

Morphology of the forelimb of *Psilopterus bachmanni* (Aves, Cariamiformes) (Early Miocene of Patagonia)

Federico J. Degrange¹ · Jorge I. Noriega² · Sergio F. Vizcaíno³

Received: 4 March 2015 / Accepted: 30 April 2015
© Paläontologische Gesellschaft 2015

Abstract Psilopterines are the smallest and most gracile predatory birds belonging to the large terrestrial Phorusrhacidae, which were abundant during the South American Tertiary. Two taxa are recognized from the Santacrucian (late Early Miocene) beds of Argentinian Patagonia: *Psilopterus lemoinei* and *Psilopterus bachmanni*. Although the first species was recently redescribed and is well known, in the case of *P. bachmanni*, the smaller of the two, the forelimb skeleton was virtually unknown until recently. The fossils described herein come from the coast of Santa Cruz Province, and were recovered from the middle levels of the Estancia La Costa Member, Santa Cruz Formation. The specimen includes associated bones of both forelimbs and a fragmentary furcula. The manus of this species, previously unknown, is described here for the first time: the *os carpi ulnare* and *radiale* are very stout bones, the carpometacarpus has *processi extensorius* and *alularis* very marked and stout and the *os metacarpale majus* and *phalanges digiti majoris* are very robust, and the *phalanx digiti minoris* is flattened. It has been proposed that some species belonging to *Psilopterus* were able to fly in a clumsy manner. While this work is not intended to certify this condition through complex

models, some considerations of the paleobiology of *P. bachmanni* based on manus movement capabilities and body mass are presented. It seems plausible that *P. bachmanni* would have had both cursorial and flying capabilities. The information provided here represents an effort to discuss features previously unknown in phorusrhacids and to provide new data that may be useful in future systematic, morpho-functional and evolutionary studies.

Keywords *Psilopterus* · Santa Cruz Formation · Forelimb · Carpometacarpus · Phorusrhacids

Kurzfassung Phorusrhacidae des taxons Psilopterinae sind die kleinsten und gräzilsten Raubvögel der großen terrestrisch lebenden Familie Phorusrhacidae, die im Tertiär von Südamerika sehr häufig war. Zwei Taxa aus dem späten Unter-Miozän (Santacrucium) von Patagonien (Argentinien) sind bekannt: *Psilopterus lemoinei* und *Psilopterus bachmanni*. Beide wurden ursprünglich sehr oberflächlich beschrieben. Während die erstere Art erst kürzlich neu beschrieben wurde, war das Skelett der Vordergliedmaßen von *P. bachmanni* bisher praktisch unbekannt. Die Fossilien, die in dieser Arbeit beschrieben werden, stammen aus der Lokalität Puesto Estancia La Costa (=Corriguen Aike), die in der Santa Cruz Provinz liegt. Sie stammen aus den mittleren Schichten der Estancia La Costa Member, Santa Cruz Formation. Das Exemplar besteht aus assoziierten Knochen beider Vordergliedmaßen und einem Fragment der Furcula. Die Hand dieser Art war bisher unbekannt und wird hier im Rahmen dieser Arbeit das erste Mal beschrieben: Ulnare und Radiale sind beide sehr kräftige Knochen, der Carpometacarpus hat kräftige und markante *Processi extensorius et alularis*. Das *Metacarpale majus* und die

✉ Federico J. Degrange
fjdino@gmail.com

¹ Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), CONICET-Universidad Nacional de Córdoba, Avenida Vélez Sársfield 1611, X5016GCA Córdoba, Argentina

² Laboratorio de Paleontología de Vertebrados, CICYTTP-CONICET, UADER, Materi y España, E3105BWA Diamante, Entre Ríos, Argentina

³ División Paleontología Vertebrados, Museo de La Plata, CONICET, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

Phalanges digiti majoris sind sehr robust, die *Phalanx digiti minoris* ist abgeflacht. Frühere Arbeiten gingen davon aus, dass einige Arten der Gattung *Psilopterus* auf eine schwerfällige Art fliegen konnten. Diese Arbeit kann diese Annahme nicht bestätigen, aber einige neue Annahmen zur Paläobiologie von *P. bachmanni* präsentieren, die auf den Fähigkeiten der Handbewegungen und der Körpermasse basieren. Es scheint plausibel, dass *P. bachmanni* sowohl Merkmale eines Laufvogels als auch für Flugfähigkeit in sich vereint. Diese neuen Erkenntnisse ermöglichen es einige Merkmale, die vorher unbekannt für die Phorusrhacidae waren, neu zu bewerten, und liefern neue Daten für zukünftige systematische, funktionsmorphologische und evolutionäre Studien.

Stichwörter *Psilopterus* · Santa Cruz Formation · Vordergliedmaßen · Carpometacarpus · Phorusrhacidae

Introduction

Psilopterines are the smallest and most gracile predatory birds belonging to the large terrestrial family Phorusrhacidae, which were abundant during the Tertiary of South America. Two taxa, *Psilopterus lemoinei* and *Psilopterus bachmanni*, are recognized from the Santacrucian age (late Early Miocene) beds of the Argentinian Patagonia, both originally described in a very ambiguous manner by Moreno and Mercerat (1891) and later by Sinclair and Farr (1932). The first species is well known, as several specimens, including skulls and fore- and hindlimb bones, were recently redescribed by Degrange and Tambussi (2011). However, in the smaller of the two, *P. bachmanni*, the forelimb skeleton was virtually unknown until a short time ago when collections were created as part of a joint project of the Museo de La Plata and Duke University (Vizcaíno et al. 2012).

Moreno and Mercerat (1891) originally described the species *Patagornis bachmanni* based on fragmentary left femur, tibiotarsus and tarsometatarsus, but provided only a brief and non-informative description. Sinclair and Farr later (1932) produced a beautifully illustrated work that included *Psilopterus* (as *Pelecyornis* Ameghino 1891), but with only vague descriptions of the genus. In that work, the forelimb description was based almost completely on *P. lemoinei*, since the only *P. bachmanni* forelimb remains known at that time was a fragmentary ulna. The last comprehensive systematic revision of the Phorusrhacidae, by Alvarenga and Höfling (2003), did not include descriptions of the forelimb of any Psilopterinae.

The fossils described in this work come from the locality Puesto Estancia La Costa (probably Corriguen Aike of the old literature, see Vizcaíno et al. 2012), situated on the coast of Santa Cruz Province between the Coyle and

Gallegos rivers, and were recovered from the middle levels of the Estancia La Costa Member (level 5.3), Santa Cruz Formation (Fig. 1). The specimen (MPM-PV4243) is housed at the Museo Regional Provincial Padre Manuel Jesús Molina, and includes associated tracheal rings, vertebrae, fragmentary hindlimbs (Fig. 2) and bones of both forelimbs (proximal and distal portions of left humerus, both fragmentary zeugopods, and a nearly complete left manus), and a fragmentary furcula (Fig. 3). Differences from *P. lemoinei* (Degrange and Tambussi 2011) in size and several other features related to the hindlimbs allow us to refer this new specimen to *P. bachmanni*.

The aim of this paper is to provide a detailed morphological description of the forelimb of *P. bachmanni*. This information will be important for developing future phylogenetic relationship hypotheses and functional morphology studies of this clade.

Materials and methods

Unless otherwise indicated, osteological terminology follows Baumel and Witmer (1993).

Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; BMNH, Natural History Museum, London, UK; FMNH, Field Museum of Natural History, Chicago, IL, USA; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Buenos Aires, Argentina; MPM-PV, Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; YPM-PU, Peabody Museum of Natural History, New Haven, CT, USA.

Description

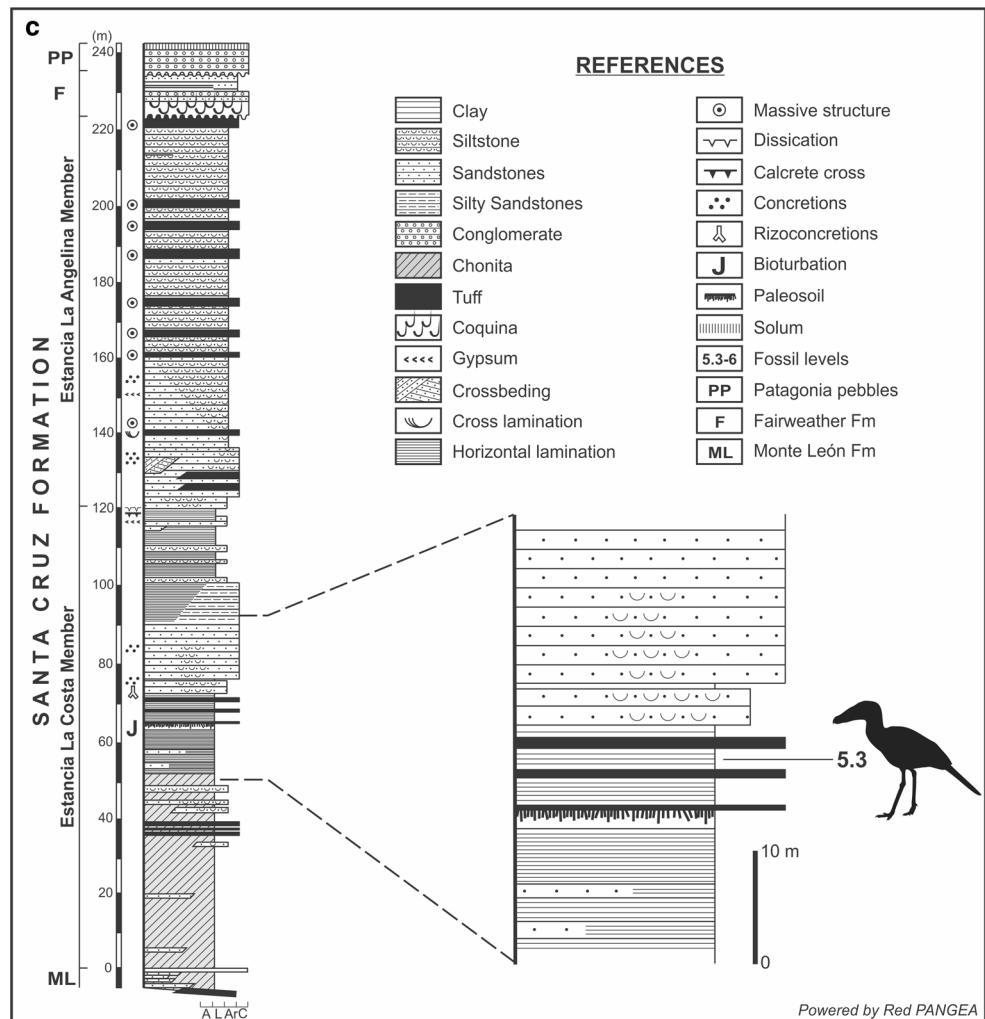
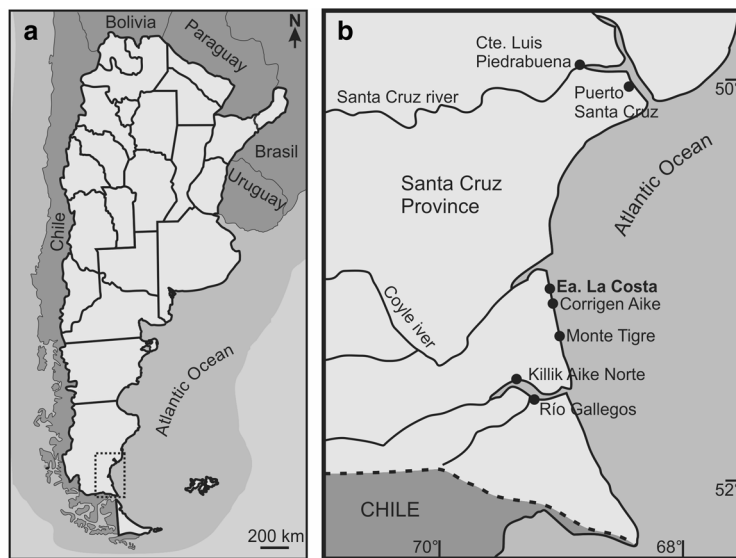
Pectoral girdle

Furcula The furcula (Fig. 3a), when viewed frontally, has a prominent “V” shape, with a very robust *corpus clavicularae*, and lacks an *apophysis furculae*. The *synostosis interclavicularae* is ossified. Both *corpi scapulorum* diverge at an angle of 66°.

Forelimb

Humerus Only the proximal and distal ends of the left humerus are preserved. Although smaller, these parts of the

Fig. 1 Geographic and stratigraphic provenance of *P. bachmanni* MPM-PV 4243. Fossil collection localities in **a** Argentina and **b** Santa Cruz Province; **c** stratigraphic profile of the Santa Cruz Formation (modified from Noriega et al. 2011)



bone (Fig. 3b) show no significant differences to *P. lemoinei* (see Degrange and Tambussi 2011), although the *fossa m. brachialis* is deeper. The *tuberculum ventrale* is very well developed, as in all phorusrhacids (Alvarenga

and Höfling 2003). The *crus dorsale* and *ventrale fossae* are wide and low, poorly marked. The *fossa pneumaticipitalis* is deep and oval in shape. The *incisura capitis* is wide and deep (narrower in *P. lemoinei*). The

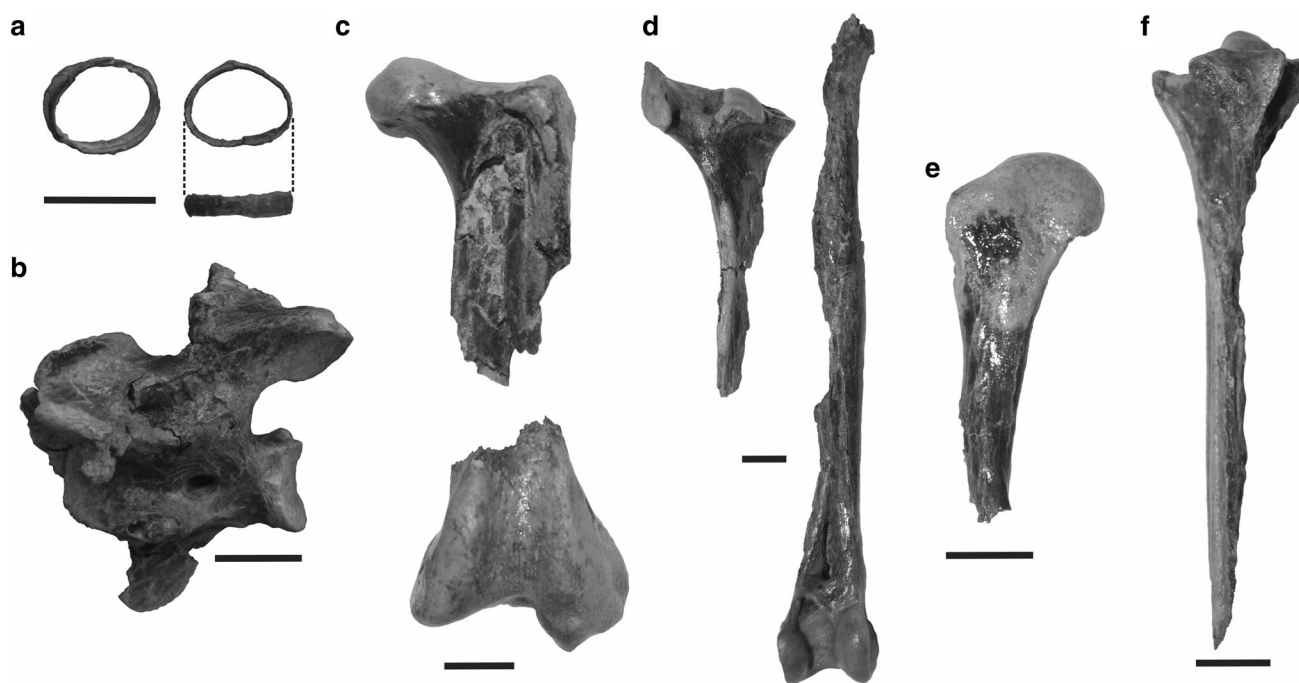


Fig. 2 Postcranial remains of *P. bachmanni* MPM-PV 4243 other than forelimb bones. **a** Tracheal rings; **b** dorsal vertebra; **c** left femur; **d** left tibiotarsus; **e** left fibula; **f** left femur. Scale bar 1 cm

tuberculum dorsale is broken in MPM-PV4243. The *caput humeri* is elongated. The *sulcus ligamentum transversus* is shortened, forming a medial circular scar and a latero-proximally oval scar. The scar of the *m. biceps brachii* is poorly marked and smaller than that in *P. lemoinei*. The *crista bicipitalis* is stout, proximomedially disposed. The *crista deltopectoralis* is not developed. The *processus flexorius* is very well developed. The *epicondylus ventralis* is prominent and oval in shape. The *incisura intercondylaris* is well marked. Both *condyli* are oval, although the *condylus ventralis* is proportionally smaller than that of *P. lemoinei*. The *fossa olecrani* is deep.

Ulna The proximal portions of both ulnae are preserved. However, only the distal portion of the left ulna is preserved (Fig. 3c–e). The *cotyla dorsalis* is shallow and oval. The *cotyla ventralis* is shallow and circular. The *crista intercotylaris* forms a poorly elevated sigmoid ridge. The *processus cotylaris dorsalis* is present and very well developed. The *olecranon* is stout but poorly salient, and it is cranially extended through a fine crest that clearly separates the dorsal and ventral aspect of the ulna, giving the *corpus* a triangular section. The *incisura radialis* is poorly marked. The *impressio m. scapulothoracalis* is present and very well marked. The *trochlea humeroulnaris* is shallow, although very well marked. The *depressio radialis* is well marked and circular in shape. The *impressio brachialis* forms a little tubercle located distal to the larger scar of the

ligamentum collateralis ventralis. The *incisura radialis* is shallow. The *sulcus intercondylaris* and the *incisura tendinosa* are poorly marked. The *condylus dorsalis ulnaris* is elongated and curved, slightly projected ventrally. The *condylus ventralis ulnaris* is stout, forming a tubercle projected distally. The *tuberculum carpale* is broken, although it is possible to appreciate that it is stout.

Radius Only the proximal portions of both radii are preserved (Fig. 3f), and show a circular cross-section. The *tuberculum bicipitale radii* is proximally located. The *cotyla humeralis* is oval in shape.

Manus The *os carpi ulnare* and *radiale* (Fig. 3g) are both very stout bones. The *os carpi ulnare* presents a wide and deep *incisura metacarpalis*, a poorly marked *processus muscularis*, a smooth and poorly delimited *facies articularis metacarpalis*, and a *crus breve* and *crus longum* of the same length.

The carpometacarpus (Fig. 3i) has *processus extensorius* and *alularis* that are very marked and stout. The *processus alularis* is also distally projected, obliquely disposed to the *processus extensorius*. The *fovea carpalis caudalis* and the *processus intermetacarpalis* are absent. The *fossa supratrochlearis* is rounded and shallow. The *trochlea carpalis* is wide and shallow. The *fossa infratrochlearis* is deep, caudally located to the *processus pisiformis* (broken in MPM-PV4243). The *fovea carpalis cranialis* seems to be deep, although the area is somewhat

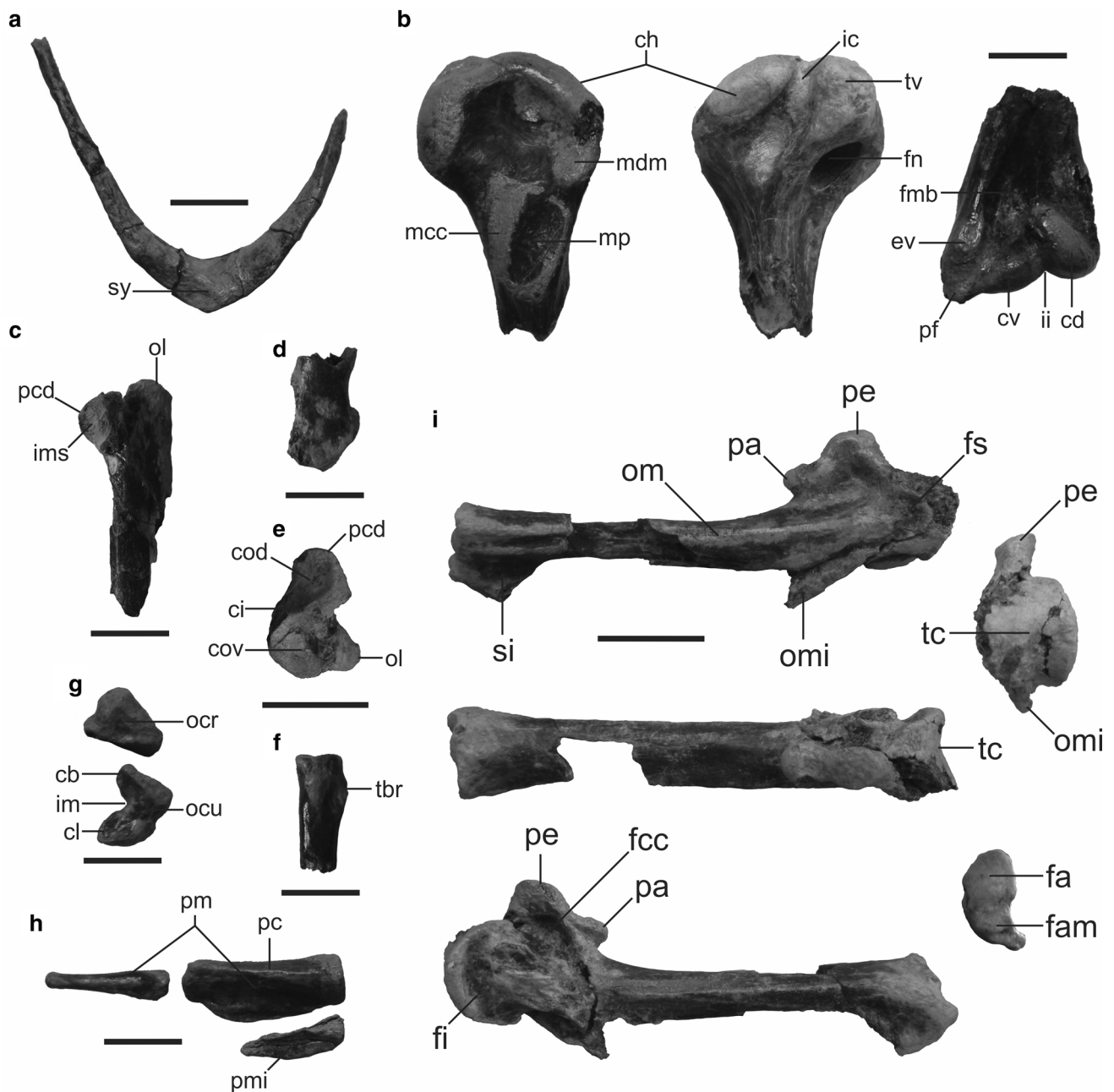


Fig. 3 Forelimb of *P. bachmanni* MPM-PV 4243. **a** Furcula; **b** proximal portion of left humerus in cranial and caudal views and distal portion in cranial view; **c** proximal portion of left ulna in lateral view; **d** distal portion of left ulna in lateral view; **e** proximal view of right ulna; **f** proximal portion of left radius in lateral view; **g** left os carpi radiale and ulnare in lateral view; **h** preserved left *ossa digitorum manus* in lateral view; **i** left carpometacarpus in lateral, dorsal, medial, proximal and distal views. *cb*, *crus breve*; *cd*, *condylus dorsalis*; *ch*, *caput humeri*; *ci*, *crista intercotylaris*; *cl*, *crus longum*; *cod*, *cotyla dorsalis*; *cov*, *cotyla ventralis*; *cv*, *condylus ventralis*; *ev*, *epicondylus ventralis*; *fa*, *facies articularis digitalis majoris*; *fam*, *facies articularis digitalis minoris*; *fcc*, *fovea carpalis cranialis*; *fi*,

fossa infratrochlearis; *fmb*, *fossa m. brachialis*; *fn*, *fossa pneu- motricipitalis*; *fs*, *fossa supratrochlearis*; *ic*, *incisura capitis*; *ii*, *incisura intercondylaris*; *im*, *incisura metacarpalis*; *ims*, *impression scapulo-tricipitis*; *mcc*, *m. coracobrachialis* attachment scar; *mdm*, *m. deltoideus minor* attachment scar; *mp*, *m. pectoralis* attachment scar; *ocr*, *os carpi radiale*; *ocu*, *os carpi ulnare*; *ol*, *olecranon*; *om*, *os metacarpale majus*; *omi*, *os metacarpale minus*; *pa*, *processus alularis*; *pc*, *pila cranialis*; *pcd*, *processus cotylaris dorsalis*; *pe*, *processus extensorius*; *pf*, *processus flexorius*; *pm*, *phalanges digiti majoris*; *pmi*, *phalanx digiti minoris*; *si*, *sulcus interosseus*; *sy*, *synostosis interclavicularis*; *tbr*, *tuberculum bicipitale radii*; *tc*, *trochlea carpalis*; *tv*, *tuberculum ventralis*. Scale bar 1 cm

damaged. The *os metacarpale majus* is very robust and wide, with a sharp medial crest. This bone is nearly straight, and is wide and depressed (not curved and

compressed laterally, as stated by Sinclair and Farr 1932). The main part of the *os metacarpale minus* is missing. The *sulcus interosseus* is wide and deep. The *facies articularis*

digitalis major is rounded and shallow. The *facies articularis digitalis minor* is elongated and horizontally disposed.

With regard to the phalanges (Fig. 3h), the *phalanx digiti alulae* is not preserved, and the *phalanx digiti minoris* is flattened. The *phalanges digiti majoris* are both very robust. The first phalanx presents a very robust *pila cranialis*, an extended ventral crest, a shallow (almost flat) *facies articularis metacarpalis*, and a convex and subtriangular *facies articularis phalangealis*. The second phalanx presents a subtriangular cross-section.

Discussion and conclusions

Comparisons

Regarding the pectoral girdle, the coracoid and scapula of *Psilopterus* are well known in the Santacrucian species and have been described by Sinclair and Farr (1932). However, to date, the furcula of phorusrhacids is known only for two taxa, a Mesembriornithinae from the Pliocene of Buenos Aires Province in Argentina (Degrange et al. 2015) and the one reported here. A major difference between Mesembriornithinae and Psilopterinae is the absence of an ossified *synostosis interclavicularae* in the former (Degrange et al. 2015). Regrettably, the *extremitas omalis claviculae* of *P. bachmanni* MPM-PV4243 is not preserved, and it is impossible to know how it connects with the coracoid and scapula. However, the morphology of the coracoid and scapula of the remains described by Sinclair and Farr (1932) shows no fusion between these elements, and there is no evidence of fusion with the furcula as in *Mesembriornis* (Kraglievich 1940; Patterson and Kraglievich 1960; Rovereto 1914).

Compared to those of the hindlimb, forelimb remains of phorusrhacids are less common. Although some fragmentary portions of the arm are recorded from observations (e.g., *Procarium simplex* Rovereto 1914; *Mesembriornis milneedwardsi* Moreno 1889; *Patagornis marshi* Moreno and Mercerat 1891; *Titanis walleri* Brodkorb 1963), complete forelimb (Fig. 4) remains are limited to only few species [e.g., *P. lemoinei*, *Paraphysornis brasiliensis* (Alvarenga 1982)], making it difficult to perform accurate comparisons among subfamilies within Phorusrhacidae. Some of the features of the forelimb of *P. bachmanni* correspond to those observed in all phorusrhacids: a sole and oval-shaped *foramen pneumaticum* in the humerus, the *crista deltopectoralis* not developed [contrary to the statement by Sinclair and Farr (1932) that it was very well developed in *Psilopterus*], the very well-developed *processus flexorius*, a triangular and deep *fossa m. brachialis*, the stout ulna with a shortened *olecranon*, and the rounded and stout *processus alularis* of the carpometacarpus.

However, there is some variation among phorusrhacids in the morphology of the forelimb. In *P. bachmanni*, the general morphology of the humerus is like that of the smaller phorusrhacids, the Psilopterinae, which is substantially different from that of giant phorusrhacids such as *Titanis*, who possesses a reduced pneumatic network of bone in the shaft (Chandler 1994: 176).

The ulna of Psilopterinae is markedly different from that of larger terror birds such as *Patagornis*, *Mesembriornis* and *Paraphysornis*, who show a substantial reduction of this forelimb bone. The ulna of *P. bachmanni* is considerably more slender than that of Mesembriornithinae. Moreover, in *Mesembriornis*, the *condylus dorsalis ulnaris* is strongly projected ventrally, a feature absent in *Psilopterus*. With regard to *Procarium simplex*, its ulna possesses a noticeable proximal pneumatic foramen in dorsal view, and the *condylus ventralis ulnaris* is not projected distally. In *P. lemoinei*, the *condylus dorsalis ulnaris* is rounder than in *P. bachmanni* in lateral view.

Among phorusrhacids, the radii are quite similar, and the only really noticeable feature is the robustness of this bone in larger taxa such as *Mesembriornis*. Slight differences occur in the *cotyla humeralis*, which is oval in *P. bachmanni* and *Mesembriornis*, wider in *Psilopterus colzecus* Tonni and Tambussi (1988), and more rounded in *P. lemoinei*.

The *os carpi ulnare* and *radiale* are quite different from those of the seriemas (Cariamidae). In the latter, the *os carpi radiale* is longer, and the *crus breve* of the *os carpale ulnare* is shorter and much more slender. Few carpal elements are known for terror birds. To date, these elements have been registered for *P. colzecus* (see Tonni and Tambussi 1988), *P. bachmanni* (this work), *P. lemoinei* (Sinclair and Farr 1932), a juvenile specimen of *P. marshi* (FMNH-P13213), and a new Mesembriornithinae taxon (Degrange et al. 2015). Among Psilopterinae, they are quite similar with regard to stiffness (Fig. 4). However, in *P. bachmanni* both *crus breve* and *crus longum* of the *os carpi ulnare* are longer than those of *P. colzecus* and *P. lemoinei*, and in the latter the *incisura metacarpalis* is dorsoventrally wider.

Superficially, the carpometacarpus of *P. bachmanni* is similar to that of the seriemas (Cariamidae), although it is sturdier (Sinclair and Farr 1932). It also differs from that of *Chunga* in that its *processus extensorius* is less projected dorsally and from that of *Cariam* by the absence of a pointed *processus* located in the base of the *os metacarpale minus* cranioventral to the *processus pisiformis*. This *processus* is present in *P. marshi* as a tubercle (see Andrews 1899), and it is highly developed in *T. walleri*, where it is ventrally directed (Chandler 1994). A major difference between Cariamidae and Phorusrhacidae is the cranial extension of the *os metacarpale minor*, which is highly projected in terror birds, especially in *Procarium*. In larger

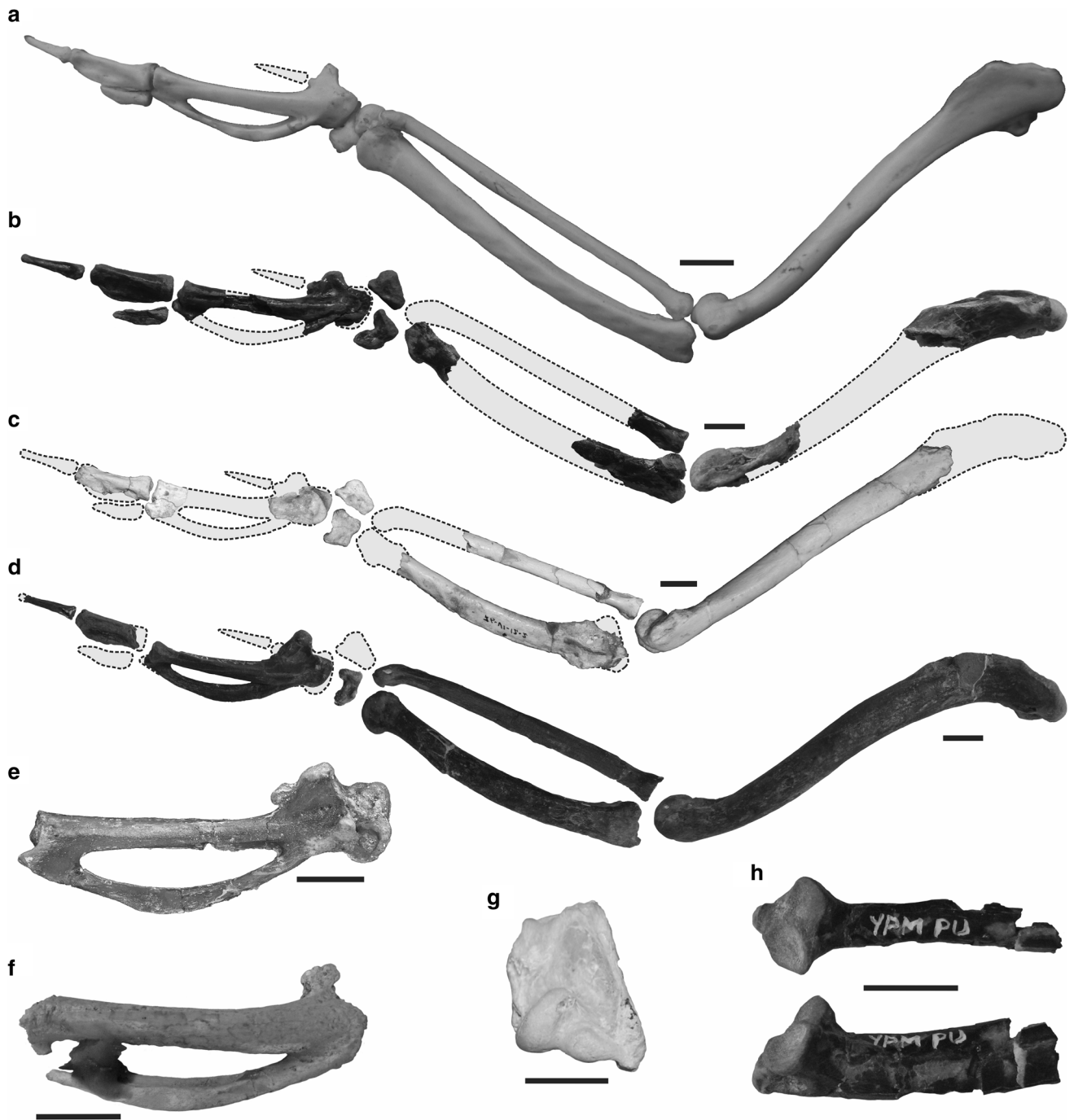


Fig. 4 Forelimbs of Cariamidae and Psilopterinae. **a** *Chunga burmeisteri* MLP 52, left forelimb; **b** *P. bachmanni* MPM-PV 4243, left forelimb; **c** *Psilopterus colzecus* MLP 76-VI-12-2, right forelimb (mirrored for comparison); **d** *P. lemoinei* YPM-PU15402, left forelimb (the manus is right, but was mirrored for comparison); **e** right carpometacarpus of *P. lemoinei* BMNH A559; **f** left

fragmentary carpometacarpus of *Ciconiopsis antarctica* MACN-A-11666 (see text for discussion of the systematic status of this taxon); **g** distal portion of right humerus of *P. bachmanni* MLP 67-XI-28-1; **h** left ulna of *P. bachmanni* YPM-PV15904 in dorsal and medial views. Grey areas with dashed lines represent parts lacking. Scale bar 1 cm

phorusrhacids such as *Titanis* and *Paraphysornis*, the *processus extensorius* is only slightly projected dorsally, and its base is larger than that of the other phorusrhacids. In

Mesembriornis milneedwardsi, the *trochlea carpalis* presents a medial pointy ventral edge, which is absent in *Psilopterus*.

With regard to the phalanges, there are no significant differences among terror birds other than the greater robustness in larger species.

There has been a history of misunderstanding concerning the carpometacarpus of phorusrhacids. Agnolín (2004) referred to the Psilopterinae the Oligocene taxon *Ciconiopsis antarctica* Ameghino 1895 (Fig. 4f), a species based on a fragmentary left carpometacarpus [not right as shown in Agnolín (2004): Fig. 12]. Later, this taxon was considered possible synonymous with *Psilopterus* (Mayr 2009), but more recently, Tambussi and Degrange (2013) stated that the combination of the preserved characters allows the assignment to Phorusrhacidae, not to Psilopterinae, postulating it should be considered as *nomen inquirendum*. It is clear that the fragmentary nature of the remain makes its systematic placement difficult. Agnolín (2004) described the *processus alularis* of *Ciconiopsis* disposed at 90° to the shaft of the *os metacarpale majus* as diagnostic of Psilopterines. However, only recently it was possible to describe this feature in any Psilopterinae (Tambussi and Degrange 2013). The specimens YPM-PU 15402, BMNH A559-1, and MPM-PV4243 undoubtedly correspond to carpometacarpi of Psilopterinae, and only in the latter two cases is the *processus alularis* preserved. In the new material herein assigned to *P. bachmanni* and in *P. lemoinei* BMNH A559-1 (Fig. 4e), the *processus alularis* is obliquely disposed to the shaft of the *os metacarpale majus* (and not perpendicular). In other words, Psilopterinae are characterized by an oblique disposition of the *processus alularis*, which is not significantly different from that of other phorusrhacids such as *P. marshi* or *T. walleri*.

More recently, Agnolín (2013) proposed that *Psilopterus* possessed a gracile and subquadrangular *os metacarpale I* (in reference to the *processus alularis*) different from the stout, rounded and protruding *processus alularis* (character 64 of Agnolín 2013) of the remaining phorusrhacids. Although there is some ambiguity in this character, its scoring in *Psilopterus* was based on the fragmentary material figured by Sinclair and Farr (1932) (see Agnolín 2013: Fig. 4), which lacks this *processus* (due to fracture). As described above, in this work we have confirmed the presence of the *processus alularis* (Figs. 3, 4d). When compared with *P. lemoinei* BMNH A559-1 (Fig. 4e), *P. bachmanni* (Figs. 3i, 4b), and the other phorusrhacids, it is evident that the presence of a stout, rounded and protruding *processus alularis* (in the sense of Agnolín 2013) is a feature common to all phorusrhacids.

In the same work, Agnolín (2013) comments on a conflictive fragmentary bone of *Mesembriornis incertus*, assigned by the author as the distal portion of a carpometacarpus of this taxon. A careful reexamination of the

material makes evident that it is distinctively different from the *M. milneedwardsis* carpometacarpus distal portion figured by Rovereto (1914)—not found in the original material. The bone is wide and depressed, with an atypical lateral extension for a phorusrhacid when viewed distally. Additionally, when viewed ventrally, the caudal extension of the *os metacarpalis minor* it is not coincident with that of a carpometacarpus, and the *sulcus interosseus* is extremely long for a terror bird. In summary, contrary to the statement of Agnolín (2013), the general morphology of this element is completely different (not coincident) with that of a phorusrhacid and its assignment to a carpometacarpus must be declined. Regrettably, a precise assignment is not possible at this time due to the fragmentary nature of the remains.

Paleobiology of *P. bachmanni*

Chandler (1994) proposed that *T. walleri* possessed a large claw on the *digitus alulae* used to subdue struggling prey (Chandler 1994: 176). This hypothesis is based on the “ball joint” morphology of the *processus alularis*. However, this theory was rejected by Gould and Quitmyer (2005), who argued that this articulation morphology is known in several species of terror birds and seriemas, in which there is no large claw associated with the *processus alularis*. We do not find any evidence here to support Chandler’s hypothesis. Moreover, Chandler (1994) stated that in *Titanis*, “the manus was held extended, as in penguins, and could not be folded under the ulna as in other birds” (Chandler 1994: 176), based on the vertical disposition of the *trochlea carpalis*. Although there are some differences, the morphology of the *trochlea carpalis* of *P. bachmanni* resembles that of Cariamidae more than that of *Titanis*. Moreover, *ossa carpi ulnare* and *radiale* are well developed in *P. bachmanni*, suggesting a capability of movement of the manus.

The avifauna recovered from the levels of Estancia La Costa Member includes other Cariamiformes. There are at least two species of seriemas (Mayr and Noriega 2015; Noriega et al. 2009) and four species of phorusrhacids (Degrange 2012): *Phorusrhacos longissimus* Ameghino 1887, *P. marshi*, *P. lemoinei*, and *P. bachmanni*. With a body mass estimation of 5 kg according to Alvarenga and Höfling (2003) and Degrange (2012), *P. bachmanni* is the smallest phorusrhacid recognized to date. Despite a difference in size of approximately 10 kg between this species and its contemporary and sympatric *P. lemoinei* (Degrange and Tambussi 2011; Degrange 2012), *P. bachmanni* probably played a very similar ecological role as a predator of small prey (Degrange 2012). To date, the Santa Cruz Formation is the only such unit with localities (e.g., Puesto Estancia La Costa) where terror birds of three different sizes (small, medium,

and large) are registered (Degrange 2012). It is plausible to infer the existence of a niche partition among the different kinds of phorusrhacids based on their supposed prey size (Degrange 2012): Psilopterinae feeding on smaller prey such as rodents, with mammals of up to 10 or 20 kg in body mass available to *Patagornis*, while *Phorusrhacos* could probably chase and kill larger prey such as *Theosodon* (~110 kg, sensu Cassini et al. 2012).

Classical theories regarding the lifestyle of phorusrhacids have proposed that these terror birds were unable to fly (Ameghino 1895; Alvarenga and Höfling 2003; Alvarenga et al. 2011; Patterson and Kraglievich 1960; Sinclair and Farr 1932), due fundamentally to their forelimb proportions and large body mass estimates for most of the species. For the larger phorusrhacids (Mesembriornithinae, Patagornithinae, Phorusrhacinae and Physornithinae), there is no doubt that this was true. Their enormous body mass and extremely shortened forelimbs are unquestionable evidence that they were strictly terrestrial and cursorial birds (Degrange 2012).

It has been proposed, however, that some species belonging to *Psilopterus* did possess the ability to fly (Degrange 2012; Tambussi and Degrange 2013; Mourer-Chauviré et al. 2011; Tonni and Tambussi 1988), albeit in a clumsy manner, as living seriemas do. This hypothesis is largely based on the absence of *processus acrocoracoideus* and *procoracoideus* of the coracoid (Alvarenga and Höfling 2003), together with the shortened forelimb.

Pennycuick (1989) proposed that the maximum weight limit above which a bird cannot fly is estimated at 12–14 kg or 16 kg (see Pennycuick 2007). However, there are living species outside this range perfectly capable of flying, such as the kori bustard *Ardeotis kori*, which can weigh as much as 19 kg (Collar 1996). Furthermore, among extinct birds, teratornithids and pelagornithids clearly surpassed that limit, doubling or tripling it (Campbell and Tonni 1981, 1983; Mayr and Rubilar-Rogers 2010; Palmqvist and Vizcaíno 2003; Vizcaíno and Fariña 1999). Even considering the weight limit exemplified by living birds, body mass would not have impeded the ability of flight in *Psilopterus*, whose mass is estimated to have ranged between 5 and 10 kg among its various species. It is possible that *P. bachmanni* (and the rest of the Psilopterinae) had both cursorial and flying capabilities, although the fore- and hindlimb proportions seem to indicate a more accentuated use of the legs (Degrange 2012, 2014). This locomotor style is present in Otidae and Cariamidae, which exhibit a similar proportion of wing bones to psilopterines.

While this work is not intended to clarify this condition, the information presented here represents an effort to provide new data that may be useful in future morpho-functional, systematic, and evolutionary studies.

Acknowledgments We thank Sandra Chapman for photographs of the materials from BMNH, and we thank Jim Holstein (FMNH), Carl Mehling (AMNH), Christopher Norris and Dan Brinkman (YPMU) for access to collections under their care. The first author thanks Claudia P. Tambussi for her constant support and advice. We also thank Heike Mewis for her assistance with German language editing. This study was supported in part by FONCYT-PICT grant 32617 and PICT 2007-392. This is a contribution to the grants PICT 26219, 0143 to Sergio Vizcaíno and NSF 0851272, 0824546 to Richard Kay.

References

- Agnolín, F.L. 2004. La posición sistemática de algunas aves fósiles de edad Eoceno (Oligoceno Medio) descritas por Ameghino en 1899. *Revista del Museo Argentino de Ciencias Naturales* 6: 239–244.
- Agnolín, F.L. 2013. La posición sistemática de *Hermosornis* (Aves, Phororhacoidea) y sus implicancias filogenéticas. *Revista del Museo Argentino de Ciencias Naturales* 15: 39–60.
- Alvarenga, H.M.F., and E. Höfling. 2003. Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papeis Avulsos de Zoologia* 43: 55–91.
- Alvarenga, H.M.F., L.M. Chiappe, and S. Bertelli. 2011. Phorusrhacids: the terror birds. In *Living Dinosaurs: the Evolutionary History of Modern Birds*, ed. Dyke, G., and G. Kaiser, 187–208. Wiley, Chichester.
- Ameghino, F. 1891. Enumeración de las aves fósiles de la República Argentina. *Revista Argentina Historia Natural* 1: 441–453.
- Ameghino, F. 1895. Sobre las aves fósiles de Patagonia. *Boletín del Instituto Geográfico de Argentina* 15: 501–602.
- Andrews, C. 1899. On the extinct birds of Patagonia, I, the skull and skeleton of *Phororhacos inflatus* Ameghino. *Transactions of the Zoological Society of London* 15: 55–86.
- Baumel, J.J. and L.M. Witmer. 1993. Osteologia. In *Handbook of avian anatomy: nomina anatomica avium*, eds. Baumel, J.J., A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge, 45–132. Nuttall Ornithological Club, Cambridge.
- Brodtkorb, P. 1963. A giant flightless bird from the Pleistocene of Florida. *The Auk* 80: 111–115.
- Cassini, G.H., S.F. Vizcaíno, and M.S. Bargo. 2012. Body mass estimation in Early Miocene native South American ungulates: a predictive equation based on 3D landmarks. *Journal of Zoology* 287: 53–64.
- Campbell Jr, K.E., and E.P. Tonni. 1981. Preliminary observations on the paleobiology and evolution of teratons (Aves, Teratornithidae). *Journal of Vertebrate Paleontology* 1: 265–272.
- Campbell Jr, K.E., and E.P. Tonni. 1983. Size and locomotion in teratons (Aves: Teratornithidae). *The Auk* 100: 390–403.
- Chandler, R.M. 1994. The wing of *Titanis walleri* (Aves: Phorusrhacidae) from the late Blancan of Florida. *Bulletin of Florida Museum of Natural History* 36: 175–180.
- Collar, J. 1996. Family Otidae (Bustards). In *Handbook of Birds of the world, Hoatzin to Auks*, vol. 3, ed. J. del Hoyo, A. Elliot, and J. Sargatal, 240–273. Barcelona: Lynx.
- Degrange F.J. 2012. *Morfología del cráneo y complejo apendicular posterior de aves fororhacoides: implicancias en la dieta y modo de vida*. Dissertation, Universidad Nacional de La Plata.
- Degrange, F.J. 2014. The hind limb morphometry of terror birds (Aves, Cariamiformes, Phorusrhacidae): their functional implications for substrate preferences and locomotory lifestyle. *Abstracts of the 4th International Palaeontological Congress*: 34.
- Degrange, F.J., and C.P. Tambussi. 2011. Re-examination of *Psilopterus lemoinei* (Moreno and Mercerat 1891), a late early

- Miocene little terror bird from Patagonia (Argentina). *Journal of Vertebrate Paleontology* 31: 1080–1092.
- Degrance, F.J., J.I. Noriega, and J.I. Areta. 2012. Diversity and paleobiology of the santacrucian birds. In *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*, eds. Vizcaíno, S.F., R.F. Kay, and M.S. Bargo, 138–155. Cambridge University Press, Cambridge.
- Degrance, F.J., C.P. Tambussi, M.L. Taglioretti, A. Dondas, and F. Scaglia. 2015. A new Mesembriornithinae (Aves, Phorusrhacidae) provides new insights into the phylogeny and sensory capabilities of terror birds. *Journal of Vertebrate Paleontology* 35: e912656. doi:10.1080/02724634.2014.912656.
- Gould, G.C., and I.R. Quimby. 2005. *Titanis walleri*: bones of contention. *Bulletin of Florida Museum of Natural History* 45: 201–229.
- Kraglievich, L. 1940. Descripción del gran ave pliocena “*Mesembriornis milneedwardsi*”. *Obras de Geología y Paleontología* 3: 639–666.
- Mayr, G. 2009. *Paleogene Fossil Birds*. Berlin Heidelberg: Springer-Verlag.
- Mayr, G., and J.I. Noriega. 2015. A well-preserved partial skeleton of the poorly known early Miocene seriema *Noriegavis santacrucensis* (Aves, Cariamidae). *Acta Palaeontologica Polonica*. doi:10.4202/app.00011.2013.
- Mayr, G., and D. Rubilar-Rogers. 2010. Osteology of a new giant bony-toothed bird from the Miocene of Chile, with a revision of the taxonomy of Neogene Pelagornithidae. *Journal of Vertebrate Paleontology* 30: 1313–1330.
- Moreno, F.P., and A. Mercerat. 1891. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. *Anales del Museo de La Plata* 1: 7–71.
- Mourer-Chauviré, C., R. Tabuce, M. Mahboubi, M. Adaci, and M. Bensalah. 2011. A Phororhacoid bird from the Eocene of Africa. *Naturwissenschaften*. doi:10.1007/s00114-011-0829-5.
- Noriega, J.I., S.F. Vizcaíno, and M.S. Bargo. 2009. First record and a new species of seriema (Aves: Ralliformes: Cariamidae) from Santacrucian (Early-Middle Miocene) beds of Patagonia. *Journal of Vertebrate Paleontology* 29: 620–626.
- Noriega, J.I., J.I. Areta, S.F. Vizcaíno, and M.S. Bargo. 2011. Phylogeny and taxonomy of the Patagonian Miocene Falcon *Thegornis musculosus* Ameghino, 1895 (Aves: Falconidae). *Journal of Paleontology* 85: 1089–1104.
- Palmqvist, P., and S.F. Vizcaíno. 2003. Ecological and reproductive constraints of body size in the gigantic *Argentavis magnificens* (Aves, Teratornithidae) from the Miocene of Argentina. *Ameghiniana* 40: 379–385.
- Patterson, B., and L. Kraglievich. 1960. Sistemática y nomenclatura de las aves fororracoideas del Plioceno Argentino. *Publicación del Museo Municipal Ciencias Naturales y Tradicionales de Mar del Plata* 1: 1–51.
- Pennycuik, C.J. 1989. *Bird flight performance*. Oxford: Oxford University Press.
- Pennycuik, C.J. 2007. *Modelling the flying bird*. London: Academic Press.
- Rovereto, C. 1914. Los estratos araucanos y sus fósiles. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 25: 1–247.
- Sinclair, W.J., and M.S. Farr. 1932. Aves of the Santa Cruz beds. Part II. *Reports Princeton University Expedition Patagonia* 7: 157–191.
- Tambussi, C.P., and F.J. Degrange. 2013. *South American and Antarctic Continental Cenozoic birds: Paleobiogeographic affinities and disparities*. Netherlands: Springer.
- Tonni, E.P., and C.P. Tambussi. 1988. Un nuevo Psilopterinidae (Aves: Ralliformes) del Mioceno tardío de la provincia de Buenos Aires, República Argentina. *Ameghiniana* 25: 155–160.
- Vizcaíno, S.F., and R.A. Fariña. 1999. On the flight capabilities and distribution of the giant Miocene bird *Argentavis magnificens* (Teratornithidae). *Lethaia* 32: 271–278.
- Vizcaíno, S.F., R.F. Kay, and M.S. Bargo. 2012. Background for a paleoecological study of the Santa Cruz Formation (late Early Miocene) on the Atlantic coast of Patagonia. In *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*, eds. Vizcaíno, S.F., R.F. Kay, and M.S. Bargo, 1–22. Cambridge University Press, Cambridge.