1950; Vuilleumier, 1970). These two works have established the presence of a longer tarsometatarsus in the Polyborinae than Falconinae; although these statements lacked empirical evidence. Only Vuilleumier (1970) measured the tarsus of the Polyborinae, but did not conduct statistical analyses supporting these observations. Additionally, hindlimb myology of the Polyborinae has been poorly studied compared with that of Falconinae. This may be due, as already mentioned above, to their different and relatively less appealing hunting strategies as well as their more restricted geographic distribution. In fact, all the bibliography dealing with these aspects belong to North American or European authors (Hudson, 1937, 1948; Goslow, 1972; Jollie, 1976, 1977a,b,c), where no Polyborinae is distributed, except *Caracara cheriway* that reaches the South of the United States. This is how it came to be thought that the *flexor cruris lateralis* muscle was absent in all the Falconidae, mainly encouraged by the classic works of Hudson (1937, 1948). However, these studies did not include members of Polyborinae. Garrod (1873) and Jollie (1976, 1977a,b,c) included Polyborine specimens but there was no mention of the presence of this muscle. In a recent description on the hindlimb myology of the caracara *Mil. chimango*, this muscle was found and was associated to a predominant terrestrial locomotion (Mosto, Carril & Picasso, 2013).

The present work aimed to (1) analyze the quantitative differences in the osseous hindlimb of Polyborinae with respect to Herpetotherinae and Falconinae and (2) characterize the differences in the myology of the hindlimb of *Mil. chimachima* and *C. plancus*, poorly studied in previous works with respect to the Falconinae.

Materials and methods

Specimens and bone measures

The proximodistal length of the femur, tibiotarsus and tarsometatarsus of several specimens of Polyborinae ($n = 40$), Falconinae ($n = 45$) and Herpetotherinae ($n = 10$) was gathered by measuring museum specimens with a digital caliper of 300 and 0.01 mm precision, combined with measurements from the literature (Supporting Information Table S1). The skeletons are housed at the Museo de La Plata, Buenos Aires, Argentina, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires, Argentina and Fundación Felix de Azara, Buenos Aires, Argentina. An extinct species, *Falco*



Figure 1 Comparison of the legs in the three subfamilies, (a) *Falco femoralis*, (b) *F. sparverius*, (c) *Caracara plancus*, (d) *Milvago chimachima*, (e) *Herpetotheres cachinnans* and (f) *Micrastur semitorquatus*. Scale bar: 1 cm.

kurochkini (Suárez & Olson, 2001) was considered in this study. This particular specimen was due to its similar features (long limbs) with that of the caracaras (Suárez & Olson, 2001). Published measurements were included from Olson (1976), Hopson (2001), Noriega, Carlini & Tonni (2001), Suárez & Olson (2001) and the web site Royal BC museum (www.royalbcmuseum.bc.ca/Natural_History).

We relativized each bone (FM, TBT and TMT) with their correspondent total leg length with the objective to compare them between Falconidae subfamilies. Each of these proportions was analyzed with one-way Kruskal–Wallis test, with subfamily as a variable. *Post hoc* comparisons were performed using Dunn's test.

Furthermore, to assess whether there is an allometric trend for each bone, a scaling relationship between bone length with body mass and total leg length was explored. This was carried out with the reduced major axis method (RMA, model II of

regression) by analyzing the log10 transformed values of FE, TBT and TMT against body mass or the total length of the hindlimb. This method is more appropriate to describe morphological relationships because it considers that the error variances for x and y are equal (Ebert & Russell, 1994). Expected coefficients under isometry are equal to 1 for comparison between bone lengths, and to 0.33 for comparisons between body mass with bones length. Data of body mass were obtained from Dunning (2008) and the total length of the hindlimb was calculated by adding the lengths of the femur, tibiotarsus and tarsometatarsus.

To analyze how each bone varied regarding function of the total hindlimb length (independent of body mass, which can also be used to estimate the contribution of each bone to total hindlimb length), the residuals of the aforementioned regressions were compared to the residuals from the scaling of the total length of the hindlimb against body mass. As the values

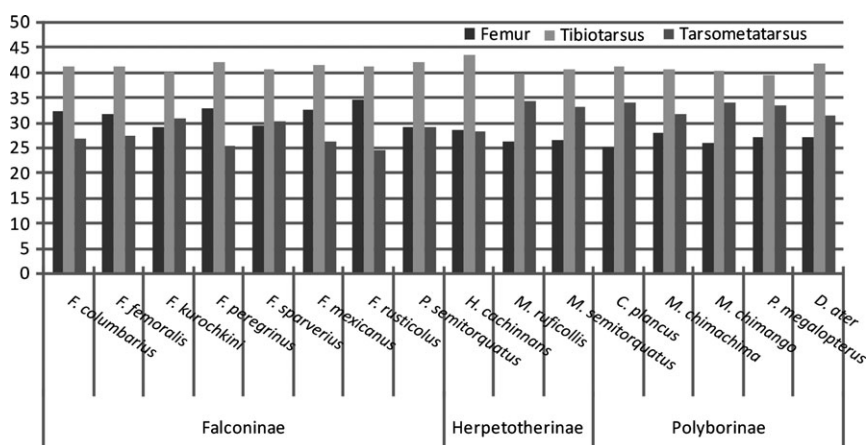


Figure 2 Proportions of the femur, tibiotarsus and tarsometatarsus in Falconidae with respect to the length of the limb.

Table 1 Mean lengths (mm) and standard deviation (SD) of the femur, tibiotarsus and tarsometatarsus of Falconidae

	Femur	SD	Tibiotarsus	SD	Tarsometatarsus	SD
Falconinae						
<i>Falco columbarius</i>	44.83	1.75	57.37	2.12	37.34	0.91
<i>Falco femoralis</i>	56.26	3.33	73.19	3.49	48.73	2.39
<i>Falco kurochkini</i>	46.90		64.40		49.60	
<i>Falco peregrinus</i>	64.45	4.93	82.37	6.40	49.39	3.13
<i>Falco sparverius</i>	36.71	1.36	50.39	1.56	37.56	3.67
<i>Falco mexicanus</i>	68.34	7.04	87.15	9.48	54.95	4.43
<i>Falco rusticolus</i>	87.92	0.31	104.26	1.64	62.09	0.73
<i>Polihierax semitorquatus</i>	27.68		39.85		27.58	
Herpetotherinae						
<i>Herpetotheres cachinnans</i>	62.26	2.73	95.44	4.80	61.96	3.28
<i>Micrastur ruficollis</i>	46.44	0.41	70.23	2.30	60.57	2.51
<i>Micrastur semitorquatus</i>	69.74	2.24	107.10	6.66	87.27	4.81
Polyborinae						
<i>Caracara cheriway</i>			111.70		91.60	
<i>Caracara creightoni</i>			101.60		82.10	
<i>Caracara plancus</i>	73.56	2.39	117.30	7.00	98.74	6.32
<i>Milvago chimachima</i>	44.97	2.25	65.58	3.51	51.06	2.20
<i>Milvago chimango</i>	46.59	1.26	72.00	2.18	60.97	1.99

are corrected by size, we used the ordinary least squares regression (Zar, 1999).

Hindlimb myology

Hindlimb myology was studied by unilateral dissections of *Mil. chimachima* (3) and *C. plancus* (4), after fixation and preservation in a 4% formaldehyde solution and in a 70% alcohol solution respectively. Two species of *Falco*, *F. femoralis* and *F. sparverius*, were also dissected for comparison. A comparison of these Polyborinae with *Mil. chimango* (Mosto *et al.*, 2013) and other diurnal raptors (Hudson, 1937, 1948) was performed, highlighting only those differences found in *Mil. chimachima* and *C. plancus*. Specimens were obtained from La Marcela farm (26°17'35"S; 59°06'67"W), Pirané, Formosa province, Argentina with authorization of Ministerio de la Producción y Ambiente, Dirección de Fauna y Parques of Formosa Province (guía de tránsito N° 003384). The specimens were euthanized following the Guidelines to the Use of Wild Birds in Research (Fair, Paul & Jones, 2010).

The anatomical nomenclature follows Baumel *et al.* (1993). The hip, knee and ankle joints refer to the pelvic girdle–femur joint, femur–tibiotarsus joint and tibiotarsus–tarsometatarsus joint respectively. The following abbreviations are used: FE (femur), TBT (tibiotarsus), TMT (tarsometatarsus), FCL (muscle *flexor cruris lateralis*) and FL (muscle *fibularis longus*). Photographs were taken with a Nikon D-40 digital camera (Nikon Corporation, Tokyo, Japan).

Results

Femur, tibiotarsus and tarsometatarsus

The TBT was the largest bone for the three subfamilies, averaging *c.* 41% of the total length of the limb (Figs 1, 2;

Table 2 Long bones of the hindlimb relativized with their correspondent total leg length between Falconidae subfamilies (factor variable), analyzed with one-way Kruskal–Wallis test

Comparison	Diff of ranks	<i>Q</i>
Femur	$H = 58.7, d.f. = 2$ ($P = <0.001$)	
Falconinae versus Polyborinae	41.5	7.3*
Falconinae versus Herpetotherinae	35.1	4.2*
Herpetotherinae versus Polyborinae	6.4	0.7
Tibiotarsus	$H = 18.9, d.f. = 2$ ($P = <0.001$)	
Falconinae versus Polyborinae	24.6	4.3*
Falconinae versus Herpetotherinae	10.3	1.2
Herpetotherinae versus Polyborinae	14.3	1.7
Tarsometatarsus	$H = 47.9, d.f. = 2$ ($P = <0.001$)	
Falconinae versus Polyborinae	38.6	6.8*
Falconinae versus Herpetotherinae	25	3*
Herpetotherinae versus Polyborinae	13.6	1.6

The *post hoc* comparisons were performed with Dunn's test.
* $P < 0.05$.

Table 1). Regarding the FE and TMT, three configurations were recovered (Fig. 2). (1) Most of the *Falco* species had a FE longer than the TMT, *F. columbarius*, *F. femoralis*,

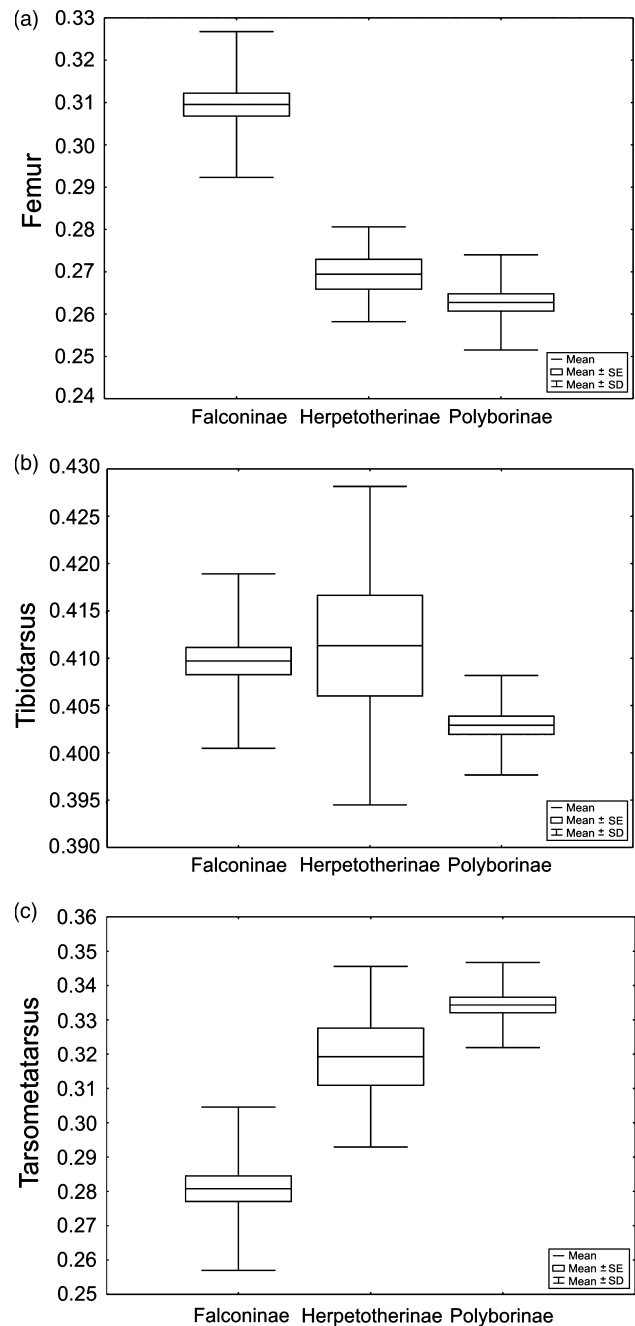


Figure 3 Box plot of the (a) femur, (b) tibiotarsus and (c) tarsometatarsus relativized with their correspondent total leg length among Falconidae subfamilies (factor variable). The femur in Falconinae was longer than in Polyborinae and Herpetotherinae, while the tarsometatarsus showed the opposite pattern. The tibiotarsus exhibited differences only between Falconinae and Polyborinae, being longest in the first subfamily. Herpetotherinae was intermediate regarding the length of this bone.

F. peregrinus, *F. mexicanus* and *F. rusticolus*; in these cases, the FE represented on average a 32.7% of the hindlimb. (2) In a few species, *F. sparverius*, *Polihierax semitorquatus* and *H. cachinnans*, the FE and TMT were the same length. (3) A

TMT longer than the FE occurred in all Polyborinae, the genus *Micrastur* and the extant species *F. kurochkini* (Fig. 2). In these species, the TMT comprised over 30% of the length of the limb.

Table 3 Reduced major axis (RMA) between femur, tibiotarsus and tarsometatarsus with body mass (bmass) or total length of hindlimb (Lleg)

	Slope a	Interc. B	Err a.	Err b.	r	p (uncorr)	Permut p	ic a	ic b
RMA									
FE/bmass	1.02	0.85	0.64	0.05	0.98	2.73E-09	<0.0001	0.88:1.12	0.76:0.97
TBT/bmass	1.01	1.01	0.09	0.07	0.95	1.14E-07	<0.0001	0.84:1.15	0.90:1.16
TMT/bmass	1.1	0.79	0.2	0.16	0.78	0.001	0.0017	0.74:1.41	0.53:1.08
Lleg/bmass	1	1.4	0.1	0.08	0.94	5.20E-07	<0.0001	0.81:1.16	1.28:1.57
Residuals									
FE/Lleg	0.3	-1.23E-03	0.16	0.01	0.48	0.098	0.102	0.08:0.83	-0.01:0.02
TBT/Lleg	0.85	-4.38E-03	0.07	2.99E-03	0.97	5.10E-08	1.00E-04	0.73:0.92	-0.01:0.001
TMT/Lleg	1.88	-3.67E-03	0.26	0.01	0.91	1.73E-05	2.00E-04	(1.12:2.31)	-0.03:0.02

FE, femur; TBT, tibiotarsus; TMT, tarsometatarsus.

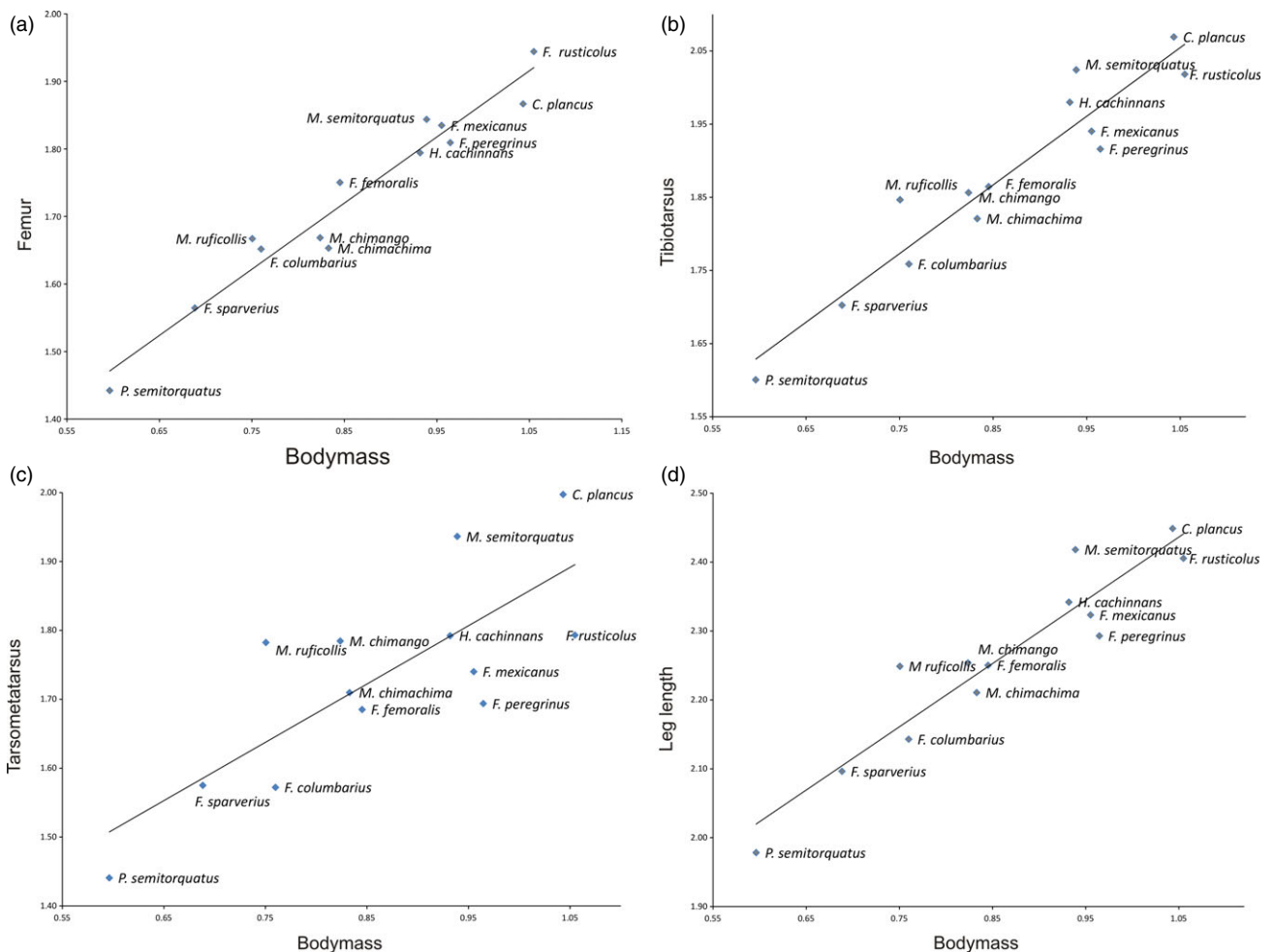


Figure 4 Scaling relationships between bone lengths and femur (a), tibiotarsus (b), tarsometatarsus (c) and total leg (d) against body mass (g). All reduced major axis regressions were positive and significant, though there was not a significant deviation from isometry (slope ranged from 1 to 1.1).

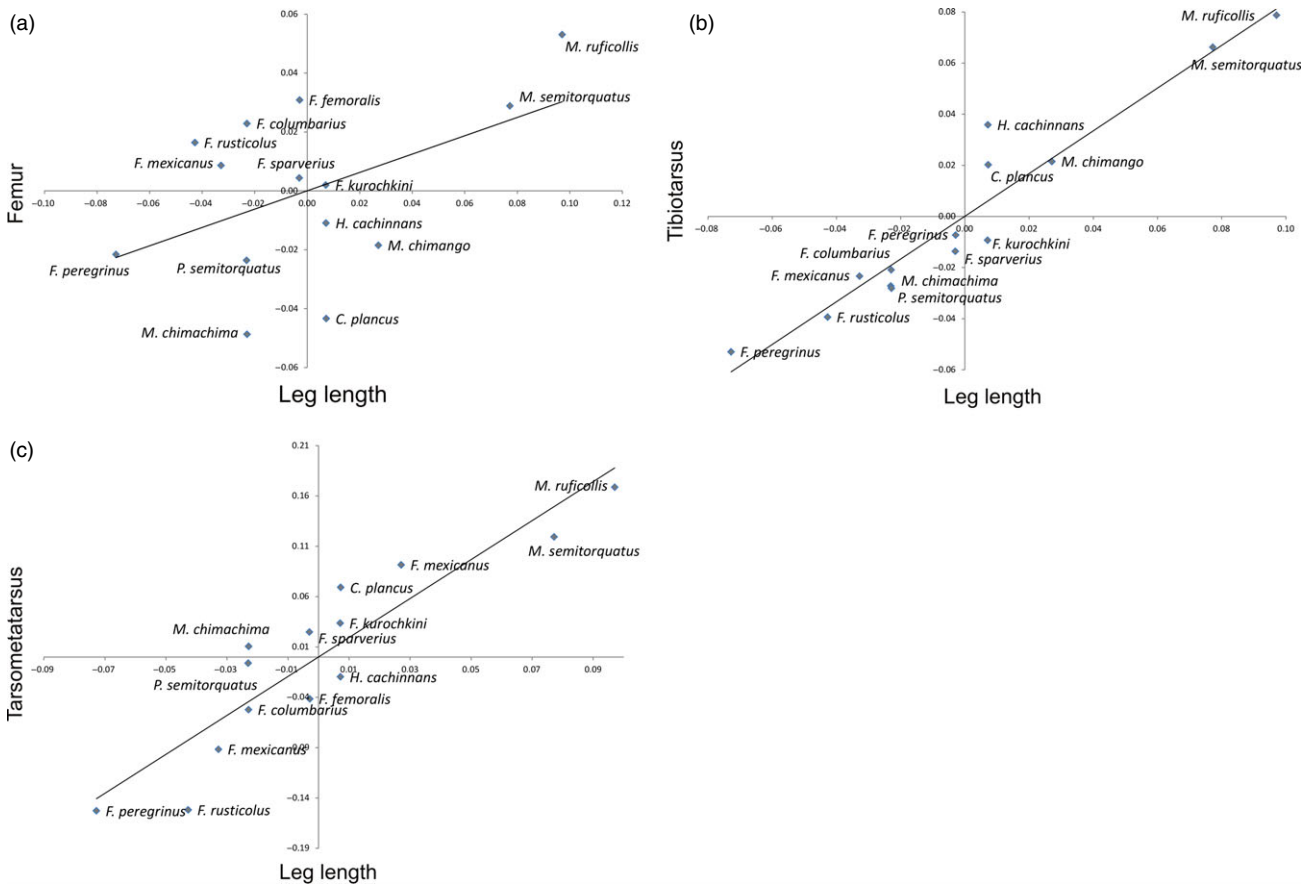


Figure 5 Scaling relationship, using reduced major axis regression, between residuals coming from the previous regressions between body mass and femur (a), tibiotarsus (TBT) (b) and tarsometatarsus (TMT) (c) against total leg length. The TBT and TMT varied significantly and positively with total leg length, with TMT being the bone with the highest regression coefficient and slope, hence explaining most of the variation in total length leg.

The Kruskal–Wallis analysis of variance revealed a significant difference in individual bone proportions between Falconidae subfamilies (Table 2). The Dunn's *post hoc* test showed that, regarding the FE, these differences occurred between Falconinae and Polyborinae and between Falconinae and Herpetotherinae, but not between Polyborinae and Herpetotherinae. As it can be seen in Fig. 3a, the *Falco* species have a relatively longer femur than Polyborinae and Herpetotherinae. Moreover, the proportion of the leg represented by the TBT only differed between Falconinae and Polyborinae. This bone was longer in Falconinae than in Polyborinae and had intermediate values in Herpetotherinae (Table 2; Fig. 3b). The proportion of the total length that corresponded to the TMT was higher for Polyborinae and Herpetotherinae than for the *Falco* species (Table 1; Fig. 3c).

The RMA regression slopes for the FE, TBT, TMT and total leg lengths with body mass were all significant but not different from an isometric expectation of 1 (Table 3; Fig. 4a–d). However, the scaling of the resultant residuals of FE, TBT and TMT (coming from the above regressions with that from leg length vs. body mass), showed different patterns for each leg

component. Thus, residuals of FE versus body mass did not vary significantly with respect to leg length. However, those belonging to TBT and TMT showed a statistically significant scaling with the residuals of leg length (Table 3; Fig. 5a–c), with the TMT slope markedly higher than that coming from the TBT. That is, deviations of the leg from the expected length according body size were better explained by deviation of TMT length than by TBT.

Hindlimb myology

The FCL was present in both species *C. plancus* (Fig. 6a, d) and *Mil. chimachima* (Fig. 6b, c). In both species it has a fleshy postacetabular origin in the dorsocaudal edge of the *ala ischii*, (Fig. 6a) and the insertion occurs by a short tendon in the proximo-medial region of the TBT (Fig. 6d), caudal to the *impression ligamentum collaterale medialis*. It is more proximal than the *m. flexor cruris medialis*. Also, in *C. plancus* the muscle has two bellies, whereas in *Mil. chimachima* presented only one.

The FL was also present in both *Mil. chimachima* and *C. plancus*. The origin occurs on the anterior aspect of the

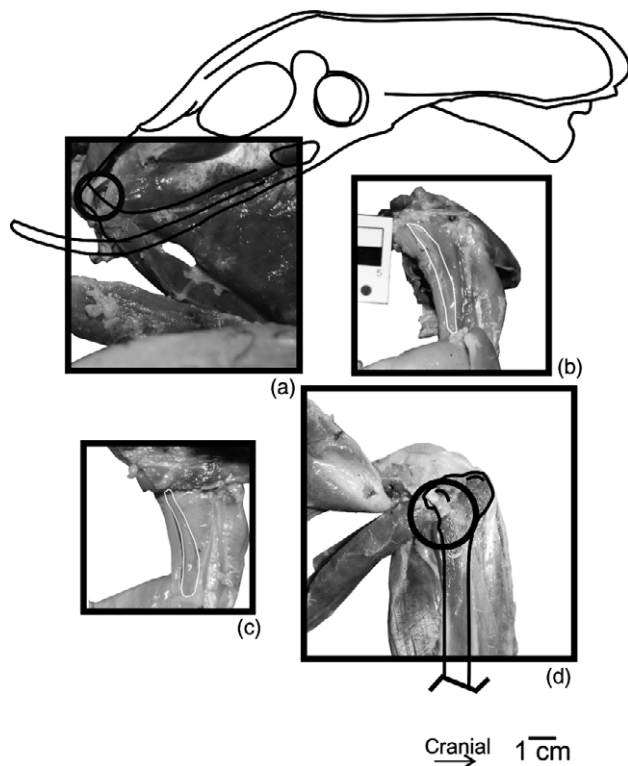


Figure 6 The muscle *flexor cruris lateralis* in *Caracara plancus* and *Milvago chimachima*. (a) Lateral view in *C. plancus* showing the origin of the muscle on the pelvis (schematic drawing); (b) and (c) lateral and medial views, respectively, of the proximal hindlimb of *Mil. chimachima*, the muscle is encircled in the white line. (d) Medial view in *C. plancus* showing the insertion of the muscle on the tibiotarsus (schematic drawing).

TBT between the *cristae cnemialis cranialis* and *lateralis* and the insertion is by a bifurcated tendon on the lateral facet of that bone. One of those tendons inserted on the *cartilage tibialis*, whereas the other fused with the *m. flexor perforatus digiti III*. In *Mil. chimachima* the FL was a well-developed muscle, whereas in *C. plancus* it was even larger, covering almost the distal half of the *m. tibialis cranialis*.

Other myological differences in *Mil. chimachima* and *C. plancus* regarding other Falcons are compared in Table 4.

Discussion

Osteology

The Polyborinae have a significantly longer limb caused by a longer TMT, thus empirically confirming the observations of previous studies (Friedmann, 1950; Vuilleumier, 1970). A long TMT increases stride length (Alexander, 1983; Kirkwood *et al.*, 1989; Bennett, 1996), allowing effective locomotion on land. It is noteworthy that Herpetotherinae also has a long TMT like that of the Polyborinae. Both subfamilies are considered basal lineages in the Falconidae phylogeny (Fuchs *et al.*, 2012; Fuchs, Johnson & Mindell, 2015) and it could be

inferred –although speculatively – that the last common ancestor of Falconidae might have been a long-legged bird with terrestrial habits. Alternatively, more terrestrial habits and elongated TMT evolved independently in the ancestral lineages of Polyborinae and Herpetotherinae.

Nevertheless, it is necessary to know with more accuracy the leg morphology of Herpetotherinae with a more thorough sampling of the representatives of this clade, together with a broader knowledge on their behavior. Our data show heterogeneity in the TMT length, the long TMT of the *Micrastur* resembles that of the Polyborinae, whereas the TMT of *H. cachinnans* is similar to that of *Falco*.

The TBT was always the longest component in all three subfamilies, considered as a distinctive characteristic for all raptors (Zeffer *et al.*, 2003). These authors compared raptors with birds belonging to different habitat groups (waders, ground dwelling or arboreal species, etc.) and concluded that this particular feature could be the result of a selective pressure for long limbs in birds of prey which increase the reaching distance for prey struck while hunting.

Long limbs were also present in the fossil species *F. kurchkini*, a feature that led Suárez & Olson (2001) to consider it as a possible terrestrial bird of open country, occupying the similar niche as a *Caracara*. Marchant & Higgins (1993) compared *F. kurchkini* with the extant *F. berigora*, an opportunistic carnivore and scavenger that may feed on the ground upon prey from the size of insects to rabbits. Regrettably, there is no morphometric data on the limb bones or myology of this species to make a comparison with the terrestrial Polyborinae which might have represented parallel evolution.

Specimens of the Polyborinae *D. ater*, *I. americanus*, *Phalcoboenus albogularis* and *P. megalopterus* were neither available at any collection nor were their measurements included in any manuscript, except for the proportions of the limb of *D. ater* and *P. megalopterus* (Hopson, 2001). However, Fig. 1 in Vuilleumier (1970) is a graph from which it can be estimated the minimum and maximum length of their TMT in several specimens. This figure shows that these four species also have large TMT, with *D. ater* (~46.9–54.4 mm) and *I. americanus* (~48.1–57.5 mm) having values similar to those of *Milvago* and *P. albogularis* (~64.5–75 mm) and *P. megalopterus* (~70.1–83 mm) with intermediate values between *Milvago* and *Caracara*. However, these are more arboreal species unlike *Caracara* and *Milvago*. It remains to be determined how this long TMT is interpreted in these genera whose habits are predominantly arboreal, and how their myology pattern would help in accomplishing this outlook.

Hindlimb myology

In general terms, the hindlimb myology of *C. plancus* and *Mil. chimachima* was similar to that of *Mil. chimango* (Mosto *et al.*, 2013) and also to those species described for Falconidae in Hudson (1937, 1948) and Berger (1956). However, the presence in these Polyborinae of a strong and well-developed *m. flexor cruris lateralis* and *m. fibularis longus* is a notorious feature that can be associated with the prevalence of the terrestrial locomotion that characterizes these birds.

Table 4 Comparative table of the muscular features of *Milvago chimachima* and *Caracara plancus* with other Falconidae

Muscle	<i>Milvago chimachima</i>	<i>Caracara plancus</i>	Falconidae ^a
Muscles with origin on the pelvis			
<i>Flexor cruris lateralis</i>	Present with one belly	Present with two bellies	Absent
<i>Pubo ischio femoralis</i>	Besides the insertion on the femur it also had a tendinous insertion on the <i>pars medialis</i> of the <i>m. gastrocnemius</i>		The <i>pars interna</i> inserts mainly as a thin aponeurotic sheet except in <i>Pandion</i> in which both parts have fleshy insertions
<i>Caudofemoralis</i>	With a fleshy origin on the femur and a wide belly	With intra-specific variation in the tendon of origin on the femur ($n = 4$), two possibilities: long and wide or short and narrow	With a short and compressed tendon on the femur
<i>Iliotibialis cranialis</i> (IC)		The origin of the <i>m. iliotibialis cranialis</i> (IC) with a small aponeurotic region and a caudal portion covered by the <i>m. iliotibialis lateralis</i> (IL)	It originates fleshy from the anterodorsal border of the ilium and from the spinous process of the last free dorsal vertebra. The origin is from the edge of the ilium only in <i>Falco</i>
<i>Iliotibialis lateralis</i> (IL)		With a fleshier cranial portion and two tendons of insertion that inserted on the patella	In these the belly does not overlap the IF. The origin in the Cathartidae is from the dorsal ridge of almost the entire length of the ilium, the belly, accordingly, overlapping most of the IF
<i>Iliofibularis</i> (IF)	The tendon of insertion is medial to the tendon of insertion of the <i>m. ambiens</i>	Presented a postacetabularly extended origin, ventral to the <i>crista dorsolateralis ilii</i> and the tendon of insertion was distant from the tendon of insertion of the <i>m. ambiens</i>	Tendon passes medial to the tendon of the <i>m. ambiens</i> , only in <i>Falco</i>
<i>Ischiofemoralis</i>		With a conspicuous dorsal portion on the belly, at the <i>crista dorsolateralis ilii</i> ; although it could not be isolated as other belly	
Muscles with origin on the distal femur or proximal tibiotarsus			
<i>Fibularis longus</i>	Present and well developed	Very large muscle with a fleshy origin	With a narrow belly in <i>Falco</i>
<i>Gastrocnemius</i> (G)		With a tendinous origin of the <i>pars medialis</i>	It arises partly fleshy from the posterior edge of the of the femur
<i>Flexor perforatus digiti IV</i> (FPDIV)	Fused at the origin with the <i>m. flexor perforatus digiti II</i> (FPDII) and the tendon of insertion of the <i>m. ambiens</i> (A)		All the flexors are intimate related
<i>Flexor perforans et perforatus digiti II</i> (FPPDII)		Tendon of origin on the lateral epiphysis of the femur and wide tendon of insertion covering the FPPDII	
<i>Flexor perforans et perforatus digiti III</i> (FPPDIII)	With a wider origin also along the fibula	With a small tendinous origin on the femur, the rest was fleshy on the fibula	
<i>Flexor digitorum longus</i>	Ossified tendon of insertion along the shaft of the tarsometatarsus (TMT)	The tendon of insertion was fused in the distal third of the TMT with the FHL. Ossified tendon of insertion along the shaft of the TMT	Ossified tendon of insertion in <i>Falco</i>
<i>Flexor hallucis longus</i> (FHL)	Two heads of origin, one fleshy and one tendinous	Three heads of origin, two larger and fleshy and one smaller both tendinous and fleshy	Two heads of origin

^aTaken from Hudson, 1937, 1948; Berger, 1956.

These muscles are extensors of the hindlimb that mainly act during the stance phase (when the foot contacts the ground; Jacobson & Hollyday, 1982; Verstappen, Aerts & De Vree,

1998; Gatesy, 1999). This phase is a crucial moment, the extensor muscles must support the body mass avoiding the hyperflexion of the joints and providing the necessary energy

to move forward (Jacobson & Hollyday, 1982; Gatesy, 1999).

The FCL is one of the most important hip extensors, together with the *m. iliofibularis*, *m. flexor cruris medialis* and *m. puboischiofemoralis* (Verstappen *et al.*, 1998), that prevent hyperextension of the knee during terrestrial locomotion (Jacobson & Hollyday, 1982; Gatesy, 1999). In those birds with no terrestrial locomotion the FCL is absent, for example Accipitriformes, Apodiformes and Strigiformes (Hudson, 1937; George & Berger, 1966; Zusi & Bentz, 1984), *Falco* (Hudson, 1937, 1948) and *P. semitorquatus* (Berger, 1956). Additionally, the FCL is a muscle with different morphology expressed on the degree of its development in relation to different locomotor habits. For example, in the Cuculidae (Cuckos) Berger (1952) found that the FCL had a greater development in those cursorial species (e.g. *Geococcyx* roadrunner) than the arboreal ones (e.g. *Coccyzus*). Mckitrick (1985, 1986) observed a similar trend in Tyrannidae (tyrant flycatcher) where species that are ground foraging like the cattle tyrant *Machetornis rixosus* presented a well-developed FCL with respect to the species that are aerial hawking like the eastern wood-pewee *Contopus virens*. The FL is an extensor of the ankle joint (tibiotarsus-tarso-metatarsus joint) and generates the propulsive force that pushes the body away (Jacobson & Hollyday, 1982). Both in *C. plancus* and *Mil. chimachima* (and also in *Mil. chimango*, Mosto *et al.*, 2013), this muscle is well developed, whereas in the more aerial and perching *Falco* it is more slender (Hudson, 1937, 1948). This same variation in the FL related to the locomotor habit has also been observed in Cuculidae and Psittaciformes (parrots). In the Cuculidae, the belly of FL is well developed and expanded in the terrestrial *Geococcyx*, whereas in the arboreal *Coccyzus* this muscle is more reduced and less expanded (Berger, 1952). In the Psittaciformes, the terrestrial and non-volant species kakapo *Strigops habroptilus*, exhibits a well-developed FL (Mitchell, 1913), whereas the rest of the studied psittacids are highly volant with no terrestrial locomotion and exhibited a lesser developed FL (Berman, 1984; Carril *et al.*, 2014).

Thus, the presence or absence and degree of development of certain hindlimb muscles are indicative of the locomotor habits in birds (Mckitrick, 1985). It is worth mentioning that other myological features were found in *C. plancus* and *Mil. chimachima*, such as the ossified tendon of the *m. flexor digitorum longus* only described for *Falco* (Hudson, 1937, 1948), the variation at the origin of the different *m. perforans et perforatus*, and a different relationship between the tendon of insertion the *m. iliofibularis* and the *m. ambiens* present in *C. plancus*. The significance of these myological variations is yet to be analyzed to determine whether they may be associated with the type of locomotion.

To conclude, several osteomyological features can be associated with terrestrial locomotion and these features become more evident when different habits are compared among falconid subfamilies. Here, we empirically demonstrated that the length of the hindlimb in the Polyborinae is larger than that of the Falconinae and this enlargement occurs on the TMT. This osteological pattern is accompanied by myology, which is related to the locomotion style that is more terrestrial than aer-

ial, with well-developed extensor muscles like the *m. flexor cruris* and *m. fibularis longus*.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Measurements (mm) of femur, tibiotarsus and tarsometatarsus measured in this work and from the bibliography.