Hind limb morphometry of terror birds (Aves, Cariamiformes, Phorusrhacidae): functional implications for substrate preferences and locomotor lifestyle

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ABSTRACT: The hind limbs of birds have long been considered a key feature in the conquest of different environments. However, the high level of morphological diversity encountered complicates the foundation of a good theoretical correlation between morphology, locomotor habits and substrate preference and this, in turn, complicates palaeobiological interpretations. Phorusrhacids (Aves, Cariamiformes) are a good example, since they have been unequivocally categorised as terrestrial birds due to their reduced forelimbs; and as apex predators with the ability to pursue prey based only on their hind limb morphology. Multivariate techniques (PCA and discriminant analysis), based on traditional metrics and geomorphometrics of the hind limb and pelvis, were applied in order to explore terrestriality and cursoriality in phorusrhacids. Although several groups of birds could be identified, when looking solely at hind limb metrics, some phorusrhacids appear to be associated with walking birds, while others are associated with cursorial birds. However, the pelvis separates cursorial birds and phorusrhacids from walking and wading birds. This scenario is complicated further by a lack of clear definition of the different locomotor modes and substrate preferences in extant birds, and this makes it difficult to confirm phorusrhacid cursoriality based solely on morphometrics. However, some qualitative features of the pelvis and foot make the picture a little clearer. To study limb adaptations in fossil birds, a more holistic study, with an emphasis on qualitative features of the whole posterior locomotor module, is necessary, since morphometrics leaves some issues unresolved. A comparison with the wings is also needed, in order to make a more complete analysis of locomotor behaviour.

KEY WORDS: ecomorphology, functional morphology, hind limbs, palaeobiology, phorusrhacids

Terror birds (Aves, Phorusrhacidae) comprise the most outstanding group of South American Cenozoic avifauna, and have been considered as apex predators in Cenozoic ecosystems (Ameghino 1895; Andrews 1899; Alvarenga & Höfling 2003; Blanco & Jones 2005; Bertelli *et al.* 2007; Degrange *et al.* 2010; Degrange 2012; Tambussi *et al.* 2012). Their terrestrial habits have been well established based on the reduction of their forelimbs (Alvarenga & Höfling 2003; Degrange 2012), although it is possible that minor species were able to fly in a clumsy manner (Degrange 2012). One of the pillars for the hypothesis of a predatory mode of life for phorusrhacids is based on the morphology of their hind limbs (Fig. 1), which seem to be suitable for pursuing prey. However, this assumption has long been based solely on the premise that phorusrhacid hind limb bones are long, which is a feature that is present in several extant birds that do not run, but walk or hop. Although previous studies on the biomechanics of the hind limbs (e.g., Tambussi 1997; Blanco & Jones 2005) and muscle reconstruction (Degrange 2012) pointed out that phorusrhacids were terrestrial birds with running abilities, a more extensive approach is needed.

Gatesy & Dial (1996) developed the concept of locomotor modules to explain the origin and evolution of flight and the diversification of locomotor styles in modern birds. According to these authors, a locomotor module is a highly integrated anatomical subregion of the muscle-skeletal system, acting as a unit during locomotion due to independent neuromuscular control. The three locomotor modules recognised by these authors (wings, tail and hind limbs) are given different priority according to different lifestyles (Gatesy & Dial 1996). However, Abourachid & Höfling (2012) recognised that legs have a multi-purpose potential based on their three-segment configuration. This configuration allows the use of legs as propulsive, paddling, foraging or grooming tools.

Following on from these concepts, and in order to explore the relationship between terrestriality, running abilities and prey pursuit in terror birds, I use the quantitative approaches of traditional morphometrics and modern geomorphometrics to study the posterior appendicular module. I will explore whether morphometrics and/or qualitative features adequately reflect the different terrestrial locomotor strategies of extant birds. This type of analysis can be used to recognise skeletal features that are crucial for terrestrial locomotion in birds, and also to infer the locomotor styles of phorusrhacids. This is the first time that geomorphometrics has been applied to any terror bird, and the results represent a major step forward in the effort to place our understanding of the ecology of terror birds on a more quantitative footing.
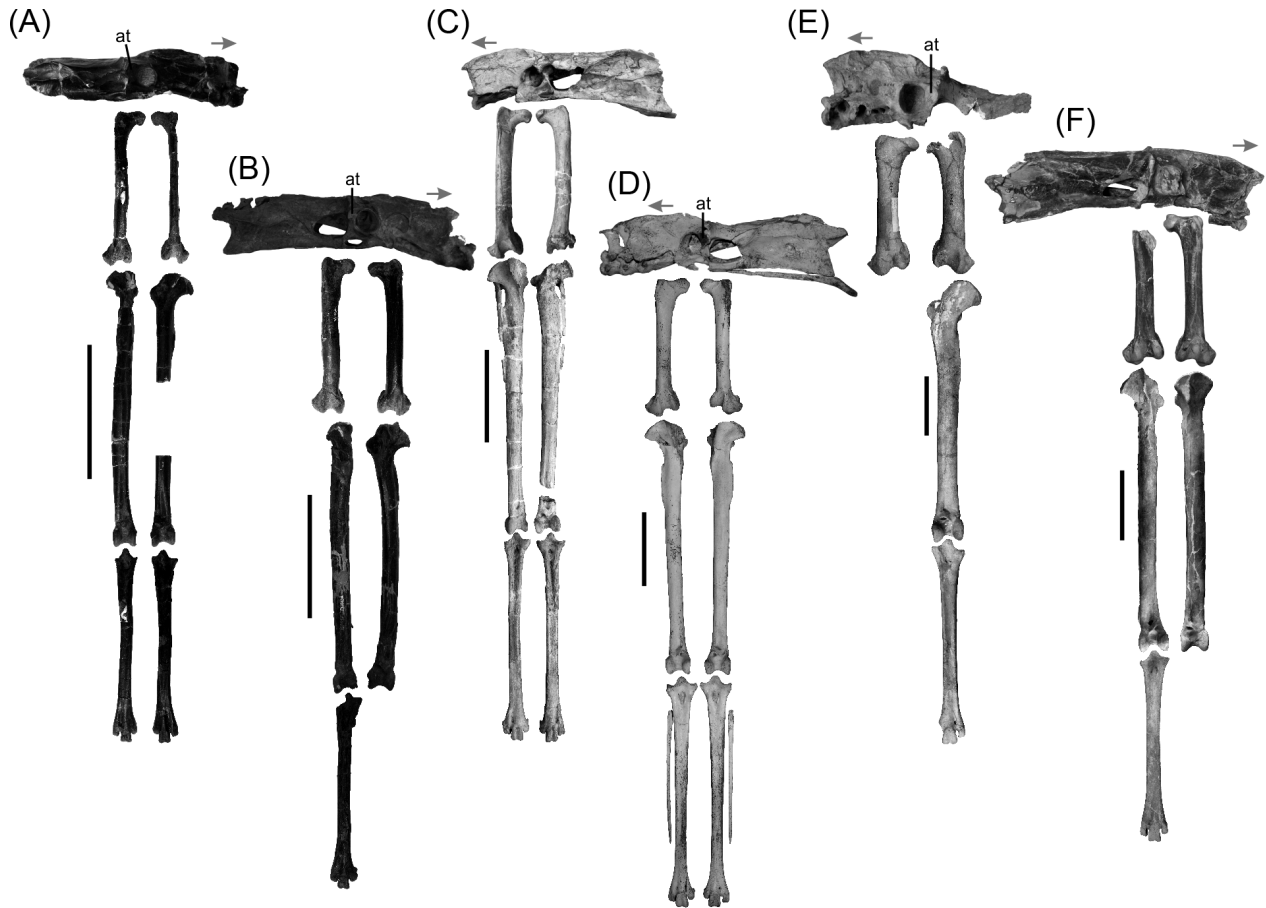
Figure 1 Phorusrhacid pelvis and hind limb: (A) *Psilopterus bachmanni*, YPM-PU 15904; (B) *Psilopterus lemoinei*, AMNH 9257 (pelvis) and YPM-PU 15402 (hind limb); (C) *Procariama simplex*, FM-P 14525; (D) *Llallawavis scagliai*, MMP 5050; (E) *Mesembriornis milneedwardsi*, MACN Pv 5944; (F) *Patagornis marshi*, NHMUK-A 516 (pelvis and femur) and AMNH 9264 (tibiotarsi and tarsometatarsus). Abbreviation: at = antitrochanter. Arrow indicates cranial part of the pelvis. Scale bars = 10 cm.

1. Materials and methods

1.1. Anatomical nomenclature
The anatomical nomenclature follows Baumel *et al.* (1993), except where noted. Latin terminology is used for muscles and osteological structures, whilst the English equivalent is also used in the Discussion.

1.2. Traditional morphometrics: measurements
The phorusrhacid femur, tibiotarsus and tarsometatarsus were measured (Fig. 2; Table 1) and analysed using the classic multivariate analysis of morpho-functional and ecomorphological analyses: PCA and discriminant analysis. The proportion that each element contributes to the whole hind limb was also analysed using ternary plots. These approaches were chosen over geomorphometrics because hind limb elements provide few homologous points for description using landmarks.

Measurements were taken using a 300 mm digital caliper with a resolution of 0.01 mm. No osteological reconstruction methods were used. As much of the material was very fragmentary, average individuals were created for each phorusrhacid species in order to use as many species as possible in the analysis. The average individual is made up from the average of each of the variables analysed (= measurement value/number of measurements carried out). All measurements are shown in Supplementary Tables 1–9.

Additionally, 22 ratios were constructed in order to obtain variables that describe the shape and features with a possible functional meaning, and to eliminate the arithmetic effect

introduced by size in calculations. These are: femur, EA/EB, EC/ED, EC/EE, EF/EG, EI/EH; tibiotarsus, ZB/ZA, ZD/ZC, ZJ/ZD, ZC/ZE, ZF/ZG, ZH/ZI; tarsometatarsus, AA/AB, AA/AC, AD/AP, AD/AE, AJ/AK, AF/AG, AH/AI, AL/AM; whole hind limb, EB/ZB, ZB/AA, EB/AA.

Angular measurements (e.g., AL and AM) were converted to radians, and all measurements were then converted by applying a decimal-based logarithm in order to reduce heterocedasticity (i.e., dispersion associated with high values; Peters 1983).

Principal component analyses (PCA) were carried out using a variance-covariance matrix. In order to check the contribution of body mass to the principal component 1 (the component that explains the most variation), a regression between the body mass and the contribution of each specimen to the component was performed. Dunning (2008) was used as a reference for extant avian body masses. For the complete hind limb, a separate analysis of PCA was also performed using the ratios. A discriminant analysis using a correlation matrix was also performed on the tarsometatarsus (Campbell & Marcus 1992) and the complete hind limb.

Two non-parametric discriminant analyses of the hind limb were carried out using a code written by Dr. A. Scarano (MLP), where the fda function of the mda package (Leisch *et al.* 2015) is used (using the MARS algorithm). The non-parametric method was chosen because the bird collection studied here is considered small (i.e., less than 250 specimens; A. Scarano pers. comm. 2011). In both analyses, a total of 67 individuals from different species were used to develop predictive models. To perform these analyses, three groups were
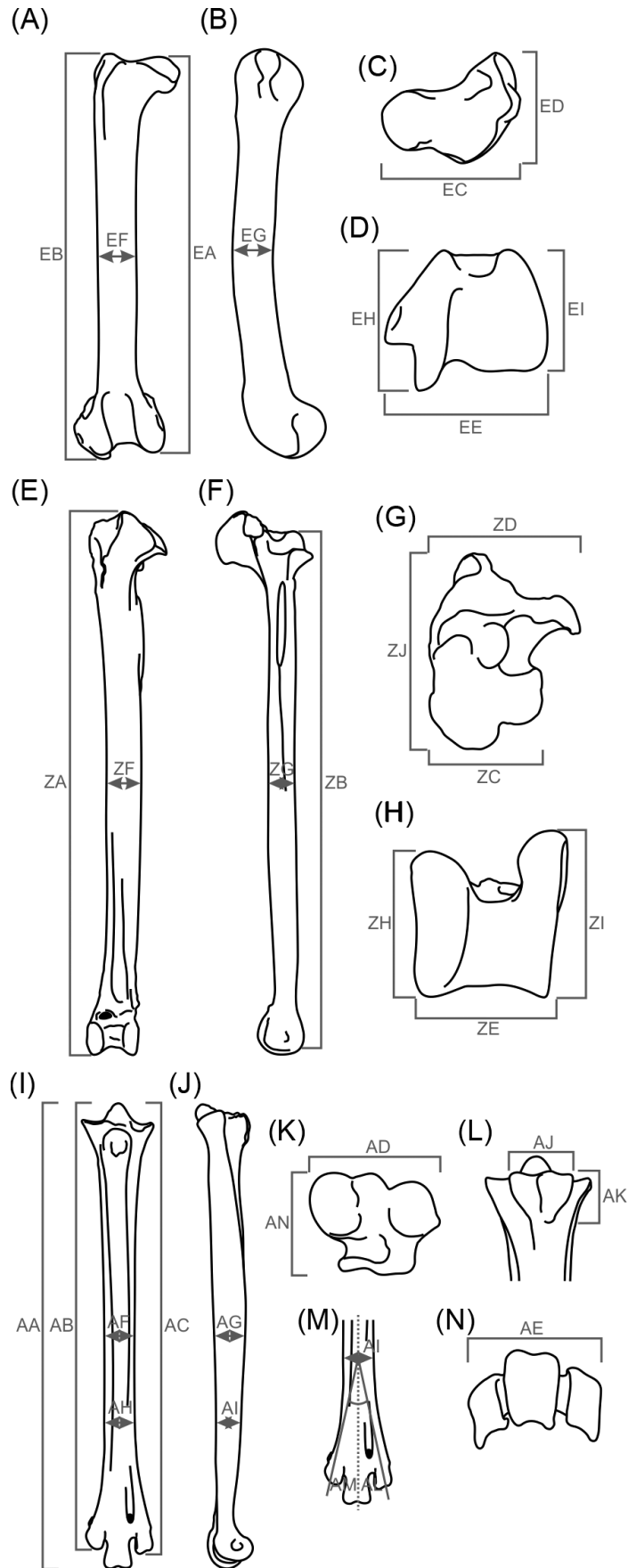
Figure 2 Measurements taken in birds' hind limbs studied herein. (A–D) femur: (A) cranial view; (B) lateral view; (C) proximal view; (D) distal view. (E–H) tibiotarsus: (E) cranial view; (F) lateral view; (G) proximal view; (H) distal view. (I–N) tarsometatarsus: (I) cranial view; (J) lateral view; (K) proximal view; (L) caudal view (*hypotarsus* measures); (M) cranial view (trochlear divarication); (N) distal view.

**Table 1** Measurements used in this work (see Fig. 2)

	Measurement name	Description	Abbrev.
Femur	Minor length	Measured between the *caput femoris* and the *condylus medialis*	EA
	Major length	Measured between the *crista trochanterica* and the *condylus lateralis*	EB
	Proximal latero–medial width	Measured between the *caput femoris* and the *trochanter femoris*	EC
	Crista trochanterica cranial extensión	Measured between the most cranial extreme of the *crista trochanterica* and its opposite point	ED
	Distal latero–medial width	Measured between the *condyli*	EE
	Corpus femoris latero–medial diameter	Measured at half of EB	EF
	Corpus femoris cranio–caudal diameter	Measured at half of EB	EG
	Condylus medialis cranio–caudal width	———————————————————————	EH
	Condylus lateralis cranio–caudal width	———————————————————————	EI
Tibiotarsus	Major length	Measured between the *crista cnemialis cranealis* and the *condylus medialis*	ZA
	Minor length	Measured between the *area interarticularis* and the space between the *condyli*	ZB
	Proximal latero–medial width	Measured between the *facies articularis*	ZC
	Latero–medial width of the *crista cnemialis lateralis*	Measured between the *facies articularis medialis* and the *crista cnemialis lateralis*	ZD
	Distal latero–medial width	Measured between the *epicondyli*	ZE
	Latero–medial diameter	Measured at half of ZB	ZF
	Cranio–caudal diameter	Measured at half of ZB	ZG
	Cranio–caudal width of the *condylus lateralis*	———————————————————————	ZH
	Cranio–caudal width of the *condylus medialis*	———————————————————————	ZI
	Cranial extension of the *crista cnemialis cranialis*	Measured between the *crista cnemialis cranialis* and the most caudal point of the *caput tibiae*	ZJ
Tarsometatarsus	Major length	Measured between the *eminentia intercotylaris* and the *trochlea metatarsi III*	AA
	Extension of the *trochlea metatarsi II*	Measured between the *eminentia intercotylaris* and the *trochlea metatarsi II*	AB
	Extension of the *trochlea metatarsi IV*	Measured between the *eminentia intercotylaris* and the *trochlea metatarsi IV*	AC
	Proximal latero–medial width	Measured between the *cotylae*	AD
	Distal latero–medial width	Measured between the *trochlea metatarsi II* and *IV*	AE
	Latero–medial diameter	Measured at half of AA	AF
	Cranio–caudal diameter	Measured at half of AA	AG
	Maximum constriction latero–medial diameter	Measured at the most thin part of the shaft	AH
	Maximum cranio–caudal diameter	Measured perpendicularly to AH	AI
	Latero–medial *hypotarsus* width	———————————————————————	AJ
	Hypotarsus length	———————————————————————	AK
	Divarication angle 1	Measured between the *trochlea metatarsi II* and *III*	AL
	Divarication angle 2	Measured between the *trochlea metatarsi III* and *VI*	AM
	Proximal cranio–caudal width	Measured between the *hypotarsus* and the cranial edge of the tarsometatarsus	AN

E = estilopod; Z = zeugopod; A = autopod

distinguished: 'waders' (W) or wading birds; 'ground birds' (G) or land birds (including birds capable of walking, running, jumping or hopping); and 'others' (X), essentially a group including flying, arboreal, predatory and swimming birds. The assignment of each species to a group was carried out according to Zeffer *et al.* (2003). This approach was used in order to explore the possibility that some phorusrhacids may have had wading habits.

The hind limb morphospace (a theoretical space that includes all morphological possibilities) of the phorusrhacids and other birds was also visualised using a ternary plot, in which the percentage contribution of each segment to the total length is
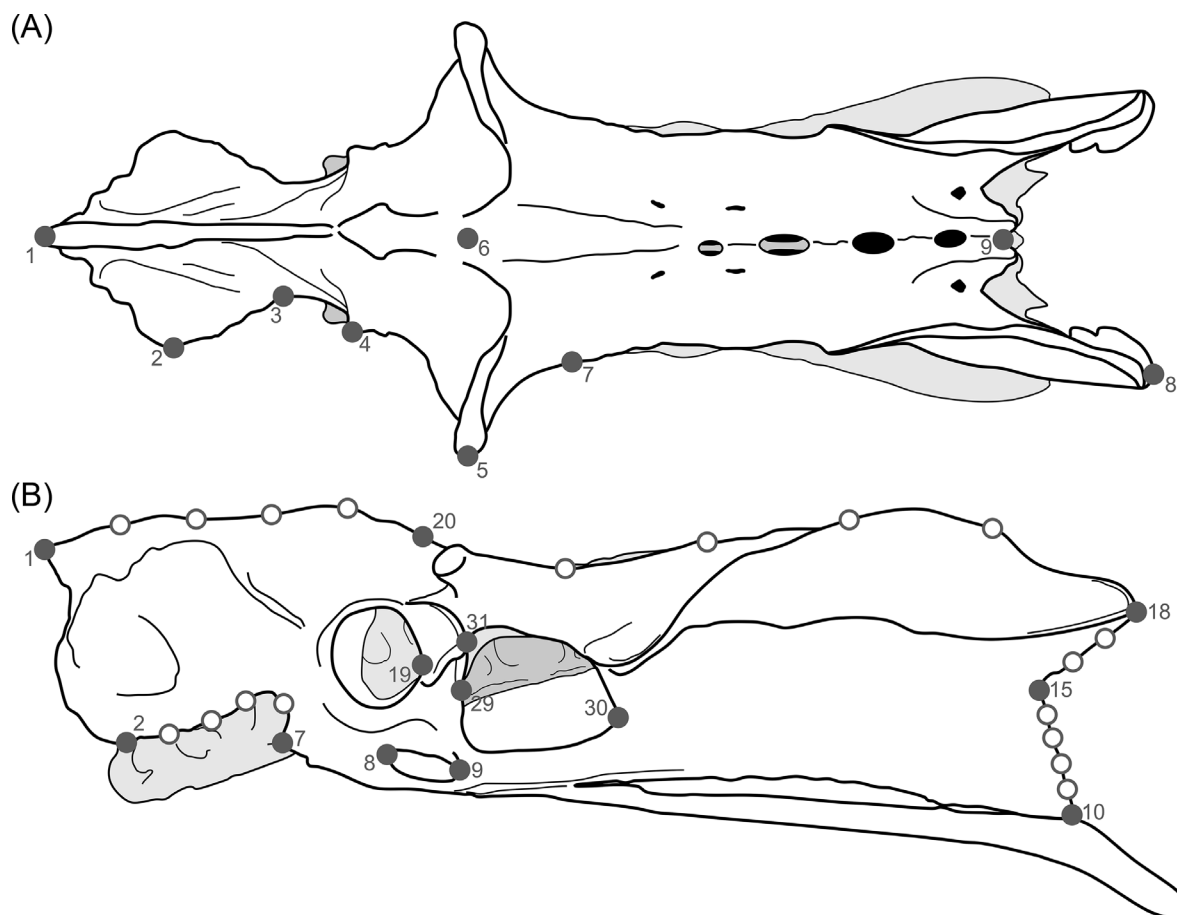
Figure 3 Landmarks used in the study of birds' pelvis: (A) dorsal view; (B) lateral view.

Table 2 Pelvic landmarks used in the geomorphometric analysis (see Fig. 3)

Pelvic view	Landmark Number	Landmark definition
Dorsal	1	Most cranial point of the *crista iliaca dorsalis*
	2	Most lateral point of the *ala preacetabularis ilii* edge
	3	Most medial point and of maximum inflexion of the *ala preacetabularis ilii*
	4	Most cranial point of the *foramen acetabuli*
	5	Most lateral point of the *crista supratrochanterica* (or analog structure)
	6	Point located on the half of the pelvis width, medially to landmark 5
	7	Maximum inflexion point behind the *antitrochanter*
	8	Most caudal point of the *spina dorsolateralis ilii*
	9	Most caudal point of the *synsacrum*
Lateral	1	Most cranial point of the *crista iliaca dorsalis*
	2	Most ventral point of the *ala preacetabularis ilii*
	3–6	Semi-landmarks over the ventral margin of the *ala preacetabularis ilii*
	7	Most cranial point of the *tuberculum preacetabulare*
	8	Most cranial point of the *foramen obturatum*
	9	Most caudal point of the *foramen obturatum*
	10	Most caudal point of the *processus terminalis ischii*
	11–14	Semi-landmarks over the caudal margin, between landmarks 10 and 15
	15	Maximum inflexion point between the *processus terminalis ischii* and the *spina dorsolateralis ilii*
	16–17	Semi-landmarks over the caudal margin, between landmarks 15 and 18
	18	Most caudal point of the *spina dorsolateralis ilii*
	19	Most caudal point of the *foramen acetabuli*
	20	Point located on the dorsal margin, vertically landmark 19
	21–24	Semi-landmarks over the dorsal margin of the *ala postacetabularis ilii*, located between landmarks 20 and 18
	25–28	Semi-landmarks over the dorsal margin of the *ala preacetabularis ilii*, located between landmarks 20 and 1
	29	Most cranial point of the *foramen ilioischiadicum*
	30	Most cranial point of the *foramen ilioischiadicum*
	31	Most caudal point of the *antitrochanter*

A

B
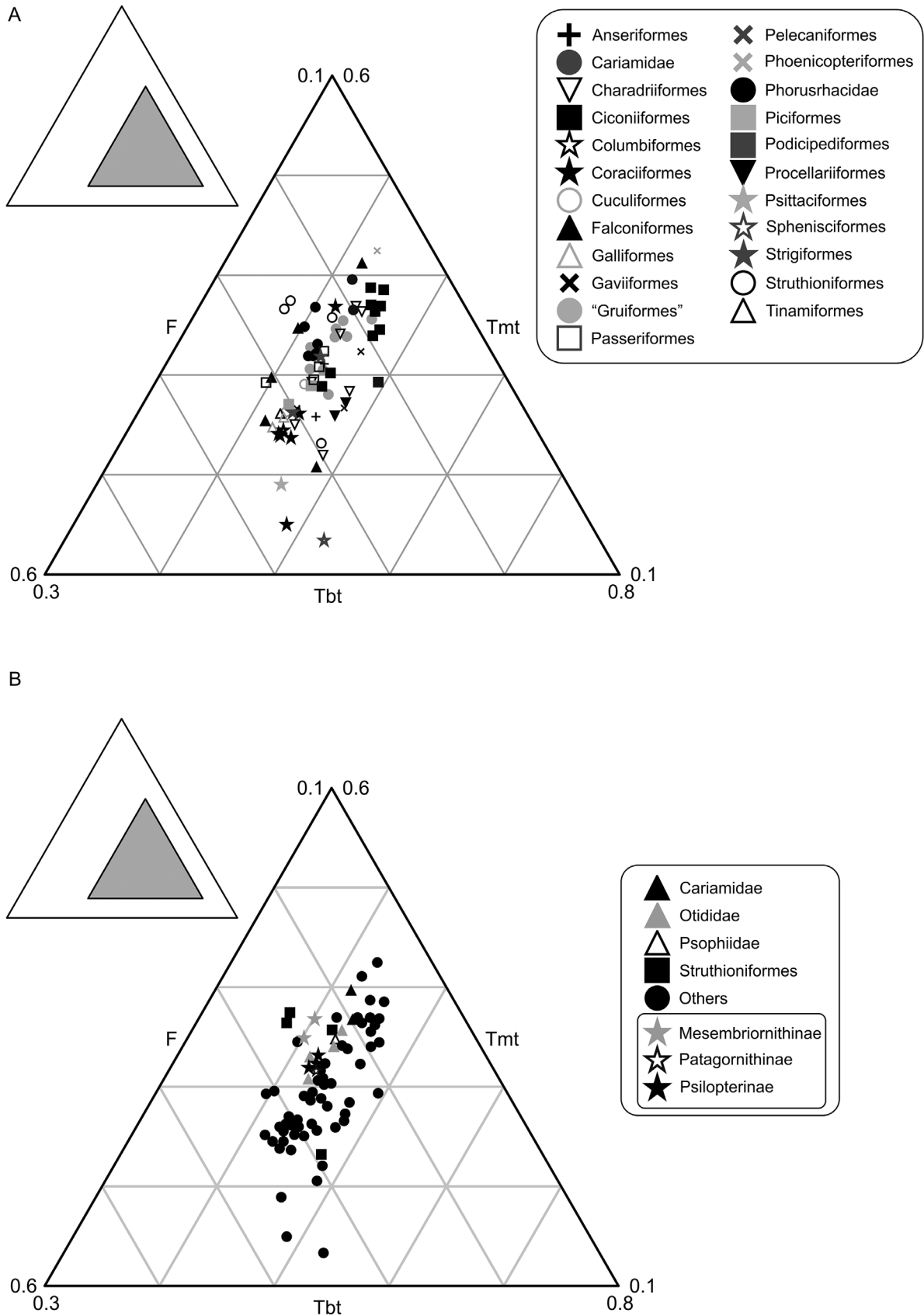
Figure 4 Neornithes' hind limb proportions: (A) graph showing the area occupied by phorusrhacids; (B) simplified graphic with phorusrhacids subfamilies discriminated. Abbreviations: F = femur; Tbt = tibiotarsus; Tmt = tarsometatarsus.

plotted in one of the three axes that define a triangle. Measurements used were EB, ZB and AA, which were added (using raw data) to obtain the total length of the posterior member. The percentages were obtained by dividing each segment's length by the total hind limb length and multiplying the result by 100. Theoretically, any appendicular design can be plotted in this way, as long as none of its segments measure 0, thus avoiding the perimeter of the triangle (Gatesy & Middleton

Table 3 Principal component analysis of the phorusrhacids and extant birds, analysed using femur, tibiotarsus, tarsometatarsus, complete hind limb and hind limb ratios measurements. Only the first five components are shown. For more details, see Supplementary Tables

	Component	Eigenvalue	% Variance	Cumulative % Variance
Femur	1	0.841961	98.48884	98.4888
	2	0.005015	0.58660	99.0754
	3	0.003353	0.39217	99.4676
	4	0.001421	0.16627	99.6339
	5	0.001130	0.13220	99.7661
Tibiotarsus	1	0.856116	97.08505	97.0851
	2	0.011359	1.28818	98.3732
	3	0.006753	0.76577	99.1390
	4	0.002727	0.30929	99.4483
	5	0.001555	0.17639	99.6247
Tarsometatarsus	1	1.264172	88.01315	88.0131
	2	0.112203	7.81172	95.8249
	3	0.018022	1.25472	97.0796
	4	0.015659	1.09017	98.1698
	5	0.008243	0.57389	98.7436
Hind limb	1	2.681229	92.44654	92.4465
	2	0.118536	4.08701	96.5336
	3	0.019340	0.66684	97.2004
	4	0.017614	0.60732	97.8077
	5	0.012625	0.43531	98.2430
Hind limb ratios	1	0.530733	51.21692	51.2169
	2	0.128818	12.43124	63.6482
	3	0.099694	9.62069	73.2689
	4	0.064833	6.25655	79.5254
	5	0.053793	5.19118	84.7166

1997; Middleton & Gatesy 2000). In the analyses performed here, the objective was to explore possible morphological similarities and discuss their functional and ecological implications.

All analyses were performed with Statistica v.6.0 and R v.2.13.1.

1.3. Geomorphometrics

It should be noted that classical morphometry has several problems: linear measurements are strongly correlated with size (Bookstein *et al*. 1985) but, meanwhile, geomorphogeometric approaches have a clear protocol to remove the arithmetic effect of dimension (centroid size), whilst an analogue method using linear measurements is not so well-established. In addition, the homology of linear measurements is usually difficult to establish; the same measurements may represent very different forms and, finally, it is difficult to generate graphs representing the studied shape based on the linear measurements taken (Adams *et al*. 2004). In addition, geomorphometric approaches are found to be very effective at the moment of capturing information about the shape of an organism (Zelditch *et al.* 2004).

Keeping these issues in mind, and also considering that the pelvis is a very complex structure (i.e., hard to represent through linear measurements), the terror birds' pelvises were analysed using 2D landmarks (homologous points), photographed from a dorsal and lateral view (Fig. 3; Table 2). *X* and *y* coordinates for each landmark were digitised using TpsDig 1.41 software (Rohlf 2005). The resulting coordinates were subjected to a generalised procrustes analysis (GPA) to remove any information unrelated to shape (Rohlf & Slice

1990; Zelditch *et al*. 2004). Localised shape changes were estimated using the partial warp scores (Bookstein 1991), and once these values were obtained, a relative warps analysis (RWA) (Rohlf 1993) was performed to examine the changes in shape of the pelvis using TpsRelw 1.35 (Rohlf 2003) and MorphoJ v. 1.03c (Klingenberg 2011) software.

The relative warps obtained were used to examine whether the morphological groups were consistent with the locomotor habit of the extant species.

1.4. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; FM, Field Museum of Natural History, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Buenos Aires, Argentina; NHMUK, The Natural History Museum, London, UK; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

2. Results

### 2.1. Hind limb diversity: ternary plot

The studied group of birds includes 75 individuals of different species that occupy only 9 % of the total area of triangular space, distributed in an area equivalent with that of Gatesy & Middleton (1997) (Fig. 4). No species are known to have femurs proportionally smaller than 27 % or bigger than 56 %. Tibiotarsus length varies between 37 % and 55 %, while the tarsometatarsus length is between 14 % and 45 %. In accordance with the proposal of Gatesy & Middleton (1997), the tarsometatarsus is the largest contributor to the variation (31%), followed by the femur (29 %) and finally the tibiotarsus (18 %), which is the most conservative in its length. When plotted (Fig. 4A), the phorusrhacids are located next to the Otididae, Passeriformes, *Polyborus plancus* (Falconiformes), *Tyto alba* (Strigiformes) and Rheidae, and away from the Cariamidae and Sagittarius, to which they have traditionally been compared (e.g., Andrews 1899).

The contribution of the femur, tibiotarsus and tarsometatarsus to the total length of the hind limb is identical in Psilopterinae and Patagornithinae, whilst in the Mesembriornithinae the tarsometatarsus is longer and the tibiotarsus is shorter. The femur of the Mesembriornithinae can be as long as in Psilopterinae–Patagornithinae, as in *Mesembriornis* or *Llallawavis*. In the latter, the tarsometatarsus is even longer, with a similar proportion to Rheidae (Fig. 4B).

2.2. Principal component analyses (PCA)

2.2.1. Femur. 74 individuals from different species were included in the analysis. The first two components account for 99 % of the total variation. PC1 explains 98.5 % (Table 3; Supplementary Tables 10–11). Whilst all variables have a strong contribution to this component, the cranial extension of the *crista trochanterica* (ED) and the cranio–caudal width of the *condylus medialis* (EH) have a slightly higher contribution. PC2 explains 0.5 % of the total variation in relation to femur length measurements (EA and EB) and the cranio–caudal diameter of *corpus femoris* (EG). In accordance with Campbell & Marcus (1992), birds are not separated by their locomotor habits, but rather by body size, represented here by body mass.

PC1 is strongly influenced by body mass (R = 0.96; R^2 = 0.93; P = 0.0000), and of the 98.5 % explained by this component, 93 % is explained by the mass of the animals analysed. It can be seen in Figure 5 that smaller birds are located to
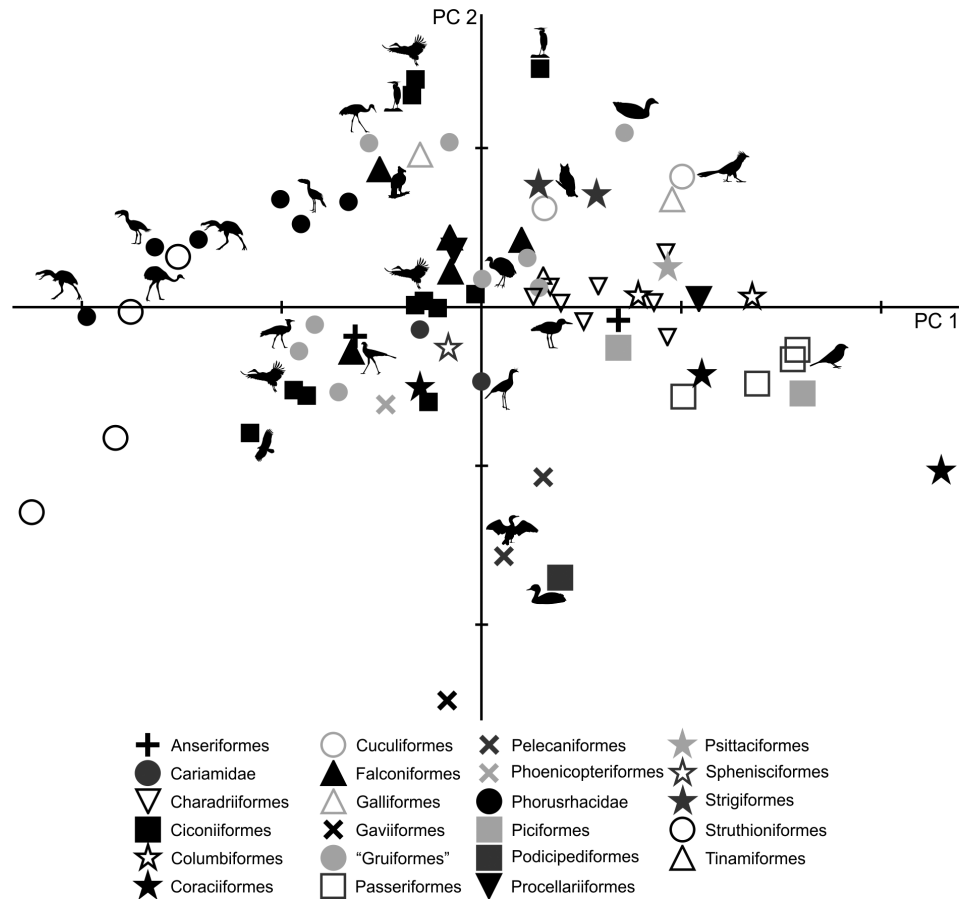
Figure 5 Principal component analysis of the femur: distribution of taxa in the morphospace defined by CP1 and CP2.

the right of the graph, whilst the largest are on the left. Phorusrhacids have negative values for PC1 and positive values for PC2. When plotted in a PC1–PC2 graph, phorusrhacids are separated into two groups (Fig. 5): *Llallawavis*, *Mesembriornis* and *Patagornis* are associated with terrestrial birds with cursor capacity such as *Pterocnemia* and *Rhea*; whilst the Psilopterinae *Psilopterus lemoinei*, *P. bachmanni* and *Procariama simplex* are grouped with flying birds, but with some connection to the terrestrial environment, whether waders or walkers (*Grus*, *Ciconia*, *Aramus*, *Ardea* and *Penelope*). Particularly striking is the membership to this group of the raptor *Geranoaetus*. PC1 distinguishes between the medium-sized phorusrhacids (*Llallawavis*, *Mesembriornis* and *Patagornis*) and the smallest ones (Psilopterinae).

PC2 distinguishes the birds with stouter and shorter femurs (with negative values) from those with more slender and elongated femora (indicated by positive values). The Psilopterinae belong to this second group, whilst the medium-sized phorusrhacids have PC2 values closer to 0, thus indicating more robust femora. *Emeus* (Struthioniformes), traditionally considered as 'graviportal' (see Tambussi *et al.* 2010 for a discussion on the incorrect application of this term in birds), has negative values for both components.

2.2.2. Tibiotarsus. The analysis included 72 individuals from different species. The first two components account for 98.3 % of the total variation. PC1 explains 97 % of the variation (Table 3; Supplementary Tables 12–13), mainly in relation to the latero-medial diameter of the *corpus tibiotarsi* (ZF), the cranio–caudal width of both condyli (ZH and ZI) and the cranial extension of the *crista cnemialis cranialis* (ZJ). Meanwhile, PC2 explains 1.3 % in relation to the tibiotarsi length measurements (ZA and ZB).
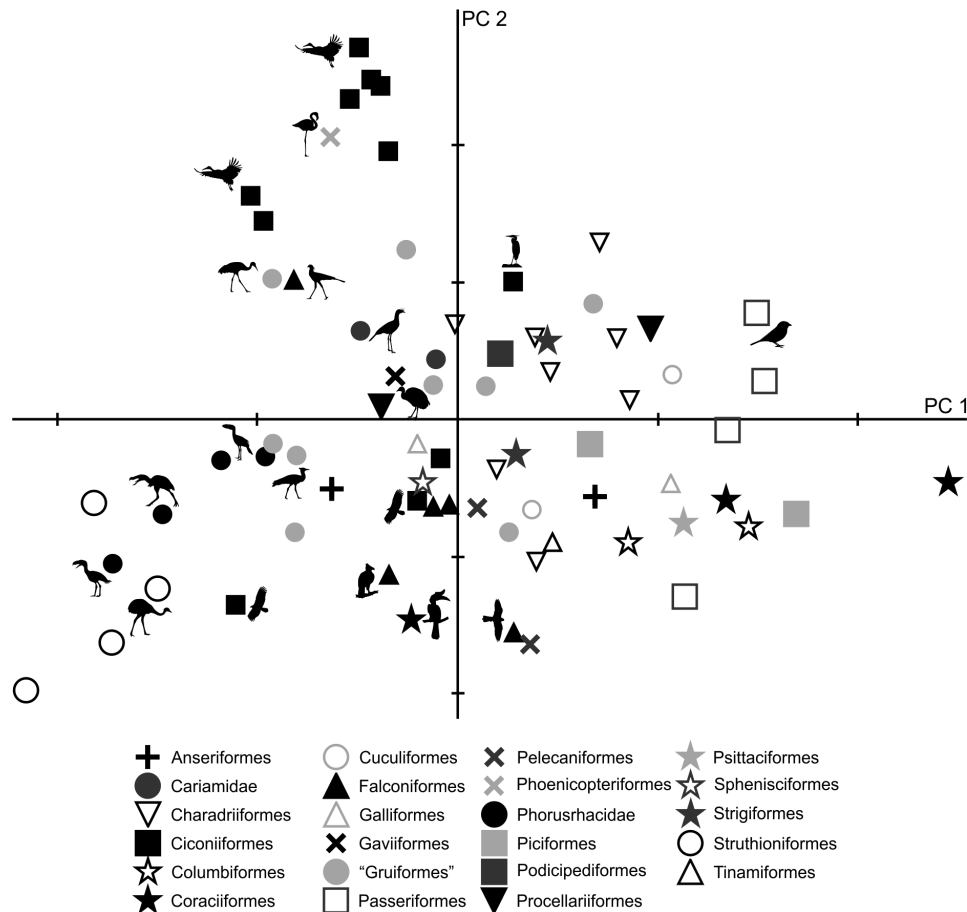
In the PC1–PC2 scatterplot (Fig. 6), a group formed of *Patagornis*, *Llallawavis* and terrestrial birds with cursor capacities (*Pterocnemia*, *Rhea* and *Dromaius*) can be separated from the group made up of Psilopterinae (*P. lemoinei* and *P. simplex*) and other terrestrial birds such as the Otididae *Ardeotis kori*, *Ardeotis arabs* and *Otis tarda*, and the Anseriformes *Chauna torquata*. These were all birds capable of flying (some are even migratory species from long distances), but that preferred to walk.

As with the femur, PC1 is strongly influenced by body mass (R $= 0.96$; R$^2 = 0.92$; $P = 0.0000$): of the 97 % explained by PC1, 92 % is correlated with mass. The larger forms are located to the left of the graph, while the smaller are located to the right. In PC1, birds can also be distinguished according to their shaft and *crista cnemialis cranialis*: negative values correspond to birds with robust shafts and extended *crista cnemialis cranialis*.

PC2 allows the identification of birds according to the length of their tibiotarsus. Wading birds such as *Phoenicopterus*, *Ciconia*, *Leptoptilos*, *Mycteria*, *Ardea* and *Aramus,* and walkers such as *Grus* (which can also wade occasionally) and *Sagittarius*, have very long tibiotarsi (high positive values). Runners such as Cariamidae have positive values close to 0, indicating longer tibiotarsi than those of Phorusrhacidae. The smaller phorusrhacids have negative values close to 0, indicating the presence of longer tibiotarsi than those of the medium-sized terror birds.

2.2.3. Tarsometatarsus. 76 individuals from different species were included in the analysis. The first two components account for 95.8 % of the total variation (Table 3; Supplementary Tables 14–15). PC1 explains 88 % of the variation in tarsometatarsus length measurements (AA, AB and AC), whilst PC2 explains 7.8 % of length measurements (AA, AB and AC), latero–medial diameters (AF and AH) and divarication angles (AL, AM).

Figure 6 Principal component analysis of the tibiotarsus: distribution of taxa in the morphospace defined by CP1 and CP2.

As in the case of tibiotarsus, in the PC1–PC2 plot (Fig. 7), a group composed of *Patagornis*, *Llallawavis* and terrestrial birds with cursor capacities (*Pterocnemia*, *Rhea* and *Dromaius*) can be observed, whereas *P. lemoinei*, *P. bachmanni* and *P. simplex* are grouped with land birds that prefer to walk, but have the ability to run, such as the Otididae *Ardeotis kori*, *Ardeotis arabs* and *Otis tarda*; although there are also other terrestrial wading birds associated, such as *Chauna*, *Grus*, *Leptoptilos crumeniferus* and *L. dubius*, and terrestrial walkers such as *Sagittarius*. The phorusrhacid *Paraphysornis* is associated with the Anseriformes *Brontornis* and the Struthioniformes *Emeus*. *Phorusrhacos longissimus* is not associated with any group, and is in between runners and 'graviportal' birds.

Although PC1 is strongly influenced by body mass (R = 0.95; R^2 = 0.90; P = 0.0000), it is less so than for the femur and tibiotarsus. Of the 95.8 % explained by PC1, 90 % is correlated with body mass. These results are consistent with Campbell & Marcus (1992), who stated that the tarsometatarsus is the bone that better reflects a bird's habit, since it is less influenced by mass. The more voluminous birds are located to the right, while the smaller are on the left of Figure 7.

With respect to PC2, positive values indicate long, slender tarsometatarsi with low angle divarication, whilst negative values indicate short, more robust tarsometatarsi shapes and a high divarication angle. In the case of phorusrhacid, the Psilopterinae, *Llallawavis* and *Patagornis* correspond to birds with long tarsometatarsi and with divarication angles which are lower than those of *Paraphysornis*, which has short tarsometatarsi with high divarication angles. *Phorusrhacos* has an intermediate length between *Paraphysornis* and Psilopterinae, but has a high divarication angle.

2.2.4. Complete hind limb. 72 individuals from different species were analysed using a total of 33 measurements of the femur, tibiotarsus and tarsometatarsus. The first two components account for 96.5 % of the total variation (Table 3; Supplementary Tables 16–17). PC1 explains 92.5 % of the variation related to the cranial extension of the *crista trochanterica* (ED), the cranio–caudal width of condyli (EH and EI), the latero–medial diameter of the *corpus tibiotarsi* (ZF), the cranial extension of the *crista cnemialis cranialis* (ZJ) and the tarsometatarsus length (AA, AB and AC). Meanwhile, PC2 explains 4 % of the variation of the tarsometatarsus length (AA, AB and AC) and divarication angles (AL and AM).

The PC1–PC2 plot (Fig. 8) shows that *Patagornis marshi* and *Llallawavis scagliai* are clearly grouped with landbirds with cursor capacities such as *Dromaius*, *Rhea* and *Pterocnemia*. *P. simplex* and *P. lemoinei* are associated with walker birds like the Otididae *Ardeotis kori*, *Ardeotis arabs* and *Otis tarda*, the Falconiformes *Sagittarius*, the Gruidae *Grus*, and the Ciconiidae *Leptoptilos crumeniferus* and *L. dubius*.

PC1 is strongly influenced by body mass (R = 0.96; R^2 = 0.92; P = 0.0000): of the 92.5 % explained by PC1, 92 % is correlated to body mass, whilst only 0.5 % is from shape. However, it should be noted that positive PC1 values indicate birds with projected femur condyli, cranially extended *crista trochanterica*, tibiotarsi with robust diaphysis, developed *crista cnemialis cranealis* and long tarsometatarsi.

As in the tarsometatarsus analysis, positive PC2 values indicate long, slender tarsometatarsi with a low divarication angle of the trochleae metatarsi. Phorusrhacids have values close to 0.
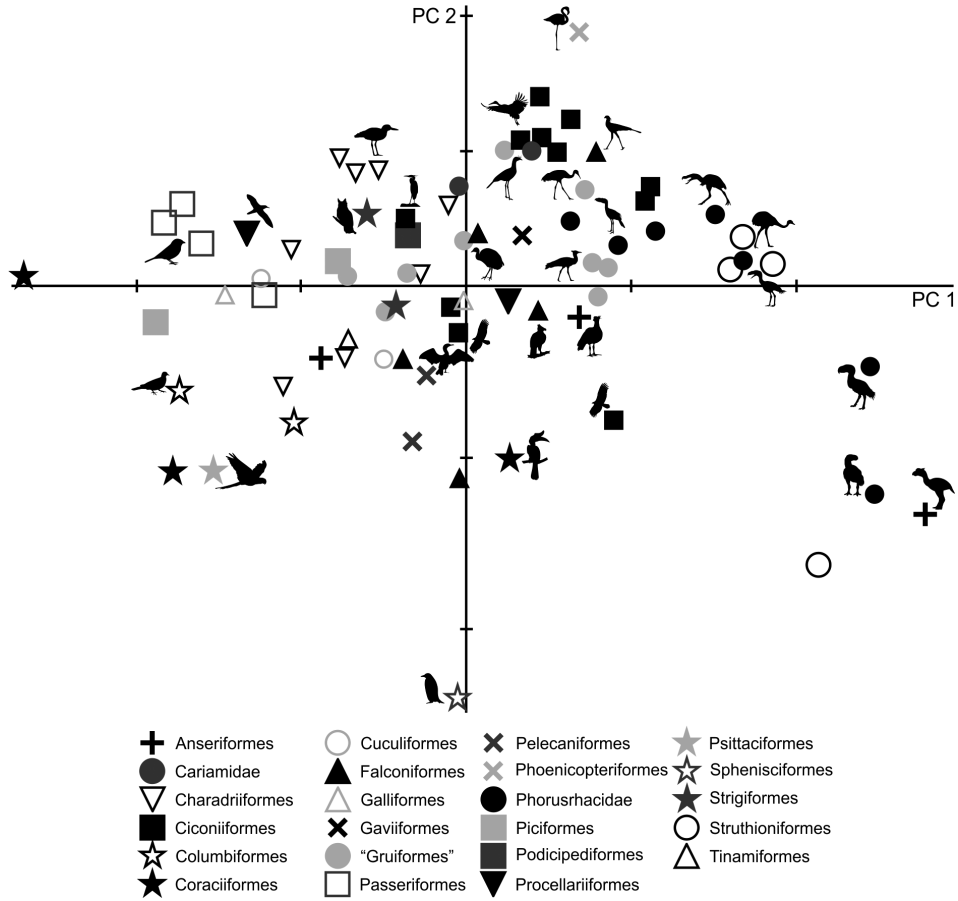
Figure 7 Principal component analysis of the tarsometatarsus: distribution of taxa in the morphospace defined by CP1 and CP2.
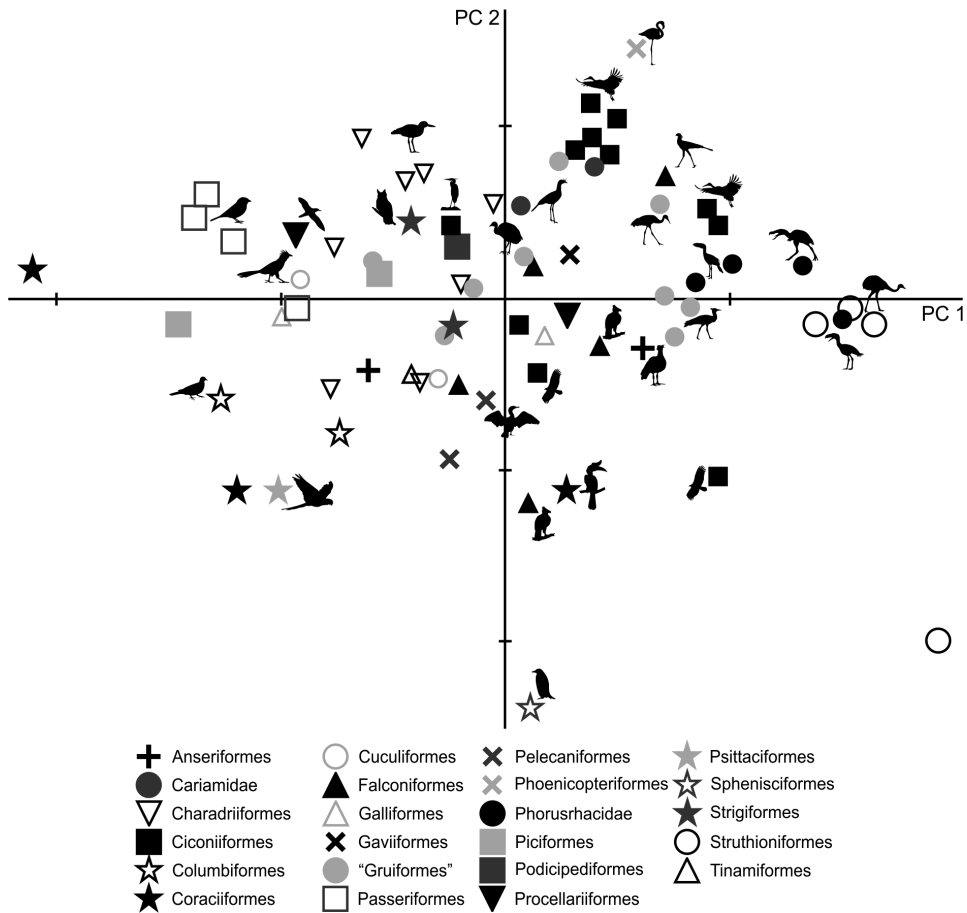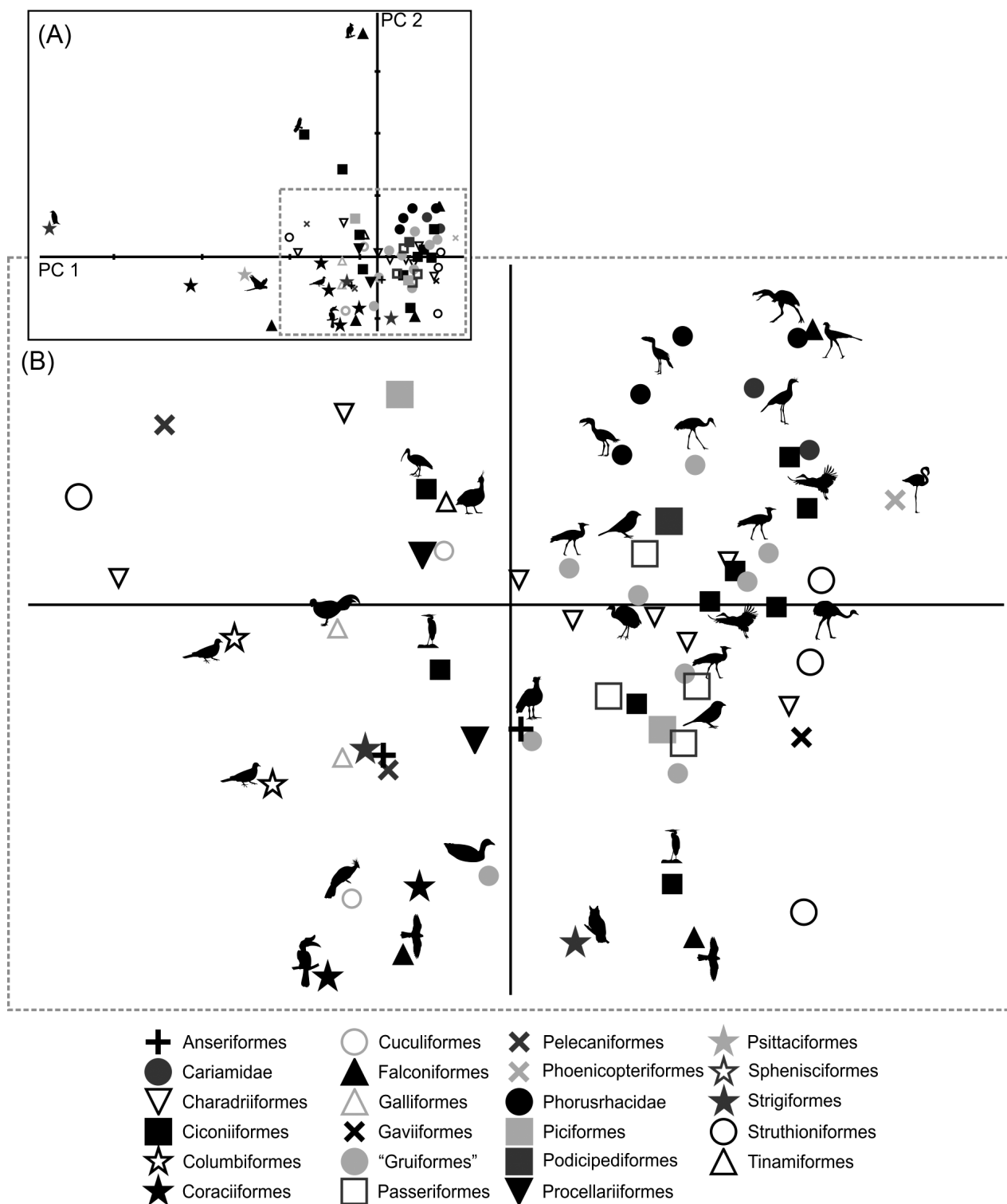

Figure 8 Principal component analysis of the complete hind limb: distribution of taxa in the morphospace define d by CP1 and CP2.

Figure 9 Principal component analysis of the hind limb ratios: (A) distribution of taxa in the morphospace defined by CP1 and CP2; (B) detail of the principal area of taxa distribution in the morphospace.

2.2.5. Hind limb ratios. Only by using the first seven components did the variation explained reach 90 % (Table 3; Supplementary Tables 18–19). Due to the removal of the arithmetic effect of dimensions by using ratios, the first two components account only for 63.6 % of the total variation. PC1 explains 51.2 % of the variation in the ratios related to limb proportions (EB/AA and ZB/AA) and the robustness of the tarsometatarsus (AF/AG and AH/AI). PC2 explains 12.4 % of the variation related to *hypotarsus* development (AJ/AK), and PC3 explains 9.6 % in relation to the cranial development of the *crista trochanterica* (EC/ED), the relative development

of the *cristae cnemialis* (ZJ/ZD) and the robustness of the tarsometatarsus (AJ/AK).

Phorusrhacids have values close to 0.4 for PC1 and PC2 (Fig. 9), and they appear to be associated with a very heterogeneous group consisting of birds such as Cariamidae, *Grus*, *Sagittarius*, *Pitangus*, *Phoenicopterus*, *Podiceps* and *Ardeotis arabs,* amongst others.

PC1 separates birds with a shorter femora and a longer, slender tarsometatarsus. A positive PC2 value indicates a wider *hypotarsus* (high AJ/AK ratio), whilst negative values indicate a narrow *hypotarsus* (low AJ/AK ratio).

Table 4 The probability of correct classification (CC) of each group based on the discriminant analysis performed on the tarsometatarsus

	G	W	X	CC
G	11	4	7	50 %
W	2	10	7	71.4 %
X	5	1	25	80.6 %

Abbreviations: G = ground birds; W = wading birds; X = "other birds". Assignments according to Zeffer *et al.* (2003)

Table 5 Phorusrhacids' probabilities of belonging to the groups used here based on the discriminant analysis made on the tarsometatarsus

	G	W	X
Psilopterus lemoinei	0.737	5.09E-04	0.211
Psilopterus bachmanni	0.533	1.71E-05	0.294
Procariama simplex	0.846	5.90E-04	0.094
Paraphysornis brasiliensis	0.977	6.63E-02	0.022
Patagornis marshi	0.873	9.45E-03	0.117
Phorusrhacos longissimus	0.993	1.90E-00	0.006
Llallawavis scagliai	0.928	3.71E-04	0.034
Brontornis burmeisteri	0.872	4.93E-04	0.127

Abbreviations: G = ground birds; W = wading birds; X = "other birds"

Table 6 The probability of correct classification (CC) of each group based on the discriminant analysis made on the hindlimb

	G	W	X	CC
G	10	1	11	45.50 %
W	3	9	2	64.30 %
X	8	1	22	71.00 %

Abbreviations: G = ground birds; W = wading birds; X = "other birds". Assignments according to Zeffer *et al.* (2003)

2.3. Discriminant analyses

2.3.1. Tarsometatarsus. The discriminant model using only the tarsometatarsus has an average probability of a correct classification of 67.3 % (model error: 0.20896; N = 67). The probability of a correct classification (CC) of each group is shown in Table 4. Probabilities that phorusrhacids belong to the groups used here are shown in Table 5.

According to the tarsometatarsus measurements, phorusrhacids are more likely to belong to group G (ground birds; Fig. 10A) than to either of the other two groups, with a probability of 53 % (*P. bachmanni*) to 99 % (*Phorusrhacos longissimus*). *Procariama*, *Patagornis*, *Llallawavis*, *Phorusrhacos* and *Paraphysornis* have the highest probability of belonging to this group. The case of the *Psilopterus* species is not so categorical. Although the chances of this species being waders are very low, the likelihood of *P. lemoinei* belonging to the group made up of all other birds is not so low (21 %), and in the case of *P. bachmanni* it is almost 30 %. Furthermore, in an estimate of the probability of *Brontornis* belonging to any of the three groups, it is shown to have an 87 % chance of being a ground bird and a 12 % chance of belonging to group X.

2.3.2. Hind limb. The complete hind limb model has an average probability of a correct classification of 60.26% (model error: 0.1791; N = 67). The probability of a correct classification (CC) for each group can be seen in Table 6, whilst the probability of phorusrhacids belonging to the groups studied here is shown in Table 7.

Table 7 Phorusrhacids' probabilities of belonging to the groups used here based on the discriminant analysis made on the hind limb

	G	W	X
Psilopterus lemoinei	0.938	3.87E-02	0.061
Procariama simplex	0.985	6.95E-01	0.014
Patagornis marshi	0.998	1.17E-02	0.001
Llallawavis scagliai	0.995	5.34E-01	0.004

Abbreviations: G = ground birds; W = wading birds; X = "other birds"

Table 8 Principal component analysis of the pelvis in dorsal and lateral view. Only the first five components are shown. For more details, see Supplementary Tables

|	Component	Eigenvalue	% Variance	Cumulative % Variance
Dorsal view	1	1.23315	65.98	65.98
	2	0.57298	14.24	80.22
	3	0.38892	6.56	86.78
	4	0.32193	4.50	91.28
	5	0.2876	3.59	94.87
Lateral view	1	0.80533	41.83	41.83
	2	0.55563	19.91	61.74
	3	0.39779	10.20	71.94
	4	0.3277	6.93	78.87
	5	0.297	5.69	84.56

Phorusrhacids should therefore belong to group G (Fig. 10B) of Zeffer *et al.* (2003), with a 93 % probability for *P. lemoinei* and a 99 % probability for *Patagornis* and *Llallawavis*.
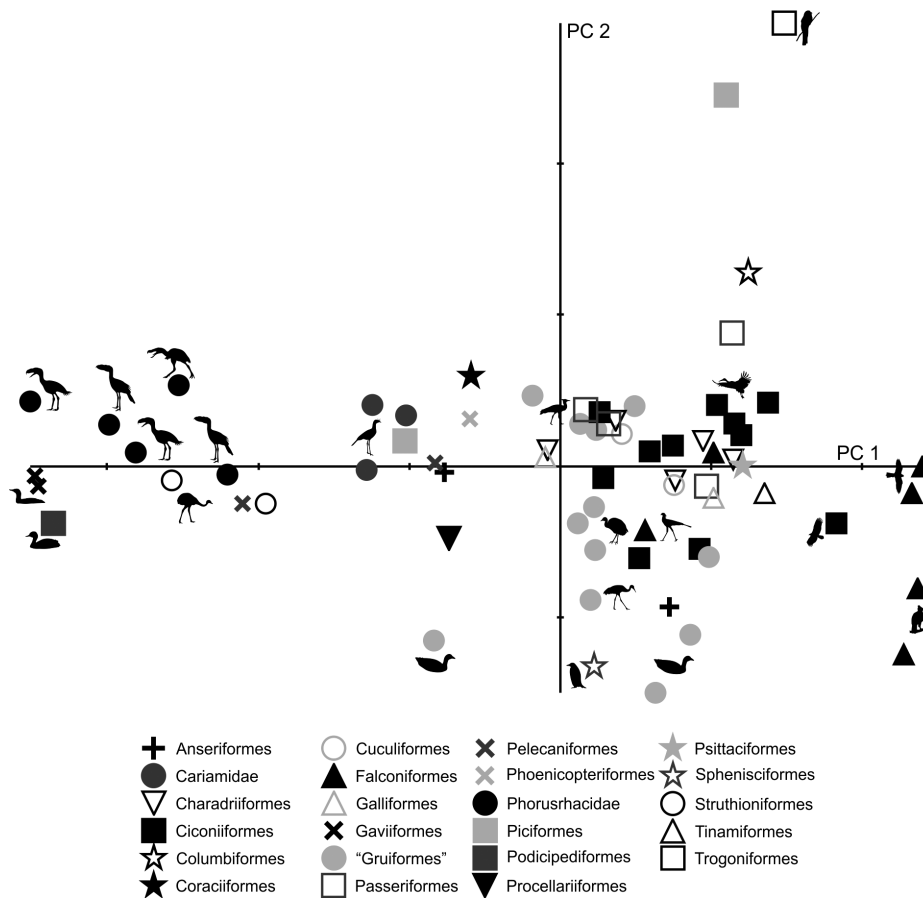
2.4. Pelvis geomorphometrics

2.4.1. Dorsal shape. 69 individuals (including five phorusrhacids) were analysed using nine landmarks (Fig. 3A). The first three components account for 86.7 % of the total variation. PC1 explains 65.9 %, PC2 explains 14.2 % and PC3 explains 6.5 % (Table 8; Supplementary Table 20). Phorusrhacids are grouped with the birds which have a narrow, elongated pelvis, which includes terrestrial birds with cursor capacities such as *Dromaius* and *Rhea*. However, they are separated from other runners (Cariamidae) and from the walker birds (e.g., Otididae and Psophiidae) due to their longer pelvis, and from the aquatic birds *Podiceps* and *Gavia*, which have an even longer pelvis (Fig. 11). The exception is *Andalgalornis*, which has a pelvis which is similar in length to that of diving birds, but can be distinguished from them by the pelvis width (Fig. 12). The two morphotypes described by Degrange (2012) are not separated.

PC1 is related to postacetabular length and pelvis width: negative values correspond to a narrow pelvis with a long postacetabular region, whereas positive values indicate a wide pelvis with a short postacetabular region. With some exceptions, this component distinguishes terrestrial birds with cursor capabilities (and swimming birds also) from non-cursorial terrestrial birds, and the non-cursorial terrestrial birds from waders. Cursorial birds have a very long postacetabular region, whilst the walking birds (Otididae and Psophiidae) have a shorter pelvis and a shorter postacetabular region, although to a lesser extent than the waders.

PC2 is dominated by pelvis width and preacetabular length: positive values indicate a wide pelvis with a short preacetabular region, whilst negative values indicate a narrow pelvis with a
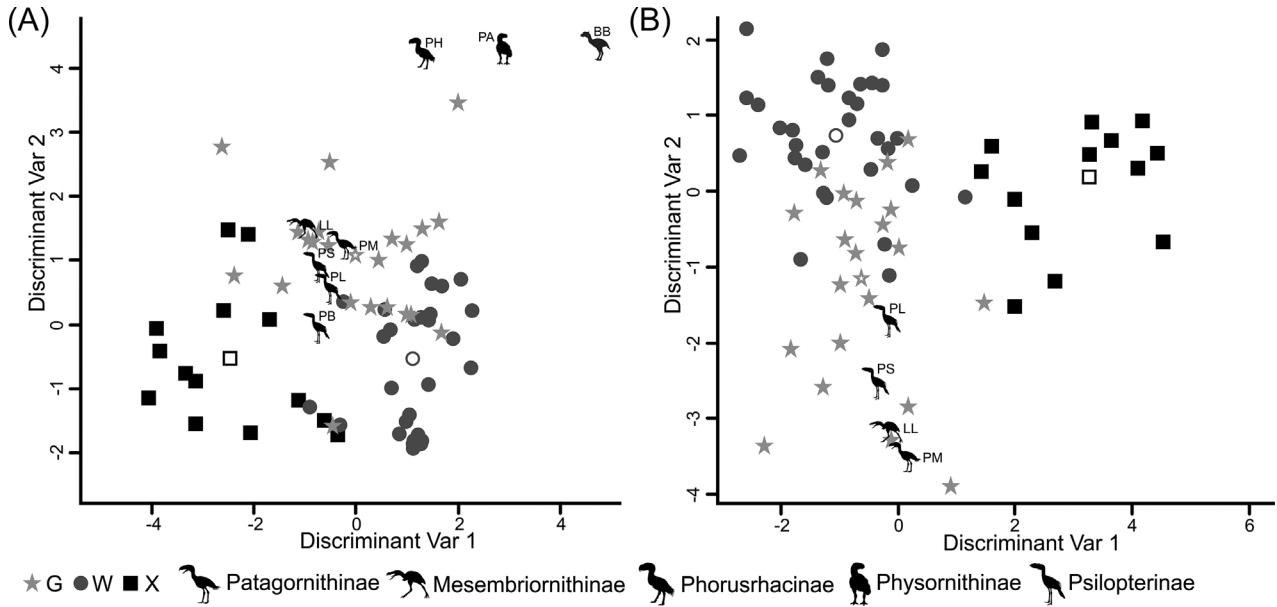
Figure 10 Discriminant analysis: (A) tarsometatarsus discriminant analysis, taxa distribution in morphospace defined by the discriminant variables 1 and 2; (B) Complete hind limb discriminant analysis, taxa distribution in morphospace defined by the discriminant variables 1 and 2. Phorusrhacids have been represented by silhouettes (which also indicate phorusrhacids' subfamily). Abbreviations: BB = *Brontornis burmeisteri*; G = ground birds; LL = *Llallawavis scagliai*; PA = *Paraphysornis brasiliensis*; PB = *Psilopterus bachmanni*; PH = *Phorusrhacos longissimus*; PL = *Psilopterus lemoinei*; PM = *Patagornis marshi*; PS = *Procariama simplex*; W = waders; X = "other birds".

Figure 11 Geomorphometric analysis of pelvis in dorsal view: distribution of taxa in the morphospace defined by CP1 and CP2.
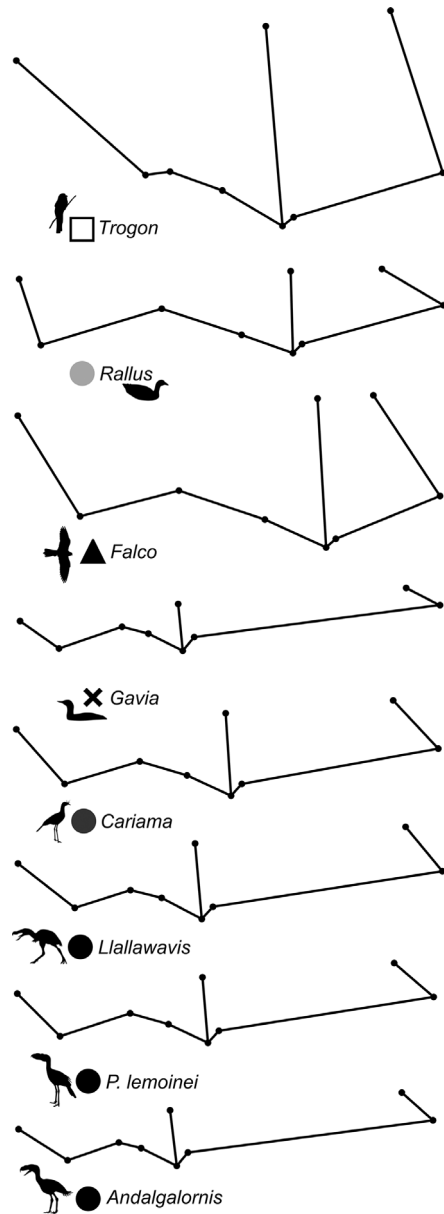
Figure 12 Deformation grid showing shape change of the pelvis (dorsal view) in different species.

long preacetabular region. In this sense, phorusrhacids have a narrow pelvis with a relatively short preacetabular region.

2.4.2. Lateral shape. 69 subjects (including five phorusrhacids) were analysed using 13 landmarks and 18 semi-landmarks (Fig. 3B). The first three components account for 71.94 % of the variation. PC1 explains 41.8 %, PC2 19.9 % and PC3 10.2 % (Table 8; Supplementary Table 21). Phorusrhacids share morphospace with *Dromaius*, *Chunga*, *Cariama*, *Gavia*, *Podiceps*, *Phalacrocorax* and *Ramphastos*, which are all birds with different locomotor habits, but with the peculiarity of having very long postacetabular regions (Figs 13, 14). No pelvic morphotypes were discerned.

PC1 is related to the proportion between the extension of the postacetabular and preacetabular regions: negative values indicate a long preacetabular region and a short postacetabular region, whereas positive values indicate a short preacetabular region and a long postacetabular region. Phorusrhacids have a pelvis with a very long postacetabular region and a very short preacetabular region. This component separates phorusrhacids from terrestrial runners (Cariamidae) and walkers (Otididae) and from the waders, whose pelvis is even shorter.

PC2 is primarily related to the height of the postacetabular region, essentially through the extension of the *processus terminalis ischii*: positive values indicate a pelvis which is poorly extended ventrally, while negative values indicate a pelvis which is highly extended ventrally. Phorusrhacids have a high pelvis, but the *processus terminalis ischii* is poorly extended ventrally.

3. Discussion and conclusions

3.1. Locomotor habits and substrate preferences

The development of the anterior locomotor module of birds relaxed the pressures on the evolution of the posterior appendicular module, thus allowing a diversification of lifestyle habits (Gatesy & Middleton 1997), from those of the hyper-aerial birds (e.g., Apodidae) to those of the exclusively terrestrial birds (e.g., Rheidae). Although the basic functions of bird legs are always landing, taking-off and walking (Habib & Ruff 2008; Abourachid & Höfling 2012), between these extremes all birds have a wide variety of locomotor habits and occupy a wide variety of environments. Locomotor behaviour can also change according to the animal's activity. Flying birds are capable of walking, running, hopping, jumping, wading, swimming or diving. In his book on primates, Oxnard (1984) claimed that a fixed locomotor categorisation is impossible, since each animal uses a wide spectrum of locomotor modes. In extant birds, a simple direct observation can identify whether a bird is able to fly or not, although the ability to fly does not necessarily mean that it will be classified as a flying bird. Some birds are ubiquitous, while others are selective in choosing the environment they frequent. Examples are the Tinamidae, the Otididae, the Psophiidae and the Cariamidae, which, although they are able to fly, are considered terrestrial or land birds because most of their time is spent on the ground. Similarly, the Anatidae and Podicipedidae are also able to fly, but they are considered swimmers because they spend much of their time in the water. Complexity of animal behaviour is so broad that it becomes almost impossible to define unique locomotor habits. Moreover, as more is learned about animal ethology, the boundaries between behavioural categories are dissolved, thus defining a continuum of possible locomotor habits (Carrano 1999), precluding their strict classification. This scenario complicates the assumptions that can be made from appendicular morphology, since this does not necessarily have a straightforward relationship with locomotor diversity or a particular habit.

There is also confusion within published literature about what a locomotor habit is, and also about the substrate type and use. This is not exclusive to birds, and affects other vertebrates such as mammals (Toledo *et al.* 2012). For example, the term 'arboreal' (i.e., lives in trees) is often referred to as a locomotor habit in certain species of Passeriformes capable of flying, when the correct locomotor term is 'climber'. Arboreal, in fact, refers to the preferred substrate. To explore an arboreal environment, birds use several types of locomotor abilities, such as walking on perches (e.g., psittaciforms), climbing branches for foraging (e.g., woodpeckers) and hopping on perches (passerines and toucans) (Abourachid & Höfling 2012). Even the term 'predatory' or 'birds of prey' is used as a mode of locomotion (e.g., Zeffer *et al.* 2003) for birds such as the Falconidae and Accipitridae, when in fact these birds travel through flight.

Despite this obscure scenario, some generalisations are possible; for example, a well developed posterior locomotor module is strongly linked to a terrestrial environment (Dial 2003). This is the case in phorusrhacids, whose very well developed posterior locomotor module is accompanied by a
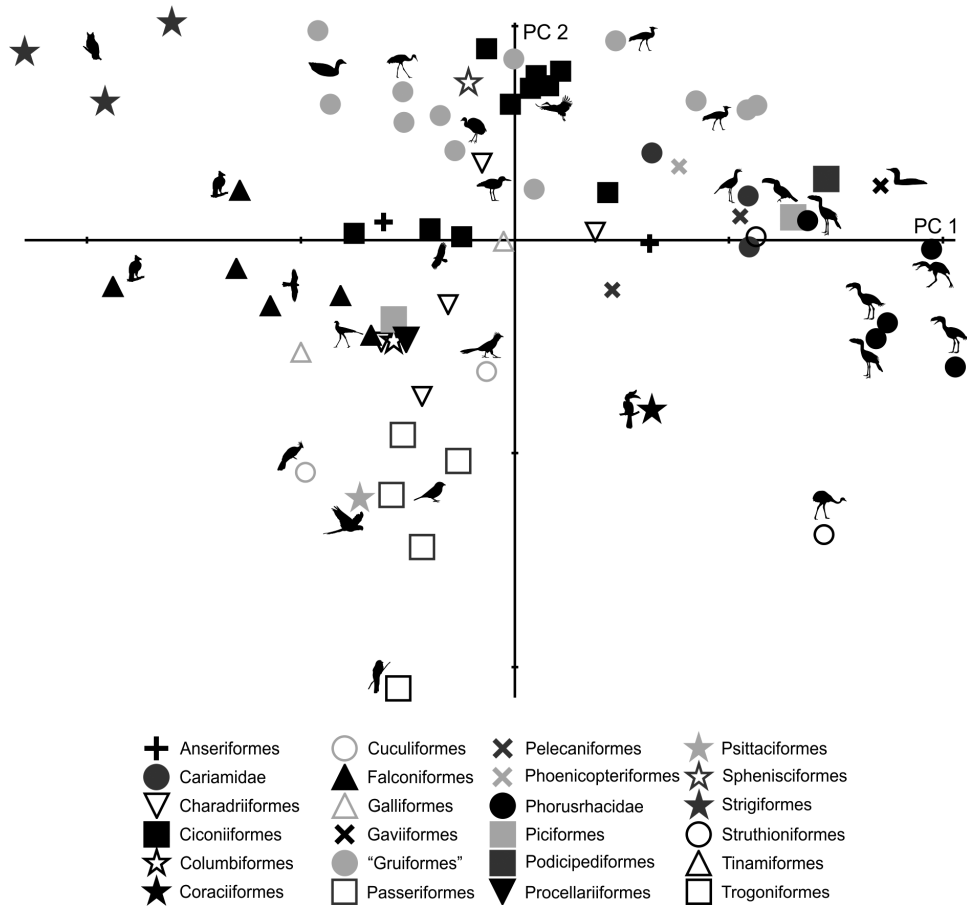
Figure 13 Geomorphometric analysis of pelvis in lateral view: distribution of taxa in the morphospace defined by CP1 and CP2.
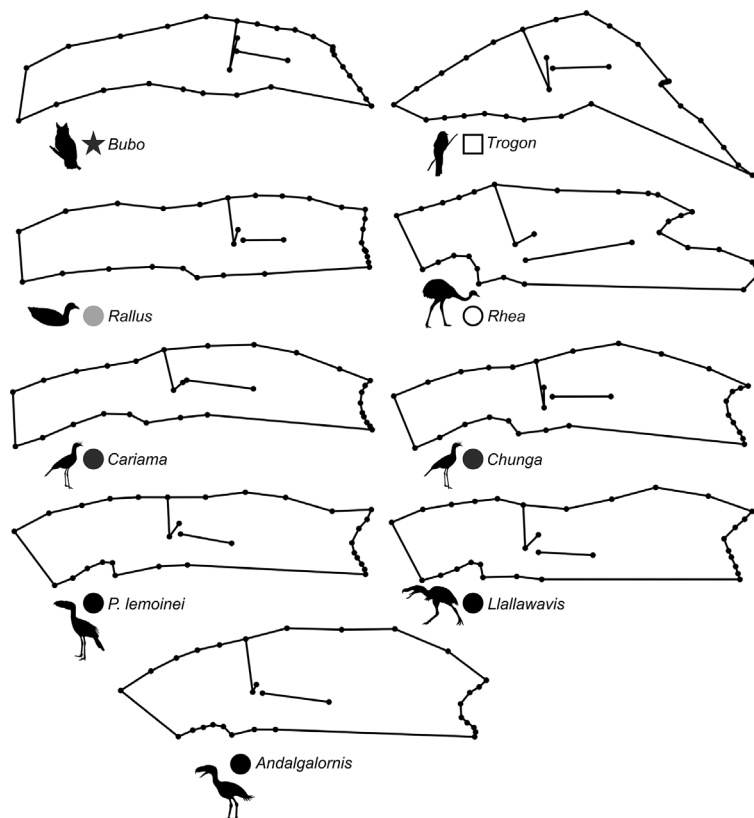

Figure 14 Deformation grid showing shape change of the pelvis (lateral view) in different species.

reduction of the forelimbs, thus indicating that most of the phorusrhacids were obligate terrestrial birds, since they were unable to fly.

Terrestrial birds, or 'ground birds', as described by Zeffer *et al.* (2003), are those that predominantly use their hind limbs for locomotion on the ground (i.e., the substrate), whether they hop, jump, walk or run (i.e., the locomotor mode). Birds move on the ground by walking, running and hopping (Hutchinson & Gatesy 2001; Alexander 2004), depending on their speed; at low speeds they walk, while at intermediate or faster speeds they can run or hop (Hayes & Alexander 1983; Verstappen *et al.* 2000; Verstappen & Aerts 2000). Wading birds (or waders), defined as those that feed while walking in waterlogged soils (i.e., wading), are technically terrestrial birds because their mode of locomotion is walking (Storer 1971; Raikow 1985). However, within the literature published on this subject, they are commonly separated from terrestrial birds (e.g., Zeffer *et al.* 2003).

With this in mind, it is evident that there is a mismatch between the assignments of a habitat through the observation of the anterior and posterior locomotor modules. As the loco-motor habit or style and the substrate on which a bird lives are not easy to identify, many ecomorphological studies use the birds' 'preferred' locomotor habit and mode of locomotion.

The recognition of some locomotor patterns in recent species has also been attributed to extinct taxa based on qualitative comparisons of skeletal features (e.g., Hinić-Frlog & Motani 2009). As previously stated, forelimb reduction in some species, associated with high body mass, indicates that most phorusrhacids were unable to fly (Ameghino 1895; Andrews 1899; Sinclair & Farr 1932; Alvarenga & Höfling 2003; Chiappe & Bertelli 2006). Several authors have stated that, beyond any doubt, phorusrhacids were cursorial birds (Alvarenga & Höfling 2003; Blanco & Jones 2005; Chiappe & Bertelli 2006) which were unable to fly (Alvarenga & Höfling 2003), or that the smaller species were able to fly for very short distances in a clumsy manner (Tonni 1977; Tonni & Tambussi 1988; Tambussi & Noriega 1996; Mourer-Chauviré *et al.* 2011; Degrange 2012; Degrange *et al.* 2015). This indicates that they were obligate terrestrial birds (Degrange 2012). However, phorusrhacid terrestriality may include different non-exclusive styles such as jumping or hopping, walking, running or even wading. Although it has been established that the hind limb length defines the cursorial ability of phorusrhacids (e.g., Tambussi & Noriega 1996; Alvarenga & Höfling 2003; Blanco & Jones 2005), the fact that a very long tarsometatarsus is shared by cursorial, walking and wading birds means that we must question the sole use of hind limb metrics to reflect phorusrhacid's cursoriality.

3.2. Hind limb proportions
Limb proportions represent a key feature in the design of any limb (Gatesy & Middleton 1997; Middleton & Gatesy 2000; Gatesy *et al.* 2009; Abourachid & Höfling 2012), and they have been used to categorise mammals specialised in racing, digging or weight support (Gregory 1912; Osborn 1929; Smith & Savage 1956; Garland & Janis 1993; Gebo & Rose 1993; Carrano 1997, 1999), and also as an indicator of cursoriality in dinosaurs (e.g., Osborn 1916; Holtz 1994; Ostrom 1976; Coombs 1978; Sereno *et al.* 1996) and even in birds (Gatesy & Middleton 1997; Zeffer *et al.* 2003). However, the actual information on locomotor habits that this can provide has been seriously questioned, particularly in the case of Neornithes. Several studies indicate that the ratios between the leg elements, or the hind limb total length, are not in themselves indicative of the type of locomotion (Gatesy & Middleton 1997;

Zeffer *et al.* 2003; Habib & Ruff 2008). Hind limb proportions differ between bird species: the lengths of the femur, tibiotarsus and tarsometatarsus are proportionally different (Abourachid & Höfling 2012). It is also not new that birds with long legs can live in very different habitats. For example, the group LL (long-legged) (Campbell & Marcus 1992) includes a very heter-ogeneous group of birds that share 'only' the great length of their legs; for example, Ciconiidae, Gruidae and Rheidae.

The critical analysis of the correlation between limb segment proportions and habitat use is also important (Abourachid & Höfling 2012). A running bird such as the greater rhea (*Rhea americana*) has a tarsometatarsus and a tibiotarsus equally as long as those of the secretary bird *Sagittarius*, which is not cur-sorial and therefore frequents grasslands, and of the flamingo *Phoenicopterus*, which is clearly a wading bird.

Patagornithinae and Psilopterinae hind limb proportions resemble those of terrestrial birds that walked like *Otis* (Otididae), whilst at the other end of the size range is the Passeriformes *Turdus* (Turdidae). By contrast, Mesembriorni-thinae proportions are similar to those of terrestrial cursorial birds, such as Rheidae. Interestingly, the seriemas *Chunga* and *Cariama* have different proportions to phorusrhacids (Fig. 4).

In a hypothetical *Psilopterus–Rhea–Cariama* series, there is a progressive increase in the relative length of the distal segments of the leg (tibiotarsus and tarsometatarsus), involving a progressive reduction in the relative length of the proximal segment (femur). Seriemas (Cariamidae), which can reach high speeds (40 km/h) and are considered agile runners (Gonzaga 1996), have a longer tibiotarsus than tarsometatarsus, short II and IV toes, and a longer third toe. Both *Psophia* (Psophiidae) and *Otis* (Otididae) have a similar hind limb proportion to that of *Psilopterus*, and can run and fly, although they more often walk (Collar 1996; Sherman 1996).

To sum up, based solely on the proportions of hind limb elements, it is not possible to establish unequivocally that all phorusrhacids were birds with cursorial capacities.

3.3. PCA and discriminant analysis
In all of the PC analyses performed using linear and angular measurements (femur, tibiotarsus, tarsometatarsus and com-plete hind limb), PC1 is strongly influenced by body mass, and it can be seen that the larger birds appear in one extreme of the graphs (Figs 5–8). However, it is clear that a correlation between body mass and terrestriality exists, since larger birds with greater body mass tend to spend more time on the ground than in the air (e.g., Collar 1996; Alexander 1998). There is a threshold value of body mass above which a bird cannot take off. This value is between 12–14 kg (Pennycuick 1989) and 16 kg (Pennycuick 2007). This is reflected in the graphs which match the distribution of larger size birds with those that are more associated with a terrestrial environment (whether they walk, run or wade).

In all analyses performed here, the Psilopterinae shared morphospace with more walker terrestrial birds such as Otididae (*Otis* and *Ardeotis*), but they are also associated with *Leptoptilos crumeniferus*, which is a wading bird according Zeffer *et al.* (2003). Meanwhile, Patagornithinae and Mesembriornithinae are associated with Rheidae and Casuariidae, which are terres-trial birds with clearly cursorial capacities (e.g., Picasso 2010).

Concerning the femur, it is clear that body mass has a high influence on its morphology (Campbell & Marcus 1992; Zeffer *et al.* 2003). However, PC2 sorts birds according to the shape of their femurs: from long and slender to short and robust. Patagornithinae and Mesembriornithinae have a similar mor-phology to Rheidae, whilst the Psilopterinae – which are similar in size to Otididae (PC1) – have longer and more slender

femurs. Wading birds have more robust and shorter femurs (e.g., *Phoenicopterus*) or, on the contrary, more slender and thinner femurs (e.g., *Ardea* and *Ciconia*) than phorusrhacids.

Psilopterinae's tibiotarsus metrics are identical to those of the walkers Otididae, and quite different from those of runners such as Cariamidae, whilst the metrics for Patagornithinae and Mesembriornithinae are similar to those of Rheidae and Casuariidae. Psilopterinae have a cranial extension of the *cristae cnemialis* and a robustness of the shaft similar to typically wading birds, but the tibiotarsus is shorter. Mesembriornithinae and Patagornithinae have a greater cranial extension of the *cristae cnemialis cranialis*, and more robust and shorter tibiotarsi than wading birds.

Tarsometatarsus morphology is strongly influenced by the habits of an animal (Campbell & Marcus 1992). However, it is evident in Figure 7 that waders, walkers and some runners (e.g., Cariamidae) have a very similar morphology; Psilopterinae are included in this association. Some waders, such as the flamingo, have a markedly longer tarsometatarsus than phorusrhacids, with less divergent *trochleae metatarsi*, whilst others such as *Leptoptilos* or *Grus,* have a very similar length and trochlear divarication. Mesembriornithinae and Patagornithinae have tarsometatarsi with similar morphometry to that of the cursorial Rheidae and Casuariidae. *Paraphysornis* and the Anseriformes *Brontornis* are associated with the moa *Emeus*, which is a fossil Palaeognathae considered 'graviportal', due to its short and robust tarsometatarsi with divergent *trochleae*. *Phorusrhacos* has shorter and more robust tarsometatarsi than Patagornithinae (Alvarenga & Höfling 2003).

When analysing the complete hind limb, it is observed that Mesembriornithinae and Patagornithinae are associated with cursorial birds, but Psilopterinae are associated with walkers and waders. Even the extant Cariamidae appears to be associated with *Mycteria* and *Ciconia*, which are considered to be wading birds. This PCA, in particular, shows that the distinction between wading birds and terrestrial birds using hind limb metric variables is extremely difficult, and quite arbitrary. This is more evident when using rates, in which the segregation of the groups is not so clear. In other words, from a morphometric viewpoint, a wading bird can be a terrestrial bird and a terrestrial bird can be a wader (Fig. 10B). This makes more sense when we take into account the fact that terrestrial and wading birds differ in the environment or substrate that they frequent, but not in the locomotor habit or style, since both walk. This finding is reinforced by the reclassifications made in the discriminant analysis carried out here. For example, in Figure 10 it can be appreciated that there is no clear separation between wading birds and terrestrial birds. However, both analyses predicted that phorusrhacids correspond to the terrestrial bird group. The prediction probabilities are generally higher for membership to group G ('ground birds') and lower for group W ('wading birds'). However, the discriminant analysis performed on the tarsometatarsus predicted that *P. bachmanni* was a ground bird with a probability of 53 %, but it has a probability of about 30 % of belonging to the heterogeneous group X (consisting of climbing birds, splatterers, divers and raptors), which may indicate that the hind limb of *P. bachmanni* is morphometrically generalist.

3.4. Pelvis morphometrics

The geomorphometric analysis performed showed that the pelvis, and particularly the postacetabular length, is a better indicator than the hind limb for discerning locomotor habits. With some exceptions (e.g., Ramphastidae), it can be stated that a long postacetabular region belongs to walking, running or diving birds. The seriemas (considered as runners) have a higher pelvis and a longer postacetabular region than Psophiidae and Otididae (considered as walking birds). In turn, these last

examples have a much longer pelvis than the wading birds (with a very short postacetabular region). Phorusrhacids have a long, high pelvis with a very long postacetabular region. This combination is unique to these birds and clearly separates them from aquatic birds (such as Podicipedidae and Gaviidae), which also have a long postacetabular region. Postacetabular extension in phorusrhacids is related to a greater development of the hip extensor muscles (Degrange 2012), which is a feature of birds with cursorial capabilities (Picasso 2010).

4. Concluding remarks

Interpreting limb function represents a step forward in elucidating the palaeobiology of vertebrates (Vizcaíno *et al.* 2008, 2010).

It is evident that appendicular morphometry is not 100 % reliable when distinguishing the different locomotor habits of birds. If hind limb morphology of a ground bird is in many cases metrically indistinguishable from that of a wading bird (and vice-versa), then why could not at least some of the phorusrhacids have been waders?

Undoubtedly, qualitative morphology remains the key when morphometry leads to ambiguous answers. Birds fly with forelimbs and move on land only with their hind limbs. In fact, in general, they can exhibit excellent performance and ground mobility regardless of their flight capabilities (Paul 2002). If the hind limb of the Otididae (bustards) is analysed on its own, it can be incorrectly assumed that it is a terrestrial bird unable to fly; whilst, on the contrary, bustards are flying birds, and some species even migrate (Collar 1996). However, it is true that cursoriality is associated with forelimb reduction (Coombs 1978; Kubo & Kubo 2012). Ratites with cursorial capabilites have an elongated, narrow pelvis, which is a feature shared with diving birds, but they also have elongated tibiotarsi and tarsometatarsi, which is a characteristic shared with wading birds (that don't have an elongated pelvis), but not with divers. The preacetabular region is short compared with the postacetabular, and the height of the pelvis is higher in cursorial Ratites. In conclusion, the shape of the pelvis and hind limbs, coupled with the development of the *cristae cnemialis* and the shape and proportions of the toes, also gives us an idea of the mode of locomotion. Obviously, it is the joint study of the whole posterior locomotor module (pelvis + hind limb) and the anterior locomotor module which truly reveals the preferential mode of locomotion used by a bird.

The hind limbs act together with the pelvis, and it is precisely this whole structure (i.e., the posterior locomotor module) which better reflects the phorusrhacid's locomotor habit. The long, high pelvis, the caudally extended postacetabular region and the highly developed, laterally extended antitrochanter (a unique structure to birds related to body support and balance maintenance during biped locomotion; Hertel & Campbell 2007) are indicators of terrestrial habit with cursorial capacities. In walking birds, the antitrochanter is also very well developed, but the pelvis is lower and less elongated. Wading birds have a low pelvis, with a very short postacetabular region and a poorly developed antitrochanter. Particularly in phorusrhacids, the lateral development of this structure reveals its relationship with the huge body mass of some of these animals; whilst its degree of verticalisation limits lateral movement of the femur, thus preventing abduction and maximising the cranio–caudal movements of the femur during locomotion.

A bird's feet are also indicative of its locomotor habit. It has been generalised that large birds associated with the terrestrial environment often have shorter digits and fewer toes (at least in the more specialised birds), thus minimising contact with the ground (Raikow 1985). Wading birds in turn, are
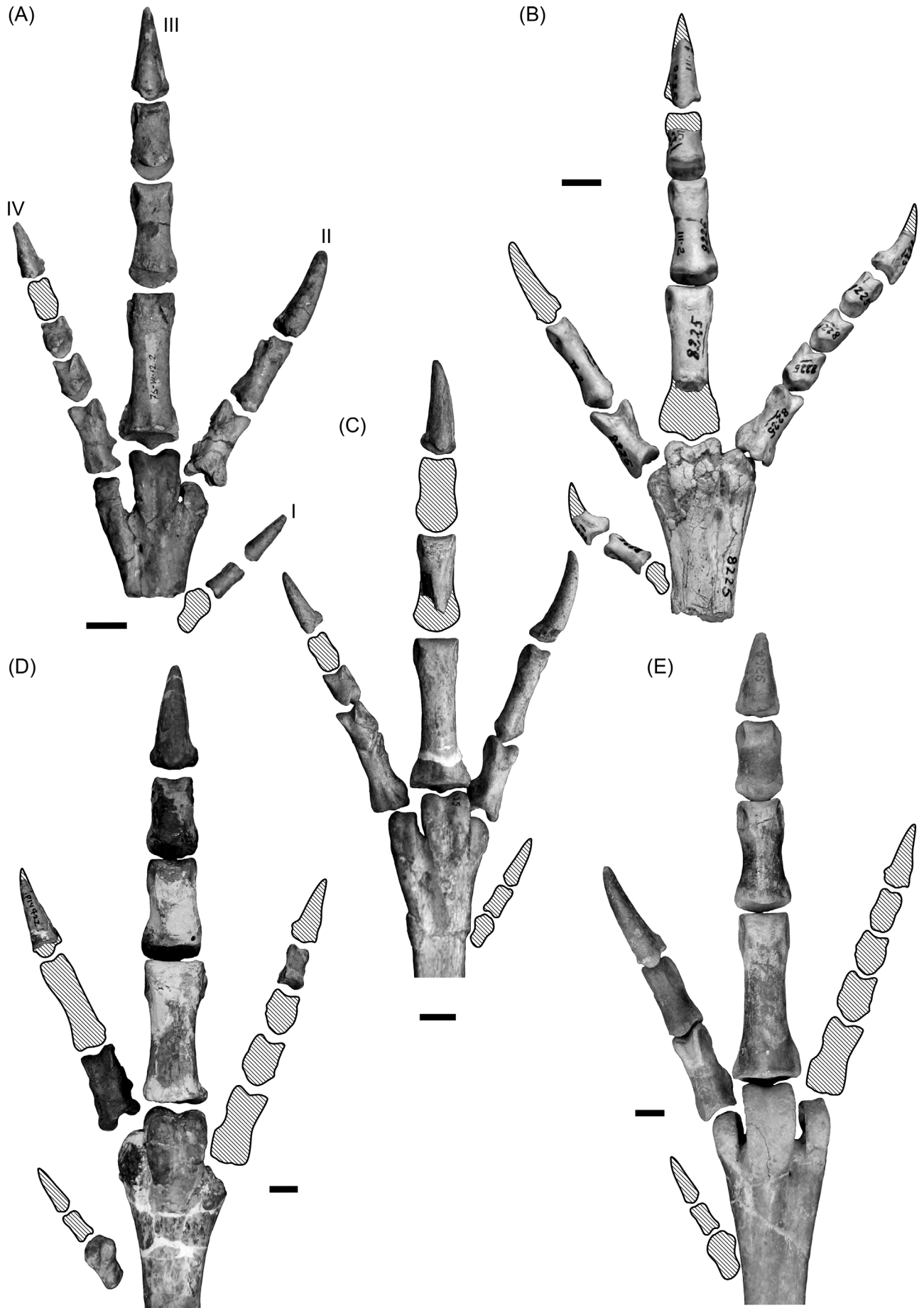
Figure 15 Phorusrhacid feet: (A) *Psilopterus colzecus*, MLP 76-VI-12-2, left foot; (B) *Procariama simplex*, MACN Pv 8225, right foot; (C) *Procariama simplex*, FM-P 14525, left foot; (D) *Mesembriornis incertus*, FM-P 14422, right foot; (E) *Patagornis marshi*, AMNH 9264, right foot. Shaded areas represent missing bones or parts of bones. Roman numerals indicate finger number. Scale bars = 1 cm.

characterised by long toes, leading to an increase in surface contact with the swampy ground (Storer 1971; Raikow 1985). Some waders have interdigital membranes between toes II, III and IV (e.g., flamingos and ducks), whilst others have a very elongated toe I, which is not elevated and is in contact with the substrate (e.g., herons). Phorusrhacids have three relatively short toes II–IV (Jones 2010; Degrange 2012) and a small, elevated toe I (Fig. 15), which is a feature related with terrestrial habits (Raikow 1985; del Hoyo *et al.* 1996). They are therefore considered tridactyl, in the sense described by Raikow (1985). This type of foot minimises friction with the ground during a race and is not suitable for mobility in waterlogged soils.

In conclusion, phorusrhacids possess morphological attributes in the posterior appendicular complex that are associated with cursorial locomotion: the high pelvis and elongated post-acetabular region; a very developed antitrochanter; elongated tibiotarsi and tarsometatarsi; the high development of the *cristae cnemialis* of the tibiotarsus; three relatively short digits pointing forward; and the elevated position of digit I, which does not touch the ground. This is consistent with the findings of Tambussi (1997), who demonstrated through an analysis of athletic capacity rates that some phorusrhacids had the same cursorial capacities as an ostrich. Cursoriality in large-sized birds is achieved with long strides through more elongated hind limbs, whilst smaller sized cursorial birds have shorter hind limbs, but a higher stride frequency (Storer 1971; Gatesy & Biewener 1991; Abourachid & Renous 2000; Picasso 2010). This shows that there is a limitation between size and, secondarily, leg length. The large sizes attained by some phorusrhacids, together with their elongated hind limbs, allowed them to develop long strides and thus succeed in a race.

Finally, to study limb adaptations in fossil birds, a more holistic study of the whole posterior locomotor module is necessary, with an emphasis on qualitative features, since morphometrics leaves some issues unresolved. A comparison with the wings is also needed, in order to make a more complete analysis of locomotor behaviour.

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