First record of Procariama simplex Rovereto, 1914 (Phorusrhacidae, Psilopterinae) in the Cerro Azul Formation (upper Miocene) of La Pampa Province; remarks on its anatomy, palaeogeography and chronological range

Raúl Ignacio Vezzosi

Available online: 06 Jan 2012

PLEASE SCROLL DOWN FOR ARTICLE

First record of *Procariama simplex* Rovereto, 1914 (Phorusrhacidae, Psilopterinae) in the Cerro Azul Formation (upper Miocene) of La Pampa Province; remarks on its anatomy, palaeogeography and chronological range

RAÚL IGNACIO VEZZOSI

New records of *Procariama simplex* in central and northwestern Argentina are reported. The fossil material includes mandibular bones, cervical vertebrae and several elements of the fore and hindlimbs. After an exhaustive comparison of anatomical characters and morphometric analysis, the fossil specimens are assigned to the psilopterine *Procariama simplex*. The specimen from La Pampa Province represents the first record of a psilopterine in this central region of Argentina and derives from upper Miocene sediments of the Cerro Azul Formation. Lithological features and biostratigraphical data allow the host bed to be assigned to the Huayquerian faunal stage (late Miocene). The La Pampa record broadens the geographical distribution of *Procariama simplex*, which was previously restricted to northwestern Argentina.

Raúl Ignacio Vezzosi [vezzosiraul@gmail.com], Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción CICYTTP-CONICET, Materi y España s/n (3105), Diamante, Entre Ríos, Argentina. Received 1.4.2011, revised 28.5.2011, accepted 14.6.2011.

PSILOPTERINE birds (Phorusrhacidae) are part of a lineage of flightless extinct terrestrial avian predators with substantial forelimb bone reduction (humerus, ulna, radius, phalanges). Commonly known as 'Fororracos', these terrestrial birds were apex predators and, together with the large terrestrial mammals, formed an endemic vertebrate association in South America during most of the Cenozoic (Pascual & Odreman Rivas 1971, Simpson 1980, Pascual & Bondesio 1982, Pascual 1984, 1998, Noriega 1994, Flynn & Wyss 1998). At the end of the 'splendid isolation' of South America by the late Pliocene–early Pleistocene, phorusrhacids also participated in the Great American Biotic Interchange across the Panamanian terrestrial bridge (Marshall 1994, Webb 2006).

These cursorial birds include five subfamilies and 13 genera (Alvarenga & Höfling 2003). They are related to the extant South American seriemas (Cariamidae). The oldest South American record of phorusrhacid birds is from the Paleocene of Brazil (Alvarenga 1985) and the youngest comes from the late Pleistocene of Uruguay (Alvarenga *et al.* 2010).

In North America, there is only one taxon, *Titanis walleri* Brodkorb, 1963, reported from the Pliocene (late Hemphillian to late Blancan) of Texas and Florida (Chandler 1994, Baskin 1995, Gould & Quitmeyr 2005, MacFadden *et al.* 2006). Chandler (1994) has indicated the presence of at least two morphotypes of *Titanis* in Florida deposits.

Procariama simplex Rovereto, 1914 is considered the largest cursorial psilopterine predator with reduced forelimbs (Alvarenga & Höfling 2003, Vezzosi 2006, 2007). The oldest remains of this taxon occur in the Miocene sediments of Catamarca Province without precise stratigraphical context (Rovereto 1914, Marshall & Patterson 1981). The present study documents the first occurrence of *P. simplex* from the late Miocene of La Pampa, extending its geographic distribution from northwest to central Argentina. New records of this taxon are also reported from the late Miocene of northwestern Argentina with precise stratigraphical context. The anatomies of the postcranial bones are reviewed, with an emphasis on the description of the humerus.

Localities and geological setting

The Pampean material (MMP-990) described in this study was collected by Alejandro Dondas at the

Salinas Grandes de Hidalgo, Atreucó Department, La Pampa Province, Argentina, about 15 km south of Hidalgo railway station (Fig. 1); this rail line connecting Carhué (Buenos Aires province) with the Pampean locality of Doblas (Campbell & Tonni 1980). The material derives from saline sediments belonging to the upper Miocene Cerro Azul Formation (Linares *et al.* 1980)—more precisely from the lowest level of the outcrop on the west side of the salt flats (A. Dondas personal observation). This site is located in a southwest–northwest depression of 3900 ha and constitutes one of the elongated salt bodies of the La Amarga-La Ernestina series represented in a larger depression (Schalamuck *et al.* 1999). To the east, it continues as a set of low salt bodies, of low economic significance, forming an ephemeral deposit up to 10 cm thick, whereas the underlying permanent layer reaches 12 m thick and contains alternating muds and slightly soluble salts, of which glauberite and gypsum are important (Cordini 1967). This formation has a loess-like appearance (Goin *et al.* 2000), containing a mixture of reddish-brown terrestrial fine sand, minor silt and sparse lenses of clay. Caliche-like concretions of irregular thickness occur at several levels, and isolated concretions also occur locally (Campbell & Tonni 1980).

These strata were originally assigned to the 'Epecuén Formation' based on several palaeontological studies (see Pascual *et al.* 1965, Campbell & Tonni 1980, Laza 1982, Montalvo *et al.* 1996),
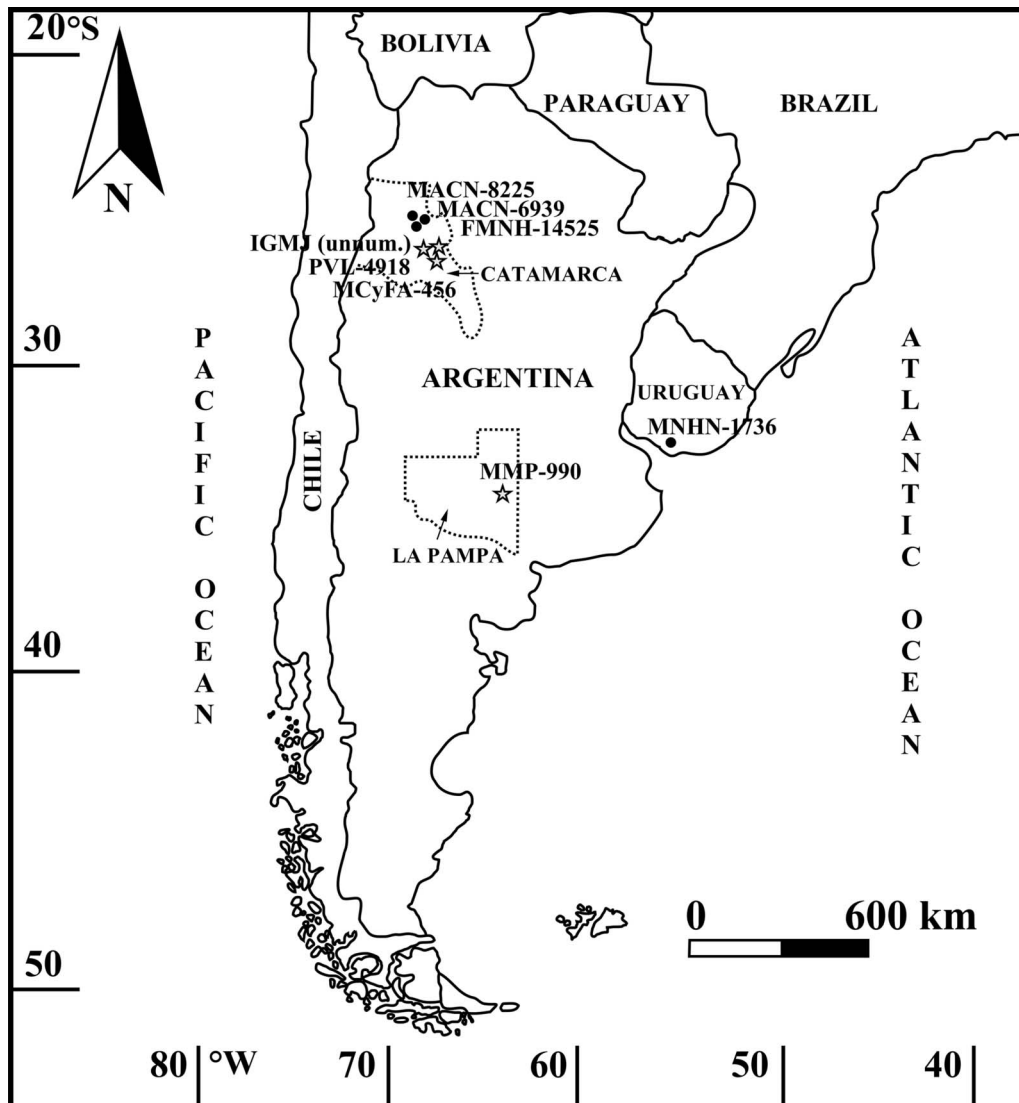

Fig. 1. Map of southern South America, the open stars indicating the fossiliferous localities from which the specimens of *Procariama simplex* were collected. Solid circles indicate records documented by previous studies.

although this unit had not been formally defined in the Salinas Grandes de Hidalgo locality (see Goin *et al.* 2000). Nevertheless, the sedimentological and stratigraphic analyses undertaken by Goin *et al.* (1997) suggest that the Cerro Azul Formation and the 'Epecuén Formation' (the latter documented at the town of Salinas Grandes de Hidalgo) are clearly correlative. Therefore, Goin *et al.* (2000) proposed to assign correlative strata from both areas previously recorded as the 'Epecuén Formation' to the Cerro Azul Formation, and this has been followed by subsequent researchers (Cerdeño & Montalvo 2002).

The late Miocene age assignment (Huayquerian SALMA *sensu* Pascual *et al.* 1965) for the Cerro Azul Formation is based on the fossil mammal fauna reported from Salinas Grandes de Hidalgo by Pascual *et al.* (1965), Zetti (1972), Montalvo *et al.* (1996), Goin *et al.* (2000), Cerdeño & Montalvo (2002).

Specimen MUCyFA-456 derives from upper Miocene (Huayquerian) sediments of the Andalhuala Formation at Wadi los Bajos, north of Chiquimil locality (Entres Ríos *sensu* Bossi & Muruaga 2009), Yocavil Valley (Castellanos 1969), Catamarca Province. Specimen PVL-4918 derives from upper Miocene (Huayquerian) sediments of the Andalhuala Formation at Entre Ríos (Bossi & Muruaga 2009). The unnumbered IGMJ specimen was recovered from upper Miocene (Huayquerian) sediments of the Andalhuala Formation at Santa María Yocavil Valley at an unspecific locality, in Catamarca Province. The fauna associated with the new material from northwestern Argentina is characteristic of the Huayquerian (*sensu* Pascual *et al.* 1965), a South American land mammal age conventionally dated as late Miocene (Marshall *et al.* 1979, Marshall & Patterson 1981, Cione *et al.* 2000).

Material and methods

The fossil remains are stored in the collections of the Museo Municipal de Mar del Plata 'Lorenzo Scaglia' (MMP), Instituto Miguel Lillo Paleontología de Vertebrados (PVL), Museo Universitario Carlos y Florentino Ameghino (MUCyFA) and the Peirano collection of the Instituto de Geología y Minería de San Salvador de Jujuy (IGMJ-unnumbered). Comparisons were made with bones of other fossil Psilopterinae, and extant and fossil taxa belonging to the Cariamidae (considered morphologically similar to psilopterines) deposited at the Departamento Científico de Paleontología de Vertebrados, Museo de La Plata (MLP), Field Museum of Natural History in Chicago (FMNH), Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN),

Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Santa Cruz province, Argentina (MPM-PV) and Museo Nacional de Historia Natural de Montevideo (MNHN) as listed below: Phorusrhacidae indet. (MNHN-1736), *Psilopterus* sp. Moreno & Mercerat, 1891 (MLP-586), *P. bachmanni* (Moreno & Mercerat, 1891) (MLP-167, MLP-168, MLP-187, MPM-PV-without numeration), *P. lemoinei* (Moreno & Mercerat, 1891) (MLP-162, MLP-188, MLP-189), *P. affinis* (Ameghino, 1899) (MACN-A-52-184), *P. colzecus* Tonni & Tambussi, 1988 (MLP-76-VI-12-2 Holotype), *Procariama simplex* (MACN-8225 Lectotype, MACN-6939; FMNH-14525), *Chunga incerta* Tonni, 1974 (MLP 71-VII-5-1 Type, MLP-71-VII-5-2, MLP-71-VII-5-3, MLP-71-VII-5-4), *Ch. burmeisteri* (Hartlaub, 1860) (MLP-535), *Cariama santacrucensis* Noriega, Vizcaíno & Bargo, 2009 (MPM-PV-3510, MPM-PV-3512), *C. cristata* (Linnaeus, 1766) (MLP-533). Taxa not available for direct comparison [i.e., *Paraphysornis brasiliensis* (Alvarenga, 1982), *Paleopsilopterus itaboraiensis* Alvarenga, 1985, *Psilopterus* sp.] were compared using published illustrations and descriptions. Anatomical terminology follows Howard (1980) and, in some cases, Baumel & Witmer (1993).

The measurements (Table 1) given in millimetres, were compiled according to the following criteria and abbreviations. In cases where the fossil is incomplete, the preserved measurement was taken and indicated by the abbreviation 'p' (preserved). *Atlas*: W-CF, condylar fossa width. W-VB, vertebral body width. *Humerus*: TL_p, total length preserved. W-SHAFT, minimum width of midshaft. D-SHAFT, minimum depth of midshaft. Circ-SHAFT, minimum circumference of midshaft. W-PROX, proximal end width. D-HEAD, head depth, taken parallel to the longitudinal axis. W-DIST, distal end width. *Femur*: TL, total length. *Tibiotarsus*: TL-FIB, fibula total length. W-FIB, fibula head width. D-HEAD-SPINE, fibular spine depth. D-COND, depth of condylae (m, medial; l, lateral). *Tarsometatarsus*: W-TROC, intertrochlear width. D-TROC, intertrochlear depth. W-HIP, width of hypotarsus. A, intertrochlear groove width. B, maximum shaft width at level of foramen magnum. C, proximal end width of trochlea metatarsi III at level of intertrochlear grooves. D, trochlea metatarsi II width. E, trochlea metatarsi III width. F, trochlea metatarsi IV width. G, trochlea metatarsi III total length. H, antero-posterior shaft length at level of foramen magnum. *Phalanges*: W-T-DIST, trochlear distal width. W-F-PROX, proximal width of trochlear fossa. D-T-DIST, trochlear distal diameter. D-T-PROX, proximal diameter of trochlear fossa.

			Procariama simplex					Phorusrhacidae indet.
	MMP-990	MACN-8225	MACN-6939	FMNH-14525	MUCyFA-456	IGMJ-unnumb.	PVL-4918	MNHN-1736
Humerus								
TL	90.90 (p)	–	–	104.00	–	88.19 (p)	–	–
W-SHAFT	8.66	–	–	–	–	9.64	–	–
D-SHAFT	9.80	–	–	–	–	–	–	–
Circ-SHAFT	29.04	–	–	–	–	–	–	–
W-PROX	17.48	–	–	–	–	–	–	–
D-HEAD	8.58	–	–	–	–	–	–	–
Femur								
TL	–	66.73 (p)	114.06 (p)	169.09	–	148.18	–	–
W-PROX	–	–	30.74	37.88	–	30.45	–	–
W-SHAFT	–	15.20	15.08	17.27	–	15.23	–	–
W-DIST	–	37.76	32.25	38.60	–	33.86	–	–
Tibiotasus								
TL	283 (p)	–	–	293.79	151.54 (p)	–	–	–
W-SHAFT	17.36	15.94	–	16.55	17.50	15.75	–	–
D-SHAFT	16.42	11.94	–	–	16.06	–	–	–
Circ-SHAFT	53.99	–	–	56.30	54.00	–	–	–
D-HEAD SPINE	20.30	–	–	23.08	–	–	–	–
W-FIB	8.43	–	–	7.97	–	–	–	–
TL-FIB	143.17	–	–	121.72	–	–	–	–
W-DIST	–	26.75	27.61	27.93	23.33	25.86	–	–
D-M-COND	–	26.85	24.74	27.77	27.36	–	–	–
D-L-COND	–	23.57	23.07	25.73	22.17	–	–	–
Tarsometatarsus								
TL	228.00 (p)	65.20 (p)	97.92 (p)	216.00	–	94.22 (p)	–	–
W-TROC	–	29.77	30.84	29.66	22.76	28.31	29.76	–
D-TROC	–	27.23	19.84	25.48	–	27.31	–	–
W-HIP	–	14.97	11.57	16.59	–	14.94	15.04	–
W-SHAFT	13.68	14.18	11.42	13.45	12.35	13.73	–	–
D-SHAFT	13.31	12.06	13.48	–	13.45	12.53	–	–
Circ-SHAFT	50.74	–	–	–	51	–	–	–
W-DIST	33.58	25.64	27.68	27.48	–	34.72	–	–
A	2.98	1.86	2.60	2.33	1.53	3.05	–	–
B	27.66	21.30	–	27.58	19.81	24.05	–	13.54 (p)
C	12.59	11.64	7.20	10.69	–	10.24	–	10.50
D	8.88	7.81	5.96	6.72	–	8.61	–	6.95
E	15.48	13.38	11.43	13.93	–	15.97	–	12.04
F	10.95	7.52	6.70	8.32	–	8.88	–	–
G	18.59	18.74	13.00	16.66	–	15.95	–	17.40
H	12.85	15.41	15.50	–	10.34	–	–	10.58
Phalanx I								
TL	45.92	35.50	–	–	–	–	–	–
W-T-DIST	15.85	11.50	–	–	–	–	–	–
W-F-PROX	20.35	14.40	–	–	–	–	–	–
D-T-DIST	12.32	–	–	–	–	–	–	–
D-T-PROX	17.45	14.30	–	–	–	–	–	–
W-SHAFT	11.47	–	–	–	–	–	–	–
Phalanx II								
TL	28.88	23.60	–	–	–	–	–	–
W-T-DIST	13.40	10.00	–	–	–	–	–	–
W-F-PROX	13.38	11.90	–	–	–	–	–	–
D-T-DIST	10.28	–	–	–	–	–	–	–
D-T-PROX	13.98	11.10	–	–	–	–	–	–
W-SHAFT	11.60	–	–	–	–	–	–	–

(*continued*)

Table 1. (*Continued*).

	Procariama simplex							Phorusrhacidae indet.
	MMP-990	MACN-8225	MACN-6939	FMNH-14525	MUCyFA-456	IGMJ-unnumb.	PVL-4918	MNHN-1736
Phalanx III								
TL	21.55	–	–	–	–	23.25	–	–
W-T-DIST	12.05	–	–	–	–	10.12	–	–
W-F-PROX	14.19	9.70	–	–	–	13.01	–	–
D-T-DIST	10.37	–	–	–	–	–	–	–
D-T-PROX	13.68	10.30	–	–	–	–	–	–
W-SHAFT	10.72	–	–	–	–	8.19	–	–

Table 1. Measurements (in mm) for specimens of Psilopterinae. The abbreviation p. indicates estimation from incomplete specimens.

A principal-components analysis (PCA) was performed from the variance–covariance matrix using INFOSTAT/P 1.1 (Fig. 2). Only 11 specimens (MACN-8225 Lectotype, MMP-990, FMNH-14525, unnumbered IGMJ, MNHN-1736, MLP-76-VI-12-2 Holotype, MACN-A-52-184, MLP-187, MLP-71-VII-5-3, MLP-533, MLP-535) and five hindlimb measurements (B, C, D, E, G) were utilized as a compromise between maximizing the number of specimens and variables that could be included.

Systematic palaeontology
Order RALLIFORMES Reichenbach, 1852
Suborder CARIAMAE Fürbringer, 1888
Family PHORUSRHACIDAE Ameghino, 1889
Subfamily PSILOPTERINAE Dolgopol de Saez, 1927

Procariama Rovereto, 1914

Procariama simplex Rovereto, 1914 (Figs 3–6)

Holotype.   MACN 8225, associated partial skeleton consisting of an incomplete skull, pelvis, proximal and distal portions of the left femur, distal portion of the right tibiotarsus, proximal and distal portions of the right tarsometatarsus, foot and ungual phalanges of the left foot (almost complete) and fragments of the phalanges of the right foot, designated by Patterson & Kraglievich (1960).

Referred material.   Portion of right mandible including a fragment of the surangular whose anterior border limits the mandibular rostral fenestra, atlas and axis with neural arcs and spines missing, shaft and proximal end of left humerus and part of right shaft, left tibiotarsus with cnemial crest, left tarsometatarsus without proximal end, left third pedal phalanges (I–II–III), MMP-990. Shaft of left femur without proximal and distal end, left tibiotarsus partially complete, left tarsometatarsus without proximal and distal end, MUCyFA-456. Proximal end of right tarsometatarsus, PVL-4918. Distal end and shaft of left humerus, both complete femora, shaft and distal end of both tibiotarsi, shaft and distal end of left tarsometatarsus, proximal and distal end of right tarsometatarsus, six podial phalanges, IGMJ (unnumbered).

Emended diagnosis.   A flightless psilopterine with slender fore- and hindlimbs, that exceeds *Paleopsilopterus* in size. Forelimbs reduced. Humerus small relative to the body of the bird and more curved than in all other psilopterines (Table 1). Pneumatic foramen large (Alvarenga *et al.* 2011) but superficial, and humerus with processus flexorius distally developed similar to the extant Cariamidae. Processus supracondylaris dorsalis deflected laterally. Hindlimbs more robust than in other psilopterines and extant cariamids, and femur proportionally shorter. Tarsometatarsal hypotarsus with two crests (medial and lateral crests). Intercondylar tuberosity prominent (Eminentia intercondylaris), oval, bulged and more convex. Deep cotylae with conspicuous and sharp edges. Anterior metatarsal groove (sulcus extensorius) deeper and concave, and proximally projected to the cotylae. Trochleae with very deep foveae ligamenti collateralia. Trochlea metatarsi III large and distally expanded with conspicuous and asymmetric rims. Outer intertrochlear groove similar to psilopterines and narrower than in extant and fossil seriemas (Cariamidae), with less lateral displacement of the outer trochlea. Trochlea metatarsi II narrow, with articular surface transversely convex without longitudinal sulcus (in dorsal and distal view), and distal displacement, being almost parallel to the trochlea III. Narrow notch between trochleae II and III. Straight
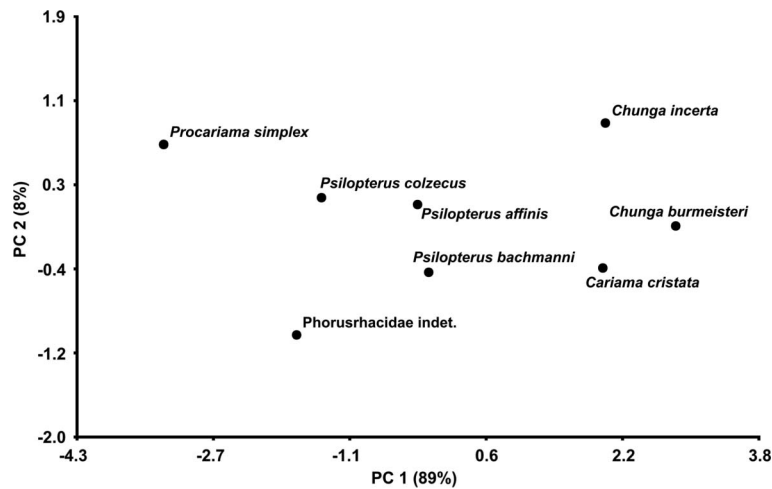
Fig. 2. Principal components analysis (PCA) of the tarsometatarsus measurements of the Psilopterinae birds. Abbreviations: PC, principal component; %, percentage of explained variation.

and subcylindrical podial phalanges, relatively gracile, with ligamental impressions rounded.

Description and comparisons

Mandible.   Only a right fragment of the mandibular symphysis and the right surangular bone, with the anterior ridge limiting the rostral mandibular fenestra, is preserved (Fig. 3A, B). Dorsally, the symphysis is concave and ventrally convex, with a subcircular rounded edge.

Cervical vertebrae.   Only the two first cervical vertebrae are preserved (atlas and axis; Fig. 3C), both fused by a secondary diagenetic process at the level of the axial odontoid. The condylar fossa of the atlas is deeply concave for reception of the occipital condyle; W-CF 5.4 mm and W-VB 10.5 mm. The hypapophysis is projected ventro-laterally and the neural arch is broken. Below, a slight median keel, flanked laterally by a ridge terminating backward on either side in a long process, is observed similar to the description given by Sinclair & Farr (1932) for *Pelecyornis australis* (synonymous with *Psilopterus lemoinei* in Alvarenga & Höfling 2003). Posteriorly, the articular surface of the axis is convex transversely and fused with the atlas (Fig. 3C).

Humerus.   The surface of the bicipital crest is reduced and part of the latter is broken. The shaft is curved with anconal and medial concavity (Fig. 3D, E), and has dimensions less than *Psilopterus* and extant Cariamidae (see Appendix A—online supporting data). The humeral head is oval and long, antero-posteriorly depressed, with anconal displacement more marked than *Psilopterus*. In relation to the longitudinal axis of

the shaft, the head is positioned transversely, which differs from the oblique orientation in *Psilopterus*. The external tuberosity (tuberculum dorsale) seems to be broken and the deltopectoral ridge (crista dectopectoralis) is not as strongly developed as in *Psilopterus*. The pneumatic fossa (fossa pneumotricipitalis) has a shallow concavity of circular section with a narrow capital groove (incisura capitalis). As mentioned by Alvarenga *et al*. (2011), the pneumatic foramen is large, but appears to be more superficial than the large and deep examples in *Psilopterus*, *Cariama* and *Chunga*. The attachment of the latissimus dorsi posterioris constitutes a simple continuous shallow depression limited by the capital shaft ridge. In palmar view, the sulcus ligamentorum transversus is a shallow lineation parallel to the head position. The sulcus (cranialis) m. coracobranchialis is elliptic, shallow and situated at the intertubercular level.

Distally, the processus flexorius is present but less prominent or developed than in *Psilopterus* (absent in *Psilopterus sensu* Sinclair & Farr 1932); a similar condition is shared with extant Cariamidae, differing from that in extinct Cenozoic Bathornithidae and Idiornithidae birds, in which it is small or not prominent (Alvarenga & Höfling 2003). This process is projected distally (Alvarenga *et al*. 2011) more than in *P. colzecus* but not so prominent as in *P. lemoinei* and *P. bachmanni*. It has an intermediate condition similar to that of *Cariama cristata*. Similarly, the lateral displacement of this process is an anatomical character also shared with Cariamidae. The internal condyle (condylus ventralis) is triangular in cross-section and straight edged as in some Psilopterinae. The external condyle (condylus dorsalis) is well developed, elongate and warped as in some psilopterines (not in *P. colzecus*), but is projected towards the
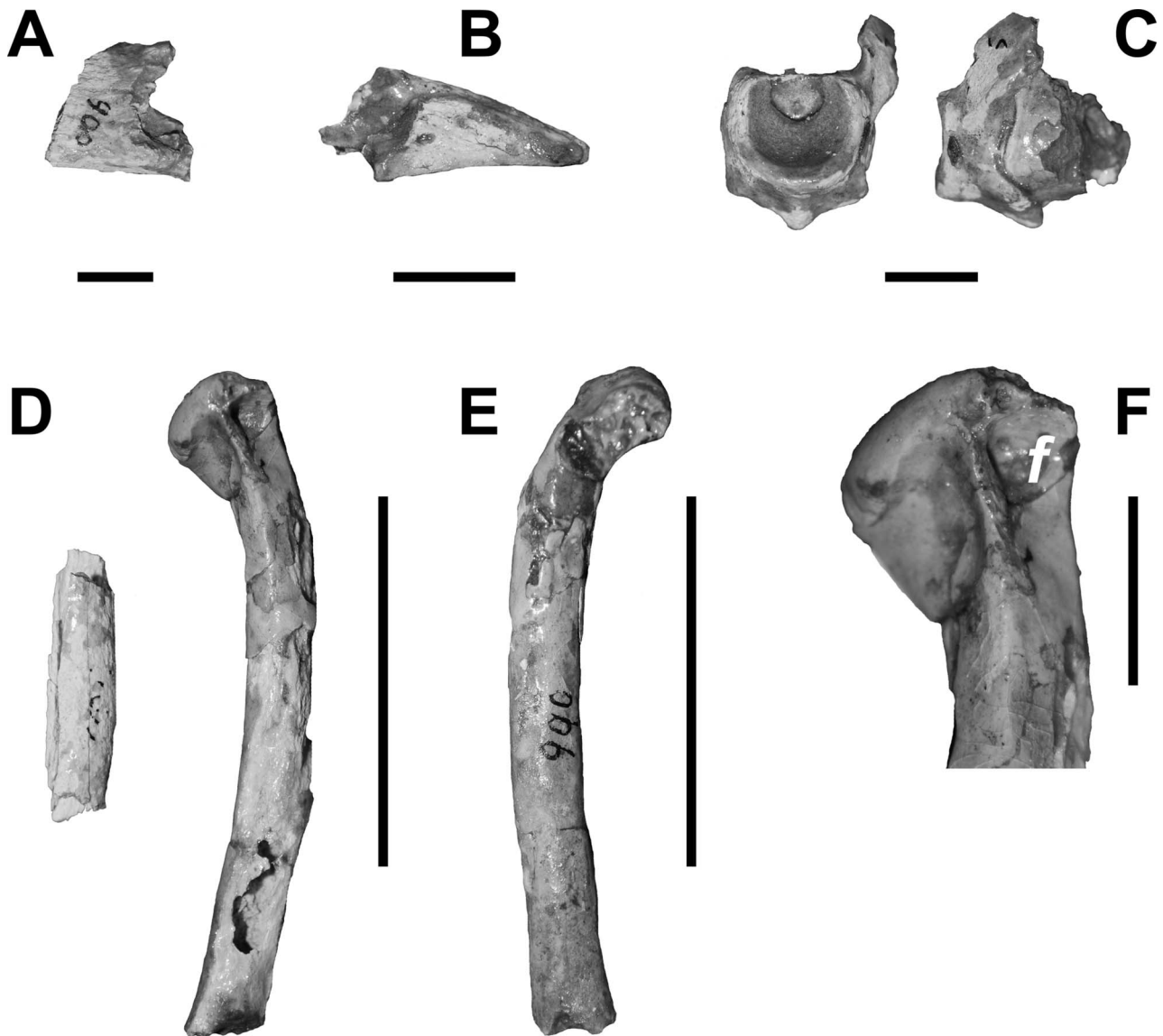
Fig. 3. Procariama simplex (MMP-990). Fragmentary mandible with right surangular (**A**) and symphysis (**B**), cervical vertebrae (**C**) (scale = 10 mm), left humerus and shaft of its right member in anconal view (**D**) and lateral view (**E**) (scale = 50 mm), detail of the proximal end in anconal view (**F**) (scale bar = 10 mm), fossa pneumatic *f*.

fossa musculi branchialis more than *Psilopterus* and extant Cariamidae. This fossa seems to be very deep and sharply delimited (Mayr & Clarke 2003) in psilopterines. Unlike most species of *Psilopterus*, the processus supracondylaris dorsalis is more deflected laterally than *Cariama cristata*. The humerus of *P. affinis* is not yet known; in fact the character could not be tested for this taxon.

Femur. In general appearance, the femora herein attributed to *Procariama simplex* (Fig. 4) resemble those of terrestrial phorusrhacid birds because they have the head and trochanter elevated to approximately the same degree (Sinclair & Farr 1932), but this

bone is proportionally shorter in *P. simplex* (Table 1). The head rises to above the level of the trochanter, the upper portion of the elevation being formed by a large blunt-pointed process, which partly divides the deep pit for the attachment of the round ligament (fovea lig. capitis) in two parts. The neck is compressed on its ventral surface. The anterior intermuscular line (linea intermuscularis cranialis) is well defined, extremely conspicuous and constitutes a notably projecting ridge of bone. The shaft is straighter than *Cariama* and differs from most rails and grues by having a rather curved shaft and the trochanter raised more proximaly than the head. The midshaft has a cylindrical section, but it is somewhat flattened
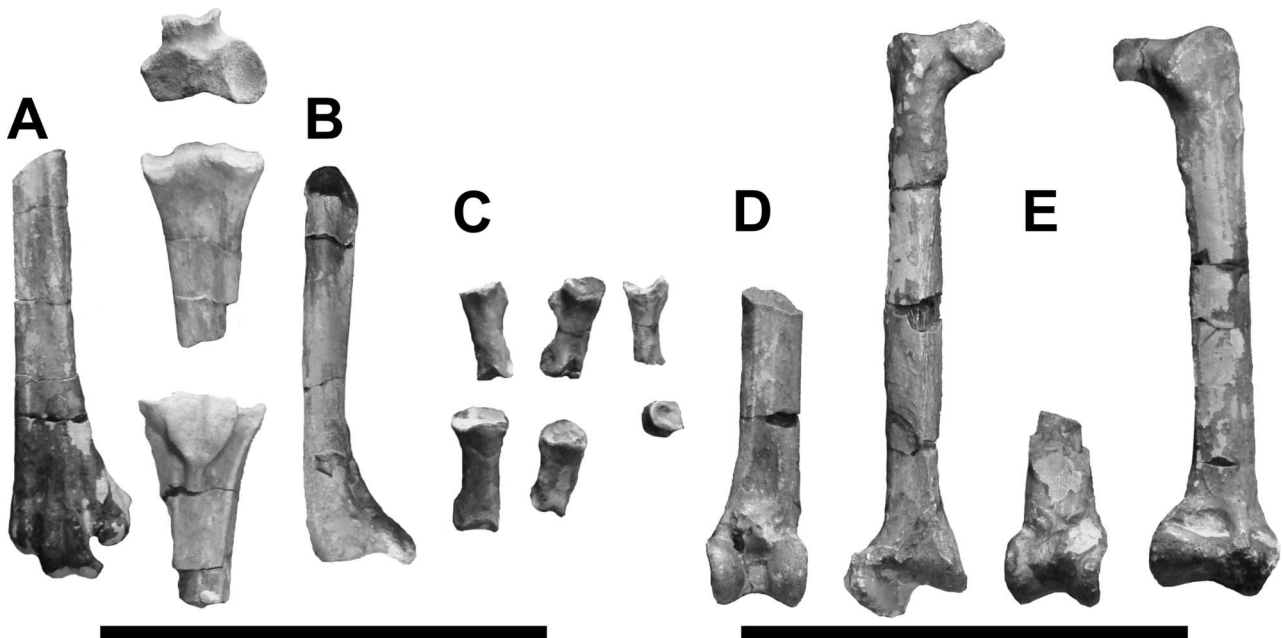
Fig. 4. Fossil record of limbs of *Procariama simplex* (IGMJ-unnumbered) from sediments of the Andalhuala Formation (late Miocene) of Santa María of Yocavill Valley, Catamarca province, Argentina. Right tarsometatarsus (**A**), left humerus (**B**), pedal phalanges (**C**), left femur and tibiotarsus (**D**), right femur and tibiotarsus (**E**). Scale bar = 100 mm.

antero-posteriorly just above the condyles. The distal end is similar to that in fossil phorusrhracids, with the outer and inner surfaces of the condyles diverging posteriorly. The popliteal area (Fossa poplitea) is oval and deeper than *Cariama*, *Grus* and *Psophia*. In dorsal view, the rotular groove (Sulcus intercondylaris) is wide and comparatively deep. The fibular groove (Trochlea fibularis) is notably wide, a feature related to running habits. As in *Phorusrhacos*, there is a well-defined rough line extending throughout its entire length on the posterior-medial border that finishes distally at the upper angle of the internal condyle (see Sinclair & Farr 1932).

Tibiotarsus. This bone is comparatively large (Table 1), slender, cylindrical in section and presents the typical configuration of psilopterines (Sinclair & Farr 1932). The midshaft is slightly cylindrical, but just above the distal end it is somewhat flattened, anticipating the beginning of a deep tendinal groove (Sulcus extensorius; Fig. 4) under the supratendinal bridge, which leads to the M. extensor digitorum longus. The fibular crest terminates distally. The beginning of the inner cnemial crest is at the level of the foramen interosseum proximal, and the supra-tendinal bridge is broken (Fig. 5). The fibular crest is one-third of the length of the fibula (Table 1). The foramen interosseum proximale is oval in dorsal and palmar views; it differs from the foramen interosseum distale, which has a triangular cross-section. The

upper surface, which articulates with the external condyle, is convex antero-posteriorly and concave latero-medially, similar to that in the phorusrhacid *Paraphysornis brasiliensis*. The D-HEAD SPINE is larger than in extant Cariamidae (Table 1).

In anterior view, the distal end has an anterior intercondylar fossa (Incisura intercondylaris) wide and deep. The tendinal groove (Sulcus extensorius) is broad and projects proximally towards the shaft (Figs 4–6), similar to Psilopterinae birds. The medial condyle projects further proximally than the lateral, it has a large and centrally placed medial ligamental prominence. The intermuscular line is marked and extends along the shaft from the level of the fibular crest to the medial condyle. It is notable that the lateral condyle, in lateral view, is rounded unlike the medial, which is elongated. Important differences from other cursorial groundbirds (i.e., Rheidae, Phorusrhacidae: Brontornithinae) are the presence of the supratendinal ridge and the internal position of the medial condyle (Moreno & Mercerat 1891, Alvarenga 1982, Tambussi *et al.* 1999).

Tarsometatarsus. This bone is one of the best known elements in the phorusrhacid anatomy with many previous extensive descriptions (Moreno & Mercerat 1891, Sinclair & Farr 1932, Alvarenga & Höfling 2003). It is thinner, but has a sturdier build than *Psilopterus* and fossil and extant Cariamidae, with similar dimensions to *Paleopsilopterus*
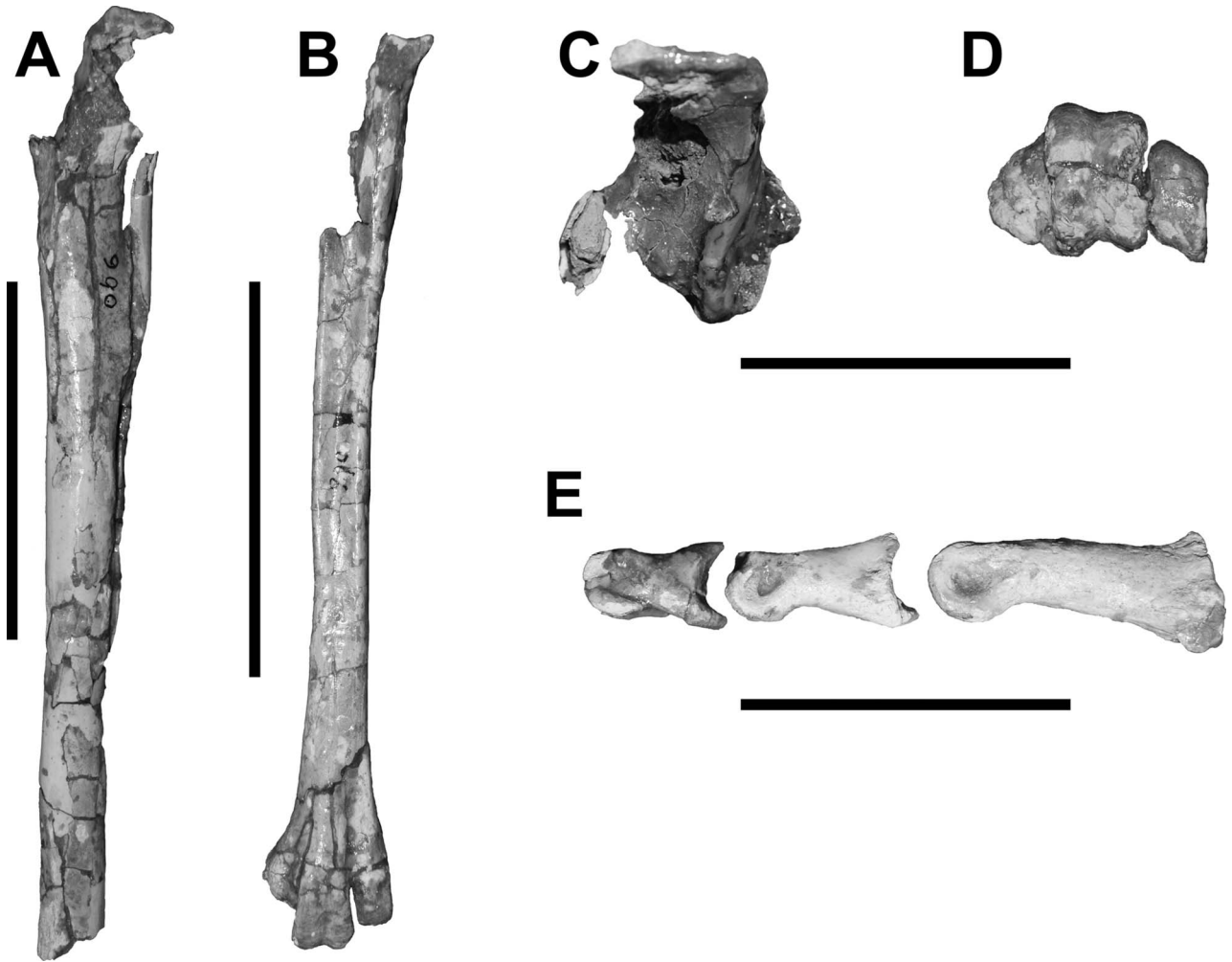
Fig. 5. Fossil record of limbs of *Procariama simplex* (MMP-990) from sediments of the Cerro Azul Formation (late Miocene) of La Pampa province, Argentina. Left tibiotarsus (**A**), left tarsometatarsus (**B**), detail of proximal end of tibiotarsus (**C**), detail of distal end of tarsometatarsus (**D**), left podial phalanx I-II-III (**E**). Vertical scale bar = 100 mm and horizontal bar = 50 mm.

(Alvarenga & Höfling 2003, table 8:82), and is relatively straight but medially curved in midshaft. The hypotarsus has the typical morphology of *Procariama simplex*, forming two expansions (lateral and medial) in the most proximal end that look like two crests (Alvarenga & Höfling 2003; Fig. 4A).

The cotylae are elliptical and deeply concave, but the external (cotyla lateralis) is clearly smaller and more squared than the medial one (cotyla medialis). The intercotylar prominence (eminentia intercotylaris) is rounded and well developed as in other phorusrhacids but is much more convex than in *Psilopterus*. The edges of the anterior metatarsal groove (sulcus extensorius) project to the cotylae, and their inner surfaces are directed towards the intercotylar prominence (Figs 4–6). In extant Cariamidae and fossil Psilopterinae, the edges of the sulcus extensorius are projected to the middle region of the

cotylae. They are attenuated distally, making them different from those in *Psilopterus*, *Cariama* and *Chunga* that have sharp, conspicuous and open edges; and even more different from that in *Paleopsilopterus*, which is somewhat attenuate and wide. The shaft is moderately slender with a subquadrangular midsection; this approaches the condition seen in Phorusrhacidae (Alvarenga & Höfling 2003, Alvarenga *et al.* 2011). The dorsal excavation of the distal vascular foramen (foramen vasculare distale) is large and funnel-shaped. It is placed between the third and fourth trochleae (trochleae metatarsi III and IV), and above the proximal end of these trochleae (Fig. 5).

Distally, the trochleae are located and arranged in a slightly curved line. The middle trochlea (trochlea metatarsi III) is larger and also more dorsal and distally expanded than the other two (Alvarenga *et al.*
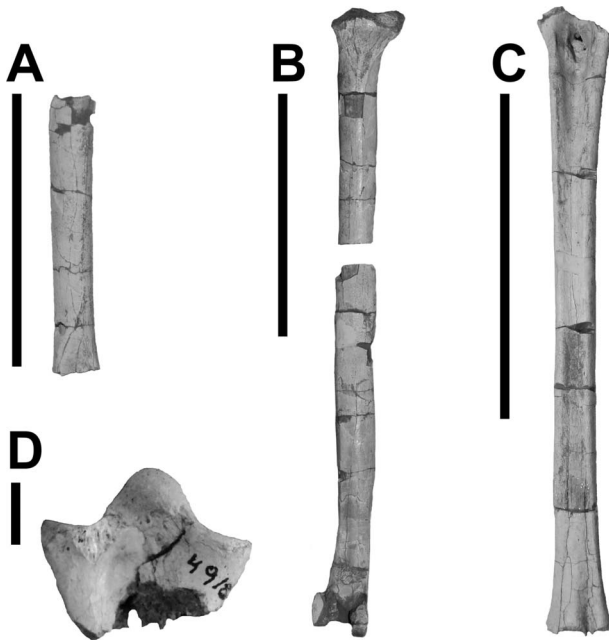
Fig. 6. Fossil record of limbs of *Procariama simplex* from sediments of the Andalhuala Formation (late Miocene) of Catamarca province, Argentina. MUCyFA-456: Left femur (**A**), left tibiotarsus (**B**) and left tarsometatarsus (**C**), Scale bars = 100 mm except for D (=10 mm). PVL-4918: Proximal end of right tarsometatarsus (**D**).

2010). It has an articular surface furrowed by a deep median groove with subparallel margins that proximally converged in dorsal and plantar view (Fig. 5D); this feature, being also present in the Phorusrhacidae specimens (MNHN-1736) from the late Pleistocene of Uruguay (Alvarenga *et al.* 2010). In dorsal view, the medial rim is more conspicuous, whereas the lateral one is more so in plantar view. This morphology is represented in all the specimens herein assigned to *Procariama* and is also noted in the Uruguay specimens (though not documented by Alvarenga *et al.* 2010). The inner trochlea (trochlea metatarsi II) is smaller, much shorter and has a less distal extent than the outer trochlea. It is important to note that in most extant predatory birds, the trochlea metatarsi II is much wider and reaches almost the same distal level as the trochlea III; this differs from the condition in some cursorial birds such as Cariamidae and Otididae, in which it is deflected medially (Alvarenga *et al.* 2010). The articular surface of the inner trochlea is transversely convex and lacks a longitudinal sulcus. In dorsal view, the inner trochlea is almost parallel to the middle one and forms a narrow notch between both (Figs 4A, 5B, D). The outer surfaces of the inner and outer trochleae, and both sides of the trochlea metatarsi III, have deep ligamental pits (foveae ligamentum collateralium) very typical of the Phorusrhacidae (Alvarenga *et al.* 2010). The foramen

vasculare distale is located more proximally than the proximal rim of the middle trochlea (Figs 4A, 5B). In palmar view, the tarsometatarsus reveals a posterior metatarsal groove (sulcus flexorius) less concave than the sulcus extensorious, and its lateral ridge is more conspicuous than the medial one.

Pedal phalanges.   These are slender, straight and subcylindrical with circular ligamental impressions (Tonni & Tambussi 1988), but larger than those of *Psilopterus* and Cariamidae (Table 1). Their distal surfaces are convex, and the proximal end of the phalanx III is more concave than that of I (Fig. 5).

Discussion

Systematic remarks.   The classification of the Phorusrhacidae is based principally on the mandibular symphysis and tarsometatarsus morphology. The latter are resistant skeletal elements, usually well preserved, and they are also used in most studies (Alvarenga & Höfling 2003) to infer feeding specialization habits and differences in force, agility and running speed (Blanco & Jones 2005).

Recently, two phylogenetic hypotheses have been proposed (see Agnolín 2009, Alvarenga *et al.* 2011) for the family. The cladistic analysis of Alvarenga *et al.* (2011) supports monophyly of the Phorusrhacidae, but this phylogeny could be revised and improved with some new characters observed in the fossil material described herein (i.e., humeri, femora, tibiotarsi, tarsometatarsi), which could fill the missing data present in the matrix for the Psilopterinae group.

In this way, the morphological and morphometric analyses of the skeletal remains studied herein, compared with phorusrhacids and fossil and extant seriemas, reveal diagnostic anatomical features in the fore and hindlimbs. They allow the assignment of all specimens to *Procariama* and the inclusion of *Procariama simplex* in the subfamily Psilopterinae. These psilopterine characters are: (1) small and curved humerus indicative of the loss of flight; (2) robust and well-developed hindlimbs with short femur; (3) hypotarsus with two very shallow crests; (4) oval, prominent and markedly convex intercotylar tuberosity; (5) deep cotylae with conspicuous edges; (6) sulcus extensorius deeply concave with conspicuous rims; (7) conspicuous mesotrochlear rims projected to the shaft (Fig. 5B); (8) trochlea metatarsi III more displaced anteriorly and distally than inner and outer trochleae; (9) articular surface of trochlea metatarsi II transversely convex and without a longitudinal sulcus (Alvarenga *et al.* 2011); (10)

gracile, straight and subcylindrical pedal phalanges with circular ligamental insertions.

In an anatomical context, the most important humerus characters described here from *Procariama simplex* are: (1) the shaft is curved more evenly than in *Psilopterus lemoinei*; (2) the head of the humerus is transverse to the longitudinal axis, similar to the position adopted with respect to the sulcus ligamental transversus with anconal displacement, but different from *P. bachmanni* and *P. lemoinei*, which have an oblique position, whereas in *Cariama cristata* it is proximally displaced; (3) the crista deltopectoralis is small, similar to *P. bachmanni* but absent in *P. lemoinei*; and (4) the condylae show morphological features that allow *P. simplex* to be grouped with some psilopterines, such as *Psilopterus bachmanni* and *P. colzecus*, i.e., an inner condyle with a straight edge and triangular shape, differing from the curved, convex and oval shape of *P. lemoinei* and *C. cristata*. These features and others outlined above strongly suggest that *Procariama simplex* was a bird unable to fly.

The humeri and tarsometatarsi morphologies described above could be considered common anatomical characters of Psilopterinae and Cariamidae, with some important differences (i.e., the proximal and distal ends of the humerus and tarsometatarsus), that may be useful in the context of a future phylogenetic analysis of living and fossil taxa of cursorial birds.

The morphometric analysis indicates that PC1 and PC2 explain 97% of the total variability (Table 2). MNHN-1736 lies at the lower end of PC1 (Fig. 2). The first component of the PCA explains 89% of the variance. PC1 would reflect the size because all variables load with the same sign and similar values (Reyment 1991, Baxter 1995). The variable E (Trochlea metatarsi III width) has the greater weight on PC1. Variables C, D and G also have a relatively greater weight on PC1. Thus, *Procariama simplex* is far from all other taxa (Fig. 2), being the largest psilopterine bird. This analysis shows that MNHN-1736 would be more related to the Psilopterinae than other Phorusrhacidae subfamilies. Thus, for PC1, the key differences among the specimens are related to the dimensions of the distal end of the tarsometatarsus.

The second component explains 8% of the total variance. The variable B has greater weight on PC2 (Table 2). Further, variables C, D, E and G have relative importance for PC2, because their weights are slightly lower and have a negative sign. Thus, PC2 is interpreted to account for shape differences (Reyment 1991, Baxter 1995). The negative sign and lower weight for D show that in large psilopterine specimens (i.e., MMP-990, FMNH-14525, MNHN-

PC	Eigenvalue	Percentage of Vx	Accumulated percentage of Vx
1	4.45	0.89	0.89
2	0.42	0.08	0.97
3	0.09	0.02	0.99
4	0.04	0.01	1.00
Loading variables	**PC1**	**PC2**	
B	−0.39	0.89	
C	−0.46	−0.30	
D	−0.46	−0.03	
E	−0.47	−0.11	
G	−0.46	−0.31	

Table 2. Eigenvalues (and proportion of variance, Vx) and loadings for the first four principal components in a principal-components analysis (PCA) based on hindlimb measurements.

1736) the morphology of the distal end of the tarsometatarsus is anatomically similar in form, and the trochlea metatarsi II in dorsal view is not turned medially, being almost parallel and much shorter than the trochlea metatarsi III, forming a narrow notch between them. Thus, for PC2, the key differences among the specimens are related mainly to the morphology of the trochlea metatarsi II and the width of the distal portion of the hindlimb.

Biostratigraphic and palaeogeographic remarks. The FMNH (14353, 14375, 14535) and MACN (8225 Holotype, 6939) specimens of *Procariama simplex* derive from sediments of early middle Pliocene age, or ['araucanense' *sensu* Marshall & Patterson (1981) or 'estratos araucanos' stage *sensu* Rovereto (1914)]. Likewise, FMNH 14525 (two specimens not one, see Marshall & Patterson 1981, table 1:40) was tentatively reported from lower Pliocene sediments (Corral Quemado Formation *sensu* Marshall & Patterson 1981). Later, Alvarenga & Höfling (2003) evaluated all these records ranging between late Miocene to early Pliocene but the accurate stratigraphic position of some was not clear. The precise geographical and stratigraphical context of the materials studied herein, according to recent lithological, stratigraphical and geochronological studies (see Bossi & Muruaga 2009), confirm that the oldest record of *P. simplex* occurs in late Miocene sediments of the Andalhualá Formation (Catamarca Province) and Cerro Azul Formation (La Pampa Province). These lithostratigraphic units are assigned to the Huayquerian land mammal stage of South America (Marshall *et al.* 1979, Marshall & Patterson 1981, Montalvo *et al.* 1996, Cione *et al.* 2000, Goin *et al.* 2000, Cerdeño & Montalvo 2002).

The presence of *Procariama simplex* in the central Pampean region at Salinas Grandes de Hidalgo (La

Pampa, Argentina) also constitutes the southernmost fossil record of this taxon, expanding its geographical range southward by more than 1400 km from northwest to southern central Argentina.

On the other hand, Alvarenga *et al.* (2010) concluded that the specimen (MNHN-1736) from Pleistocene sediments (Dolores Formation, middle–late Pleistocene Antón & Goso 1974) of Uruguay belongs to a large, cursorial phorusrhacid without confident taxonomic placement and may have a close relationship with some among the phorusrhacid subfamily. Based on new analyses and comparisons presented herein, this fossil could be assigned to cf. *Procariama* sp. and would represent the youngest occurrence of this genus.

Thus, it is concluded that *Procariama simplex* was a predatory bird with less flying capacity than *Psilopterus* and seriemas, with good visibility and thinner hindlimbs but sturdier build to provide good cursorial agility and speed for running, prey capture and moving through the extensive open areas that were supposed to dominate central to northwestern Argentinian environments during the late Miocene. If new evidence confirms assignment of the Uruguayan specimen to *Procariama*, the genus would have survived until the Pleistocene with a temporal range of at least 6 million years.

Acknowledgements

References

AGNOLÍN, F., 2009. *Sistemática y filogenia de las aves fororracoideas (Gruiformes, Cariamae)*, Fundación de Historia Natural Félix de Azara, Buenos Aires, 79 pp.

ALVARENGA, H., 1982. Uma gigantesca ave fóssil do Cenozóico brasileiro: *Physornis brasiliensis* sp. n. *Anais da Academia Brasileira de Ciências 54*, 697–712.

ALVARENGA, H., 1985. Um novo Psilopteridae (Aves: Gruiformes) dos sedimentos Terciários de Itaboraí, Rio de Janeiro, Brasil. Proceedings of the Congresso Brasileiro de Paleontologia, 8. Rio de Janeiro, 1983, *NME-DNPM sér. Geol. V, 27*, 17–20.

ALVARENGA, H. & HÖFLING, E., 2003. Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papeis Avulsos de Zoologia. Museu de Zoología da Universidade de São Paulo 43*, 55–91.

ALVARENGA, H., JONES, W. & RINDERKNECHT, A., 2010. The youngest record of Phorusrhacid birds (Aves: Phorusrhacidae) from the late Pleistocene of Uruguay. *Neues Jahrbuch für Geologie und Paläontologie 256,* 229–234.

ALVARENGA, H., CHIAPPE, L. & BERTELLI, S., 2011. Phorusrhacids: The terror birds. In *Living Dinosaurs: The Evolutionary History of Modern Birds,* 1st edition, G. DYKE & G. KAISER, eds, Wiley, Hoboken, NJ, 187–208.

AMEGHINO, F., 1889. Contribuición al conocimiento de los mamíferos fósiles de la República Argentina. *Actas Academia Nacional Ciencias de Cordoba 6*, 1–1028.

AMEGHINO, F., 1899. Sinópsis geológico-paleontológica. Suplemento (adiciones y correcciones). La Plata, 13 pp.

ANTÓN, D. & GOSO, H., 1974. *Estado actual de los conocimientos sobre el Cuaternario en el Uruguay*, Dirección de Suelos y fertilizantes, Montevideo, 12 pp.

BASKIN, J.A., 1995. The giant flightless bird *Titanis walleri* (Aves: Phorusrhacidae) from the Pleistocene coastal plain of south Texas. *Journal of Vertebrate Paleontology 15*, 842–844.

BAUMEL, J. & WITMER, L., 1993. Osteologia. In *Handbook of Avian Anatomy: Nomina Anatomica Avium,* 2nd ed., J.J. BAUMEL, A.S. KING, J.E. BREAZILE, H.E. EVANS & J.C. VANDEN BERGE, eds, Publications of the Nuttall Ornithological Club, Cambridge, 45–132.

BAXTER, M.J., 1995. Standardization and transformation in principal component analysis, with applications to archaeometry. *Applied Statistics 44*, 513–527.

BLANCO, R.E. & JONES, W.W., 2005. Terror bird on the run: a mechanical model to estimate its maximum running speed. *Proceedings of the Royal Society (B) 272*, 1769–1773.

BOSSI, G.E. & MURUAGA, C.M., 2009. Estratigrafía e inversión tectónica del 'rift' neógeno en el Campo del Arenal, Catamarca, NO Argentina. *Andean Gegology 36*, 311–341.

BRODKORB, P., 1963. A giant flightless bird from the Pleistocene of Florida. *Auk 80*, 111–115.

CAMPBELL, K.E. JR & TONNI, E.P., 1980. A new genus of Teratorn from the Huayquerian of Argentina (Aves: Teratornithidae). *Contributions in Science, Natural History Museum of Los Angeles County 330*, 59–68.

CASTELLANOS, A., 1969. Notas de la estratigrafía terciaria del valle de Yocavil en las provincias de Catamarca, Tucumán y Salta (Argentina). *Publicación del Instituto de Fisiografía y Geología Rosario 54*, 1–42.

CERDEÑO, E. & MONTALVO, C., 2002. Los Hegetotheriinae (Hegetotheriidae, Notoungulata) del Mioceno superior de la provincia de La Pampa. *Revista del Museo Argentino de Ciencias Naurales 4*, 35–43.

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.

CIONE, A.L., AZPELICUETA, M., BOND, M., CARLINI, A., CASCIOTTA, J.R., COUZZOL, M.A., DE LA FUENTE, M., GASPARINI, Z., GOIN, F.J., NORIEGA, J.I., SCILLATO YANÉ, G.J., SOIBELZON, L., TONNI, E.P., VERZI, D. & VUCETICH, M.G., 2000. Miocene vertebrates from Entre Ríos province, eastern Argentina. In *El Neógeno de Argentina*, F.G. ACEÑOLAZA & R. HERBST, eds, INSUGEO, Serie Correlación Geológica, Tucumán 14, 191–237.

CORDINI, R., 1967. Reservas y Salinas de Argentina. *Secretaría de Estado de Energía y Minería, Anales 13*, 1–106.

DOLGOPOL DE SAEZ, M., 1927. Las aves corredoras fósiles del Santacrucense. *Anales de la Sociedad Científica Argentina 103*, 145–64.

FLYNN, J.J. & WYSS, A.R., 1998. Recent advances in South American mammalian paleontology. *TREE 3*, 449–454.

FÜRBRINGER, M., 1888. *Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane*. Tj. van Holkema, Amsterdam, Netherlands, 1751 pp.

GOIN, F., MONTALVO, C.I. & VISCONTI, G., 1997. Los Marsupiales de la Formación Cerro Azul (Mioceno Tardío), provincia de La Pampa, Argentina. *Ameghiniana 34R*, 536.

GOIN, F., MONTALVO, C.I. & VISCONTI, G., 2000. Los Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (provincia de La Pampa, Argentina). *Estudios Geológicos 56*, 101–126.

GOULD. G. & QUITMYIER, I., 2005. *Titanis walleri*: bones of contention. *Bulletin of the Florida Museum of Natural History 45*, 201–229.

HARTLAUB, C.J.G., 1860. On a new form of grallatorial bird nearly allied to the Cariama (*Bicholophus cristatus*). *Proceedings of the Zoological Society of London 28*, 334–336.

HOWARD, H., 1980. Illustration of avian osteology taken from 'The avifauna of Emeryville Shellmound'. *Contributions in Science, Natural History Museum of Los Angeles County 330*, 27–38.

LAZA, J.H., 1982. Signos de actividad atribuibles a *Atta* (Myrmicidae, Hymenoptera) en el Mioceno de La Pampa, república Argentina. Significación paleogeográfica. *Ameghiniana 19*, 109–124.

LINARES, E., LLAMBIAS, E. & LATORRE, C., 1980. Geología de la provincia de La Pampa, República Argentina y Geocronología de sus rocas metamórficas y eruptivas. *Asociación Geológica Argentina 35*, 87–146.

LINNAEUS, C., 1766. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I, editio duodecima, reformata*, Laurentii Salvii, Holmiae 532 pp.

MACFADDEN, B., LABS-HOCHSTEIN, J., HULBERT, R. & BASKIN, J., 2006. Refined age of the late Neogene Terror Bird (*Titanis*) from Florida and Texas using rare earth elements. *Journal of Vertebrate Paleontology 26*(Supplement 3), 92A.

MARSHALL, L.G., 1994. The terror birds of South America. *Scientific American 270*, 90–95.

MARSHALL, L.G. & PATTERSON, B., 1981. Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. *Fieldiana. Geology, New Series 9*, 1–78.

MARSHALL, L.G., BUTLER, R.F., DRAKE, R.E., CURTIS, G.H. & TEDFORD, R.H., 1979. Calibration of the Great American Interchange. *Science 204*, 272–279.

MAYR, G. & CLARKE, J., 2003. The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics 19*, 527–553.

MONTALVO, C.I., CARDONATTO, M.C., VISCONTI, G., VERZI, DH. & VUCETICH, M.G., 1996. Vertebrados de la Formación Cerro Azul (Mioceno tardío) del valle de Quehué, provincia de La Pampa, Argentina. *VI Jornadas Pampeanas de Ciencias Naturales, Abstracts 1*, 159–165.

MORENO, F.P. & MERCERAT, A., 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.

NORIEGA, J.I., 1994. *Las aves del 'Mesopotamiense' de la provincia de Entre Ríos, Argentina*. Tesis Doctoral. Facultad de Ciencias Naturales y Museo. Universidad de La Plata, 135 pp. (unpublished).

NORIEGA, J.I., VIZCAINO, S.F. & BARGO, M.S., 2009. First record and new species of seriema (Aves: Ralliformes: Cariamidae) from Santacrucian (early–middle Miocene) beds of Patagonia. *Journal of Vertebrate Paleontology 29*, 620–626.

PASCUAL, R., 1984. La sucesión de las Edades-mamífero, de los climas y del diastrofismo sudamericano durante el Cenozoico: fenómenos concurrentes. *Anales de la Academia Nacional de Ciencias Exáctas, Físicas y Naturales 36*, 15–37.

PASCUAL, R., 1998. The history of South American land mammals: The seminal Cretaceous–Paleocene transition. *Asociación Paleontológica Argentina. Publicación Especial 5*, 9–17.

PASCUAL, R. & BONDESIO, P., 1982. Un roedor Cardiatheriinae (Hidrochoeridae) de la edad Huayqueriense (Mioceno tardío) de La Pampa. Sumario de los ambientes terrestres de la Argentina durante el Mioceno. *Ameghiniana 19*, 19–35.

PASCUAL, R. & ODREMAN RIVAS, O.E., 1971. Evolución de las comunidades de los vertebrados del Terciario Argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados. Mesa Redonda. *Ameghiniana 7*, 372–403.

PASCUAL, R., PISANO, J. & ORTEGA HINOJOSA, E.J., 1965. Un nuevo Octodontidae (Rodentia, Caviomorpha) de la Formación Epecuén (Plioceno medio) de Hidalgo (provincia de La Pampa). Consideraciones sobre los Ctenomyinae Reig, 1958 y la morfología de sus molariformes. *Ameghiniana 4*, 19–30.

PATTERSON, B. & KRAGLIEVICH, L., 1960. Sistemática y nomenclatura de las aves fororracoideas del Plioceno Argentino. *Publicación del Museo Municipal de Ciencias Naturales y Tradicionales de Mar del Plata 1*, 1–52.

REICHENBACH, H.G.L., 1852. *Handbuch der specieleln Ornithologie*, Lieferung 3, Dresden, 434 pp.

REYMENT, R.A., 1991. *Multidimensional Palaeobiology*, Pergamon Press, Oxford, 377 pp.

ROVERETO, C., 1914. Los estratos araucanos y sus fosiles. *Anales del Museo Nacional de Historia Natural, Buenos Aires 25*, 1–249.

SCHALAMUCK, I.B., DEL BLANCO, M., MARCHIONNI, D., ROMERO, S. & CÁBANA, C., 1999. Salinas y sulfateras de la región pampeana, Buenos Aires y La Pampa. In *Recursos Minerales de la República Argentina*, E.O. ZAPPETTINI, ed., Instituto de Geología y Recursos Minerales SEGEMAR, Anales 35, 1947–1962.

SIMPSON, G.G., 1980. *Splendid Isolation: the Curious History of South American Mammals*. New Haven, CT, Yale University Press, 266 pp.

SINCLAIR, W.J. & FARR, M.S., 1932. Aves of the Santa Cruz Beds. In W.B. SCOTT, ed., *Reports of The Princeton University Expeditions to Patagonia (1896–1899)*, 7, W.B. SCOTT, ed., Princeton University Press, Princeton, NJ, 157–191.

TAMBUSSI, C., UBILLA, M. & PEREA, D., 1999. The youngest large carnassial bird (Phorusrhacidae, Phorusrhacinae) from South America (Pliocene–Early Pleistocene of Uruguay). *Journal of Vertebrate Paleontology 19*, 404–406.

TONNI, E.P., 1974. Un nuevo cariamido (Aves, Gruiformes) del Plioceno superior de la provincia de Buenos Aires. *Ameghiniana 11*, 366–372.

TONNI, E.P. & TAMBUSSI, C., 1988. Un nuevo Psilopterinae (Aves: Ralliformes) del Mioceno tardio de la Provincia de Buenos Aires, Republica Argentina. *Ameghiniana 25*, 155–160.

VEZZOSI, R.I., 2006. Primer registro de *Procariama simplex* Rovereto, 1914 (Phorusrhacidae: Psilopterinae) en la Formación Cerro Azul (Mioceno tardío) de la provincia de La Pampa, Argentina. In *Reunión Argentina de Ciencias Naturales y IX Jornadas de Ciencias Naturales del Litoral, Abstracts 1*, 93.

VEZZOSI, R.I., 2007. *Historia natural y análisis morfológico comparado de las especies de cariámidos (Aves: Ralliformes) vivientes y extintos de Argentina: el caso particular de un ejemplar de Salinas Grandes de Hidalgo*. Tesis de Grado, Facultad de Humanidades y Ciencias. Universidad Nacional del Litoral, 91 pp. (unpublished).

WEBB, S.D., 2006. The Great American Biotic Interchange: patterns and processes. *Annals of the Missouri Botanical Garden 93*, 245–257.

ZETTI, J., 1972. *Los mamíferos fósiles de edad huayqueriense (Plioceno medio) de la región pampeana*. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 86 pp. (unpublished).