

## ORIGINAL ARTICLE

# Qualitative and Quantitative Analysis of Talons of Diurnal Bird of Prey

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**Summary**

The aim of this work is to establish qualitative and quantitative differences and similarities among talons lacking the keratin sheath in diurnal raptors. We set out to find a tool that allows for the determination of toe (I-IV) and hindlimb (left or right) identity. Different methodologies were used, such as classical anatomical descriptions and Fourier analysis of the medial contour of the ungual phalanx. A series of measurements and ratios were obtained and analysed using *t*-tests and principal components analysis. The qualitative descriptors are more important than quantitative analyses for assessing ungual phalanx identity. They allowed us to differentiate between hindlimbs and among toes corresponding to the talons of D-I, D-II and D-III, while the assignment of D-IV was complicated by its symmetry. The *t*-test showed that digits I and II did not differ in any measurement or ratio, whereas it showed several differences among the other digits. Fourier analysis was useful only when it was applied to one species with a large number of specimens. This work is an important contribution to the paleontological field where it is common to find isolated phalanges, and consequently, their identification is very difficult.

**Introduction**

Falconidae (falcons) and Accipitridae (kites and hawks) are diurnal raptors that predate upon other vertebrates, such as mammals, birds, fish and also invertebrates (Thiollay, 1994; White et al., 1994). They have previously been included within the order Falconiformes, but currently, they are considered separate phylogenetic entities based on molecular phylogenies (Ericson et al. 2006, Hackett et al., 2008). Both rely on their hindlimbs to obtain their food, with great importance of the feet and aided by the bill (Sustaita, 2008; Sustaita and Hertel, 2010). The digits have an anisodactylous arrangement and their claws, commonly known as talons for birds of prey, show a particular morphology: they are strongly curved, with great development of the flexor and extensor tubercle with a robust corpus that tapers towards the distal end (Richardson 1942 in Pike and Maitland, 2004 Fig. 1). Talons, both in Accipitridae and Falconidae, seem to have an important

role when killing and grasping their prey (Goslow, 1971; Thiollay, 1994; White et al., 1994), although there are variations in the use of the digits during these activities (Harris, 1984; Csermely and Gaibani, 1998 Csermely et al., 1998; and Fowler et al., 2009).

As Fowler et al. (2009) stated 'Claw morphology has received virtually no attention at all, which is surprising given its importance to predatory success' (Fowler et al., 2009:2); however, there are several works where talons were part of such analysis. To name a few, Csermely and Rossi (2006) and Csermely et al. (2012) studied the morphology of digits I and III to compare among Strigiformes, Falconidae, Accipitridae and non-raptorial birds; Pike and Maitland (2004) analysed the claw geometry of digit III in several families of birds to predict their mode of life; Einoder and Richardson (2007) analysed the four digits of Australian raptors with an ecomorphological focus; Fowler et al. (2009) carried out a study analysing the curvature of the inter-digital variation of the talons

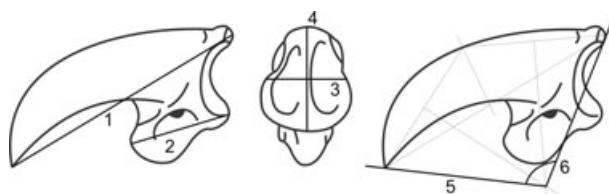


Fig. 1. Sketch of a talon in lateral and proximal articular facet view showing the analysed measures. (1) Length of the phalanx (2) length of the flexor tubercle (3) width (4) height (5) radius of curvature (6) angle of curvature.

within the raptor families and found taxonomical differences (see also Fowler et al., 2009; and bibliography cited there). In all these studies, talons were analysed with the keratin sheath intact, but the ungual phalanx (the osseous structure) has not been studied. Few palaeontological contributions are focused on the anatomy of this structure in raptors (e.g. Mourer-Chauviré, 1983; Tambussi et al., 2003; Agnolin, 2006; Mayr, 2006). The lack of information on this subject precludes an understanding of the distinctive anatomical features (both descriptive and by measurement) possessed by each digit, or that allows identification of the hindlimb to which they belong. It is also unknown whether phalanges can be identified to species through the bony anatomy. This kind of information is relevant both in paleontological studies as in neontological ones. In paleontological sites, isolated phalanges are much more frequent than articulated limbs, but more difficult to identify (Tambussi, 2011). Such analyses require a database of the anatomy of talons of extant birds, and this research is intended as a contribution towards this goal.

The objectives of this work are (1) to evaluate whether the morphology of the ungual phalanges can be used to identify the digit and the hindlimb to which they belong, (2) to evaluate the taxonomic value of the morphology on a species level and (3) to quantitatively and qualitatively analyse this morphology with the aim to explore whether or not there is agreement on these two types of methods.

## Materials and Methods

The ungual phalanx of each digit (I–IV) of both limbs was studied in 56 specimens from nine species of the Falconidae (number of specimens): *Caracara plancus* (7), *Falco femoralis* (3), *Falco sparverius* (6), *Falco tinnunculus* (1), *Falco peregrinus* (3), *Falco columbarius* (1), *Milvago chimachima* (2), *Milvago chimango* (4) and *Spizapteryx circumcinctus* (1); and ten of the Accipitridae: *Accipiter striatus* (2), *Buteo albicaudatus* (3), *Buteo magnirostris* (7), *Buteo ventralis* (1), *Buteo jamaicensis* (1), *Ictinia plumbea* (1), *Geranoaetus melanoleucus* (10), *Elanoides forficatus*

(1), *Elanus leucurus* (1) and *Rostrhamus sociabilis* (1). The selection of the specimens listed above was mainly restricted to their presence in the collections, and it was considered that the sample was representative of the two families, Accipitridae and Falconidae.

Materials are housed at Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and Fundación de Historia Natural Félix de Azara (FHN) of Ciudad Autónoma de Buenos Aires, Argentina. The exclusive condition for including the materials in the analyses was that it was possible to discern the toe number (expressed here with Roman numeral, e.g., D-III for digit III) and the limb (left of right) to which they belong. Following Fowler et al. (2009), we assume there is no variation in the gross morphology of the talons due to gender or ontogenetic stage.

## Qualitative analysis

Anatomical descriptions were made by direct observation and magnifying glass. The osteological terminology follows Baumel and Witmer (1993) with its English equivalents. D-I was described as if it was anteriorly orientated, rather than posteriorly as in life, with the purpose of making the comparison easier.

## Quantitative analysis

The following measurements were obtained (Fig. 1) with a Vernier Caliper (0.02 mm precision):

1. Length of the phalanx, from the extensor tubercle to the tip of the claw.
2. Length of the flexor tubercle, from the middle ventral margin of the articular facet to the most distal part of the flexor tubercle.
3. Width of the articular facet.
4. Maximum height of the articular facet.

The (5) radius and (6) angle of curvature were measured following the methodology used by Pike and Maitland (2004) with modifications. As these talons lack the keratin sheath, the outer curve of each ungual was traced from the distal tip to the proximal extensor tubercle (Fig. 1). The angles were taken in degrees and then converted to radians. For species with more than one specimen, the average of the measurements was obtained. The following ratios were calculated because of the large size variability between the species.

1. Height/width of articular facet.
2. Length of the phalanx/length of the flexor tubercle.
3. Length of the phalanx/radius of curvature.
4. Length of the phalanx/angle of curvature.

T-tests were performed (software: STATISTICA 7.1; Statsoft 2005) to compare absolute measurements and ratios. This

test was chosen to identify the measurements that best differentiate among the digits (Fowler et al., 2009). For these analyses, data were log-transformed, and an alpha level of 0.05 was assigned. A Bonferroni correction was made to adjust for the increased risk of type I errors.

The original measurements and ratios of the four digits of the right foot of the species were also explored using a principal components analysis (PCA; with the Pearson correlation matrix; software: PAST; Hammer et al., 2001) to examine groupings among digits. We applied this method because it does not use *a priori* groupings and maximizes variance explained among specimens collectively when assessing the contribution of each variable.

The contour of the talons was evaluated using elliptic Fourier analysis (software: SHAPE 1.2; Iwata and Ukai, 2002). The medial side of the four talons of the right foot was studied, and in the case of absence of any talon, a reflection image of the left foot was used. Also, we examined the variation within each of two species for which a sufficient number of species were available for the analysis: *Geranoaetus melanoleucus* (Accipitridae) ( $n = 10$ ) and *Caracara plancus* (Falconidae) ( $n = 7$ ). The Fourier method decomposes the contour into harmonically related ellipses (Kuhl and Giardina, 1982). From each ellipse, or harmonic, four coefficients are obtained:  $A_n$  and  $B_n$ , and  $C_n$  and  $D_n$  for  $x$  and  $y$ , respectively. Finally, the incremental changes of the  $x$  and  $y$  coordinates are analysed. Herein, 20 harmonics were subjected to a PCA except for the three first coefficients of the first harmonic, following the suggestion of Crampton (1995). These three are used to standardize translation, size and the first digitized point, and therefore, all specimens share the same value.

We did not employ phylogenetic-correction methods to account for shared ancestry, and therefore caution that the significance of some of our analyses may be inflated due to issues of non-independence. However, the taxonomic 'group' comparisons are among fairly well-supported and somewhat distant phylogenetic entities. In addition, our primary analyses are within-taxon comparisons of ungual features among toes and between limbs. Furthermore, given the high levels of significance obtained for some of the tests that were significant, we feel that the results are unlikely to differ substantially had we explicitly controlled for phylogeny. In addition, the primary analyses are comparisons of ungual features within groups, among toes and between limbs.

## Results

### General description of the ungual phalanges

The ungual phalanges of diurnal birds of prey commonly show asymmetry. All talons are characterized by

being highly curved and having a distally oriented and well-developed flexor tubercle, and also a large extensor tubercle. Relative size diminishes from digit I to IV (Figs 2 and 3), more noticeably from digit II to III, whereas the pairs I-II and III-IV are more similar. The transverse section of the corpus exhibits a markedly convex dorsal region, flattening on the lateral and medial aspects and terminating with a flat ventral facet by two well-marked edges. This edge is more marked in Accipitridae than Falconidae, being the unique feature that differentiates one family from the other; although *Elanoides forficatus* does not have the ventral facet as delimited as the rest of the Accipitridae (for example, Fig. 2g,h).

The articular facet is concave, limited dorsally by the extensor tubercle and ventrally by the flexor tubercle (Fig. 4a). Commonly, in this facet, there is a dorsoventrally extended ridge (Fig. 4b) that delimits two cotylae (Fig. 4b). However, the development of this ridge differs among the digits by being absent in all the digits (e.g. *Falco sparverius*) or only slightly developed (e.g. *Caracara plancus*). In other cases, such as *Accipiter striatus*, both cotylae are well differentiated only in digits I and II, but not in III and IV. Where the dorsoventral ridge contacts the ventral ridge, a prominence is developed, referred to here as the middle prominence (Fig. 4c). The articular facet, in proximal view, is laterally rotated with respect to the corpus in some digits. In some cases, the contour varies by having a dorsoventrally rectangular, circular or pear shape.

On both sides of the flexor tubercle, there are pairs of ventral foramina, for the passage of nerves and vessels (Fig. 4a,c). In some specimens, two additional smaller foramina are located in the middle of the lateral margin of the articular facet (Fig. 4b). These smaller foramina are present in some specimens of different species, and when they are present, they occur in every digit, representing individual variation. There is a pair of lips dorsal to the ventral foramina, with their origin on the lateral margin of the articular facet that extends towards the flexor tubercle; it corresponds to the proximal portion of the keratin sheath. It can appear differentially developed when both sides are compared.

A characteristic of few species, such as *Geranoaetus melanoleucus* or *Buteo jamaicensis*, is the presence of small fossae in the ventral portion of each cotyla located at different levels with respect to one another (Figs 2c,d and 4b). These correspond to the joint of the articulating non-ungual phalanx. The phalanges of *Rostrhamus sociabilis* are unusual because compared with other raptors, they are relatively longer (see also next section), and the flexor tubercle is less developed. *Ictinia plumbea* also shows a relatively longer phalanx in digits I and II.

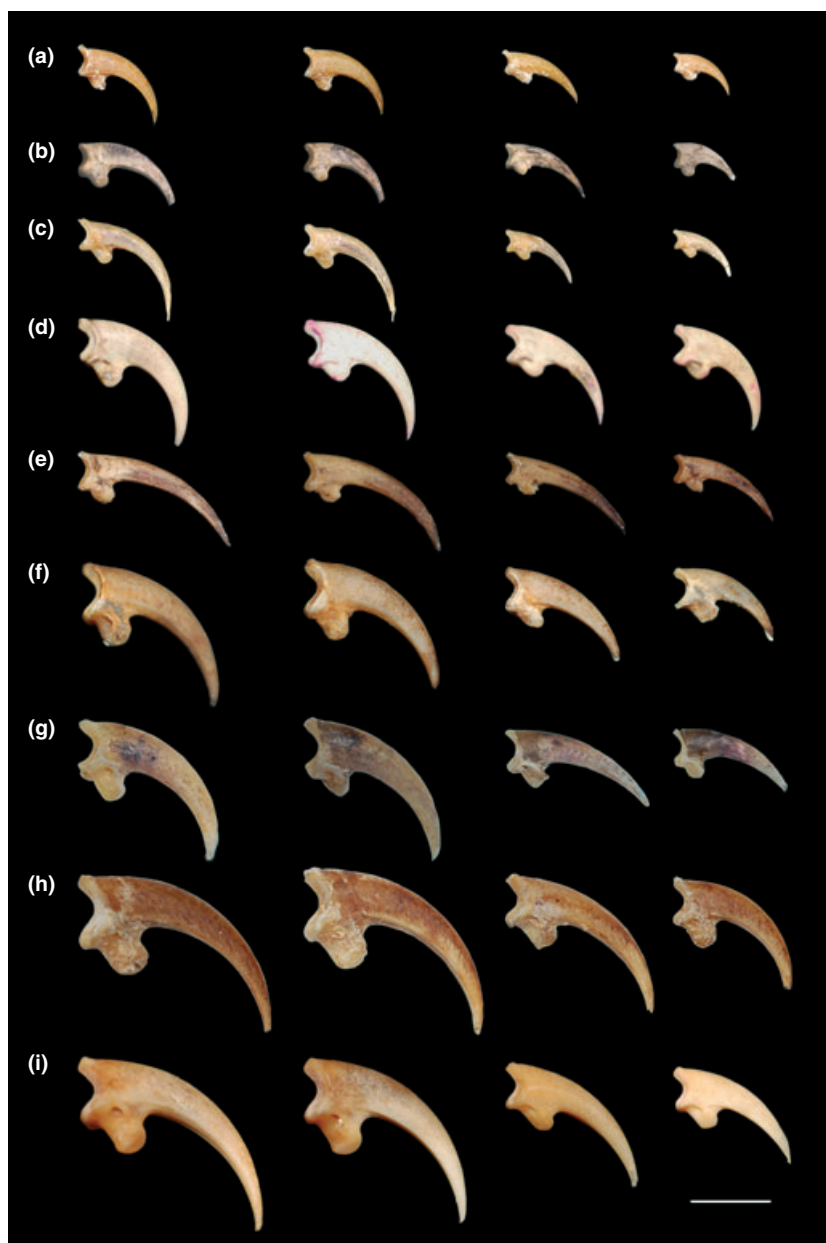


Fig. 2. Medial and lateral view of the ungual phalanges of (a) *Ictinia plumbea* (L), (b) *Elanus leucurus* (R), (c) *Accipiter striatus* (L), (d) *Falco peregrinus* (R), (e) *Rostrhamus sociabilis* (L), (f) *Buteo albicaudatus* (R), (g) *Caracara plancus* (R), (h) *Geranoaetus melanoleucus* (L), (i) *Buteo jamaicensis* (L). (L) left, (R) right foot; from left to right column digits I to IV, respectively. Scale 1 cm.

There are several characteristics that highlight the bilateral asymmetry of the ungual phalanx: the cotylae of the articular facet can differ in size and relative position, or one cotyla may be more proximodistally or dorsoventrally displaced with respect to the facies plantaris. In ventral view, the middle prominence may be medially or laterally displaced, and the orientation of the flexor tubercle may be lateral or medial. Finally, the ventral foramina of the flexor tubercle are differentially located in that relative to the ventral margin of the articular facet, a foramen can be more distally displaced than the other. In distal view, with the flexor tubercle dorsally orientated, a foramen can be more dorsally displaced (Fig. 4c).

### Digit I

The medial cotyla is more distal and ventral than the lateral one. Also, in Falconidae, the medial cotyla is larger, although just for the left foot. The middle prominence is laterally displaced. The medial foramen is more distal and ventral than the lateral one, and the flexor tubercle is medially orientated (Fig. 3).

In *Caracara plancus*, the right cotyla is the larger one, no matter the side of the foot; also the medial cotyla has a straight dorsolateral margin, which allows the assignment of toe number and hindlimb. A medial prominence beneath the ventral foramen is the characteristic of *C. plancus* (Fig. 4b,c).

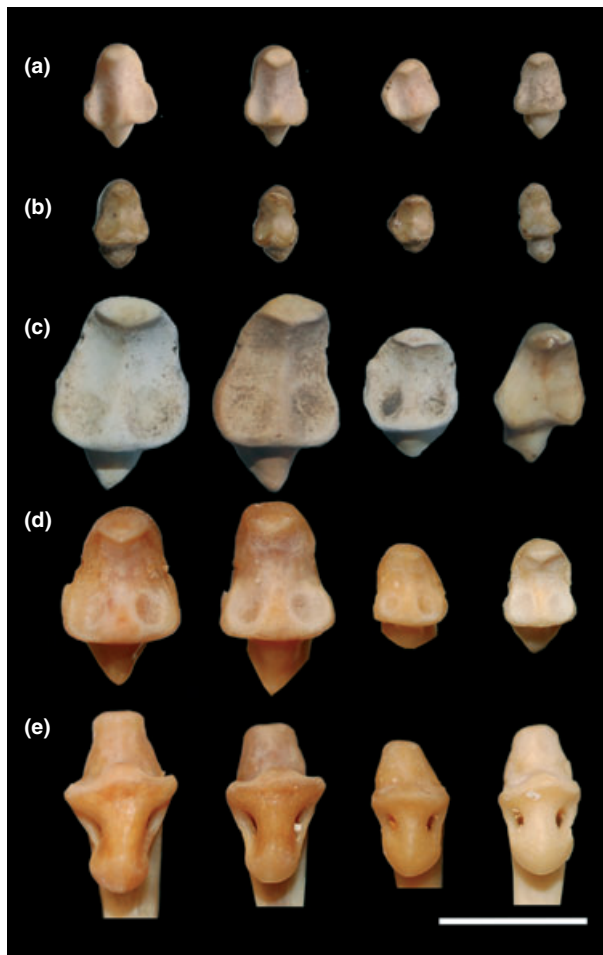


Fig. 3. Articular facet of the ungual phalanges (a) *Buteo magnirostris* (R), (b) *Elanoides forficatus* (R), (c) *Geranoaetus melanoleucus* (R), (d) *Buteo jamaicensis* (L), (e) proximal half in ventral view of *Buteo jamaicensis* ungual phalanges, (L) left, (R) right foot; from left to right column digits I to IV, respectively. Scale 1 cm. Several features described on the text can be appreciated when different species, and all digits are compared; for example, the different size of the ungual, more noticeably from digit II to III; the first row shows the tubercle flexor medially oriented (notice the difference of a–c against d, e) and the second one laterally oriented; the enlarged articular facet of digit III (third column) due to the lateral ridge, among others.

## Digit II

The articular facet is quite symmetric except that the lateral cotyla is more distally located. The middle prominence is located medially, and the medial foramen is more distally and dorsally placed than the lateral one, although in Accipitridae, these foramina are sometimes located at the same level. The flexor tubercle is laterally orientated (Fig. 3). In dorsal view, the phalanx of *C. plancus* shows a distinctive lateral protrusion of this tubercle; this allows for discrimination of toe number and

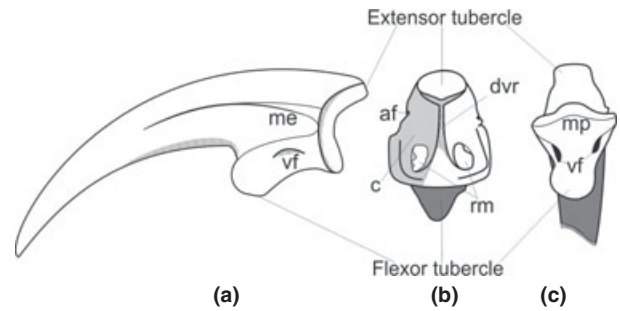


Fig. 4. Sketch of the ungual phalanx from DIII of the right foot and DI of the left foot of *Buteo jamaicensis* (a) DIII in medial view; (b) articular facet of DIII; and (c) ventral view of DI. Accessory foramina (af), cotyla (c), (painted with grey), dorsoventral ridge (dvr), medial edge (me), middle prominence (mp), rounded marks (rm), ventral foramina (vf).

hindlimb side. Also in this species, the medial lip, dorsal to the foramen, is well developed in D-II.

## Digit III

The presence of an edge along the medial facet of the corpus is the characteristic of D-III (Figs 3 and 4a), facilitating the unequivocal identification of both toe number and limb side. The edge is located in the middle of the medial margin of the articular facet, viewed in proximal view. This occurs in most of the species with very few exceptions (e.g. *Falco peregrinus*). As a consequence, this feature enlarges the medial cotyla leading to a more circular contour of the articular facet, unlike the other digits. This medial cotyla is more distally and ventrally located than the lateral one. The middle prominence is usually not displaced but might be laterally displaced, as occurs in most of the Accipitridae studied here. The medial foramen is more distally and dorsally located than the lateral one. The flexor tubercle might be laterally orientated although not always (Fig. 3).

## Digit IV

The variability in this digit in the specimens analysed is large, making the assignment difficult where the asymmetry is present. When we observe an asymmetric ungual phalanx from this digit, the middle prominence is laterally located (Fig. 3). The medial cotyla is more ventrally located with respect to the lateral one and only in the right foot more distally located. The lateral foramen is more distal only in the right foot. The medial foramen in the left foot could be more dorsal. The orientation of the flexor tubercle is lateral although just in the left foot.

This phalanx is the most symmetric of the talons. Despite these differences found in some specimens, a



Table 1. Summary of the descriptions for each digit

Digit	I	II	III	IV
Articular facet (relative displacement of the cotylae)				
Facies plantaris	M	x	M	x
Distal	M	L	M	x
Middle prominence	L	M	L	L
Ventral foramen				
Distal	M	M	M	L
Dorsal	L	M	L	x
Flexor tubercle orientation	M	L	L	x

L, lateral; M, medial.

morphological generalization of D-IV is not possible because these differences are not strongly marked or there are no differences at all in all the species.

See Table 1 for a summary of these descriptions.

### Quantitative methods

The results of the *t*-test can be seen in Tables 2 and 3. As an overview, the width of the articular facet, length of the flexor tubercle, radius of curvature and ratio of phalanx length to angle of curvature did not show any significant differences among digits. Digit I did not show any significant difference with digit II in any measurement nor ratio and showed the greatest difference with digit IV: the height of the articular facet, the length of the phalanx, the angle of curvature and the ratio length phalanx/radius of curvature. The PCA of the different measurements and ratios of the four digits of the right foot indicated that there was no segregation by digit number, together or separately. The talons of *Rostrhamus sociabilis* were the only exception in the PCA of the ratios, each of its digits was differentiable. The same occurred for the PCA performed using the Fourier harmonics with the exception of *Geranoaetus melanoleucus* and *Caracara plancus*, where the variation within the species was studied. In the former, D-III is segregated from D-I, D-II and D-IV (Fig. 5a); the first two PCs explained the 76.62%. In *Caracara plancus*, there was a good clustering of D-I and D-II from D-III and D-IV (Fig. 5b) with a 70.19% of the total variance explained by the first two PCs.

### Discussion

The qualitative osseous features allowed differentiation of the ungual phalanges of each digit. The talons of D-I and D-II are very similar (Figs 2 and 3). However, taking into account all their characteristics, identification is possible. D-III and D-IV have particular features that easily allow their discrimination; D-III has a medial edge, while D-IV has the symmetry of its osseous features (Fig. 3).

Regarding the second and third goal of this contribution (to evaluate the taxonomic value of the morphology on a species level and to quantitatively and qualitatively analyse this morphology with the aim to explore whether or not there is agreement on these two types of methods), the quantitative analyses had limited success discriminating among talons, especially the PCA where no segregation was found. The *t*-tests (Tables 2 and 3) performed with the measures, and ratios of D-I and D-II also did not show significant differences, in concordance with the homogeneous anatomy previously described. The Fourier analysis was useful to analyse intraspecific variation in those species where a large number of specimens were available (*G. melanoleucus* and *C. plancus*). The segregation of D-I and D-II from D-III and D-IV in *C. plancus* agrees with that previously reported and reinforces the considerably homogeneous nature of the morphology of these digits. Fourier analysis, which involves a large number of specimens of very few species, has proven to be a powerful tool for detecting complex differences that are not easily observed (e.g. Costa et al., 2008, 2010; Momtazi et al., 2008). Instead, when using Fourier analysis with many species and relatively few specimens, the results were misleading with the diurnal raptors. Our expectations were not fulfilled, and we considered that the number of specimens is not a problem but the tool we tried here does not allow us to distinguish one ungual from another with a low morphological variation.

Other workers have found differences in claw morphology between diurnal raptors and other groups (Csermely and Rossi, 2006; Csermely et al., 2012). Talons of Accipitridae and Falconidae are superficially similar to those of Strigiformes: they are strongly curved with a robust corpus that tapers towards the end and exhibit great development of the flexor and extensor tubercles (which are associated with the muscles responsible for the movement of the digits; *m. flexor digitorum longus*, *m. flexor hallucis longus*, *m. extensor digitorum longus*, *m. extensor hallucis longus*). They also share the presence of ventral foramina (an independent autapomorphy of these three groups, see Mayr and Clarke, 2003). Together, these features allow differentiation of birds or prey from other birds. However, talons of Accipitridae and Falconidae show two well-marked edges that delimit the ventral surface of the talon, whereas these are absent in Strigiformes (Mourer-Chauviré, 1983) and in the osprey (Pandionidae) giving the corpus an oval shape. With the exception of *Elanoides forficatus* in which the edge is absent, this edge is much more marked in Accipitridae than Falconidae. This highlights the importance of analysing the anatomical variation in as many species and specimens as possible. The analysis of more specimens of *Elanoides*

Table 2. Measurements and ratios ( $P < 0.05$ ) among digits analysed with a *t*-test and then Bonferroni correction. Toe number in Roman numerals

	Mean group 1	Mean group 2	<i>t</i> -value	df	<i>P</i>	Valid <i>N</i> group 1	Valid <i>N</i> group 2	Std.Dev. group 1	Std.Dev. group 2	F-ratio Variances	<i>P</i> variances	<i>P</i> -value Bonferroni
Height of articular facet												
I/II	-0.324	-0.33	0.134	38	0.894	19	21	0.164	0.157	1.088	0.85	No Sign
I/III	-0.324	-0.434	2.206	35	0.034	19	18	0.164	0.137	1.421	0.473	No Sign
I/IV	-0.324	-0.468	3.027	37	0.004	19	20	0.164	0.133	1.504	0.385	Sign
II/III	-0.33	-0.434	2.165	37	0.037	21	18	0.157	0.137	1.307	0.582	No Sign
II/IV	-0.33	-0.468	3.018	39	0.004	21	20	0.157	0.133	1.383	0.484	Sign
III/IV	-0.434	-0.468	0.786	36	0.437	18	20	0.137	0.133	1.058	0.899	No Sign
Width of articular facet												
I/II	-0.502	-0.53	0.519	38	0.606	19	21	0.175	0.16	1.197	0.693	No Sign
I/III	-0.502	-0.542	0.722	35	0.475	19	18	0.175	0.156	1.252	0.647	No Sign
I/IV	-0.502	-0.639	2.576	37	0.014	19	20	0.175	0.158	1.232	0.655	No Sign
II/III	-0.53	-0.542	0.235	37	0.815	21	18	0.16	0.156	1.046	0.934	No Sign
II/IV	-0.53	-0.639	2.211	39	0.033	21	20	0.16	0.158	1.029	0.953	No Sign
III/IV	-0.542	-0.639	1.916	36	0.063	18	20	0.156	0.158	1.016	0.98	No Sign
Length of the phalanx												
I/II	0.207	0.19	0.337	38	0.738	19	21	0.17	0.16	1.133	0.781	No Sign
I/III	0.207	0.118	1.702	35	0.098	19	18	0.17	0.149	1.293	0.601	No Sign
I/IV	0.207	0.04	3.338	37	0.002	19	20	0.17	0.142	1.438	0.439	Sign
II/III	0.19	0.118	1.45	37	0.155	21	18	0.16	0.149	1.14	0.791	No Sign
II/IV	0.19	0.04	3.162	39	0.003	21	20	0.16	0.142	1.269	0.607	Sign
III/IV	0.118	0.04	1.633	36	0.111	18	20	0.149	0.142	1.113	0.816	No Sign
Length of the flexor tubercle												
I/II	-0.342	-0.377	0.713	38	0.48	19	21	0.152	0.159	1.102	0.841	No Sign
I/III	-0.342	-0.26	-1.664	35	0.105	19	18	0.152	0.145	1.102	0.845	No Sign
I/IV	-0.342	-0.288	-1.182	37	0.245	19	20	0.152	0.133	1.305	0.57	No Sign
II/III	-0.377	-0.26	-2.372	37	0.023	21	18	0.159	0.145	1.215	0.691	No Sign
II/IV	-0.377	-0.288	-1.94	39	0.06	21	20	0.159	0.133	1.438	0.433	No Sign
III/IV	-0.26	-0.288	0.606	36	0.548	18	20	0.145	0.133	1.184	0.717	No Sign
Radius of curvature												
I/II	0.02	0.02	0.006	38	0.995	19	21	0.174	0.161	1.161	0.742	No Sign
I/III	0.02	-0.004	0.427	35	0.672	19	18	0.174	0.168	1.071	0.891	No Sign
I/IV	0.02	-0.092	2.263	37	0.03	19	20	0.174	0.134	1.692	0.264	No Sign
II/III	0.02	-0.004	0.449	37	0.656	21	18	0.161	0.168	1.084	0.855	No Sign
II/IV	0.02	-0.092	2.407	39	0.021	21	20	0.161	0.134	1.458	0.416	No Sign
III/IV	-0.004	-0.092	1.796	36	0.081	18	20	0.168	0.134	1.58	0.335	No Sign
Angle of curvature												
I/II	0.256	0.239	0.985	38	0.331	19	21	0.06	0.048	1.554	0.34	No Sign
I/III	0.256	0.163	4.514	35	0	19	18	0.06	0.065	1.156	0.762	Sign
I/IV	0.256	0.195	2.906	37	0.006	19	20	0.06	0.069	1.312	0.569	Sign
II/III	0.239	0.163	4.181	37	0	21	18	0.048	0.065	1.797	0.21	Sign
II/IV	0.239	0.195	2.347	39	0.024	21	20	0.048	0.069	2.039	0.122	No Sign
III/IV	0.163	0.195	-1.486	36	0.146	18	20	0.065	0.069	1.135	0.799	No Sign
Height/width of articular facet												
I/II	1.521	1.592	-1.164	38	0.252	19	21	0.202	0.186	1.175	0.722	No Sign
I/III	1.521	1.289	4.346	36	0	19	19	0.202	0.115	3.105	0.021	Sign
I/IV	1.521	1.49	0.554	37	0.583	19	20	0.202	0.14	2.087	0.121	No Sign
II/III	1.592	1.289	6.115	38	0	21	19	0.186	0.115	2.641	0.043	Sign
II/IV	1.592	1.49	1.977	39	0.055	21	20	0.186	0.14	1.775	0.217	No Sign
III/IV	1.289	1.49	-4.892	37	0	19	20	0.115	0.14	1.488	0.404	Sign
Length of the phalanx/Length of the flexor tubercle												
I/II	3.555	3.7	-1.343	38	0.187	19	21	0.354	0.327	1.174	0.724	No Sign
I/III	3.555	3.744	-1.489	36	0.145	19	19	0.354	0.426	1.451	0.438	No Sign
I/IV	3.555	3.389	1.598	37	0.118	19	20	0.354	0.295	1.44	0.437	No Sign
II/III	3.7	3.744	-0.375	38	0.71	21	19	0.327	0.426	1.703	0.25	No Sign

Table 2 (continued)

	Mean group 1	Mean group 2	t-value	df	P	Valid N group 1	Valid N group 2	Std.Dev. group 1	Std.Dev. group 2	F-ratio Variances	P variances	P-value Bonferroni
II/IV	3.7	3.389	3.193	39	0.003	21	20	0.327	0.295	1.226	0.66	Sign
III/IV	3.744	3.389	3.043	37	0.004	19	20	0.426	0.295	2.089	0.12	Sign
Length of the phalanx /radius of curvature												
I/II	1.545	1.483	1.516	38	0.138	19	21	0.146	0.114	1.624	0.294	No Sign
I/III	1.545	1.341	3.176	35	0.003	19	18	0.146	0.236	2.64	0.048	Sign
I/IV	1.545	1.366	3.504	37	0.001	19	20	0.146	0.172	1.396	0.483	Sign
II/III	1.483	1.341	2.433	37	0.02	21	18	0.114	0.236	4.286	0.002	No Sign
II/IV	1.483	1.366	2.574	39	0.014	21	20	0.114	0.172	2.267	0.077	No Sign
III/IV	1.341	1.366	-0.369	36	0.714	18	20	0.236	0.172	1.891	0.182	No Sign
Length of the phalanx /angle of curvature												
I/II	0.974	0.957	0.139	38	0.89	19	21	0.418	0.365	1.316	0.55	No Sign
I/III	0.974	0.953	0.169	35	0.867	19	18	0.418	0.333	1.578	0.353	No Sign
I/IV	0.974	0.738	2.155	37	0.038	19	20	0.418	0.249	2.829	0.03	No Sign
II/III	0.957	0.953	0.034	37	0.973	21	18	0.365	0.333	1.199	0.711	No Sign
II/IV	0.957	0.738	2.233	39	0.031	21	20	0.365	0.249	2.15	0.101	No Sign
III/IV	0.953	0.738	2.269	36	0.029	18	20	0.333	0.249	1.793	0.22	No Sign

Table 3. Summary of *T*-test results. A cross indicates the measurements and ratios with significant differences between digits. Number of toe I–IV

Digit	I/II	I/III	I/IV	II/III	II/IV	III/IV
Height of articular facet			x		x	
Width of articular facet						
Length of the phalanx			x		x	
Length of the flexor tubercle						
Radius of curvature						
Angle of curvature		x	x	x		
Height/width of articular facet		x		x		x
Length of the phalanx/Length of the flexor tubercle					x	x
Length of the phalanx /radius of curvature		x	x			
Length of the phalanx /angle of curvature						

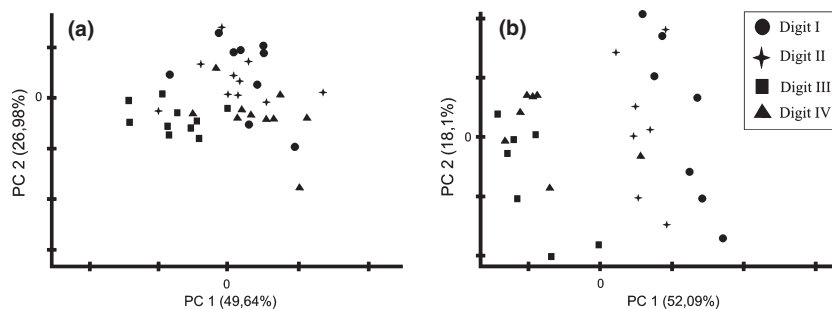
*forficatus* would help to know whether this is an isolated case or a typical feature of the species.

Regarding the differentiation at the species level, we could not find any unambiguous character, qualitative or quantitative, that gives certainty to the species assign-

ment. Only in *Rostrhamus sociabilis* (Fig. 2e), the talons are unequivocally distinguished both in the analysed PCA of the ratios as in the observation of the anatomical features. This bird is highly specialized on its diet, limited to freshwater snails of the genus *Pomacea* (Thiollay, 1994). Its relatively longer and slender talon morphology may be useful for snatching its prey. Finally, the overall size and shape of the ungual phalanges allow an approximation to the species that they belong to, namely larger claws probably belong to larger species, and vice-versa.

As Fowler et al. (2011) stated ‘The morphology of inter-phalangeal articulation surfaces is indicative of strategy for countering stress incurred during foot use’. Whether the differences described in this work are due to weight bearing, the use of the foot when obtaining their prey or a compromise between both remains to be studied. When a bird of prey is perching, it can be clearly seen that digit III is rotated medially along its long axis. Given that it is the main weight-bearing digit of the foot during terrestrial locomotion (Hopson 2001 in Glen and Bennett, 2007) and also during perching, it is plausible that the particular morphology of this digit, the medial edge and other features above described are due to this

Fig. 5. Principal components analysis graphs of the results of the Fourier analyses. (a) *Geranoaetus melanoleucus* (b) *Caracara plancus*. Coded by digit number. Note in (a) that, except for one specimen, digit III was clearly separated of the other digits; the same occurs in (b) with digits I and II separated of III and IV, in both cases across PC1.





reason. However, owing to the dearth of studies focused on qualitative and quantitative inter-digital variation in osseous features in diurnal birds of prey, it is difficult to draw comparisons with these data.

To conclude, through different techniques, we sought to determine limb and digit identity in diurnal birds of prey. Qualitative methods allowed discrimination of both attributes except for digit IV. But from the quantitative methods used here, we could not distinguish the left from the right limb in any case, and only a few characters (e.g. height of articular facet) distinguished some phalanges. There was no measurement that identifies isolated unguals, while this was qualitatively possible. The qualitative attributes that best allowed the discrimination were the relative displacement of the cotylae, the middle prominence of the articular facet, the relative position of the ventral foramina and the orientation of the flexor tubercle (Table 1). It is the sum of all these features, which differentiates both among digits and between limbs. These findings are relevant for the identification of fossil phalanges, which commonly appear isolated and fragmentary. The study performed here shows that the qualitative descriptors are more important than quantitative analyses for assessing ungual phalanx identity of the diurnal raptors.

The present work is a first contribution to the knowledge of the variation of the morphology of the ungual phalanx in species of diurnal birds of prey. Further studies with a larger number of specimens of each species will provide a more representative sample that will extend and enrich the present findings. Accordingly, studies are currently underway to examine variation in the contour of the talons within additional species.

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