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## Alcheringa: An Australasian Journal of Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/talc20>

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Available online: 25 Jul 2011

**To cite this article:** Marcos Martín Cenizo, Claudia Patricia Tambussi & Claudia Inés Montalvo (2011): Late Miocene continental birds from the Cerro Azul Formation in the Pampean region (central-southern Argentina), *Alcheringa: An Australasian Journal of Palaeontology*, DOI:10.1080/03115518.2011.582806

**To link to this article:** <http://dx.doi.org/10.1080/03115518.2011.582806>



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# Late Miocene continental birds from the Cerro Azul Formation in the Pampean region (central-southern Argentina)

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CENIZO, M.M., TAMBUSI, C.P. & MONTALVO, C.I., *iFirst Article*. Late Miocene continental birds from the Cerro Azul Formation in the Pampean region (central-southern Argentina). *Alcheringa*, 1–22. ISSN 0311-5518.

The oldest known birds from the Cerro Azul Formation are described, including the oldest records for the genera *Eudromia* and *Nothura* (Tinamidae), *Milvago* (Falconidae), *Pterocnemia* (Rheidae) and an undetermined Tyrannidae. The first remains of Phorusrhacidae for this formation are reported and a specimen previously referred to the giant teratorn *Argentavis magnificens* is reassigned to this family. We outline and update the current knowledge of the groups studied herein. The palaeornithological record from the Cerro Azul Formation is congruent with palaeoenvironmental inferences previously drawn from mammalian assemblages recovered from this unit, which point to the existence of open environments, possibly xerophyllous shrubby steppes, perhaps with some trees. These records are the first indications of a typically Pampean bird fauna at the end of the late Miocene in central-southern Argentina.

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Key words: Rheidae, Tinamidae, Falconidae, Tyrannidae, Phorusrhacidae, Teratornithidae, Huayquerian.

PALAEONTOLOGICAL research on the upper Miocene Cerro Azul Formation (Linares *et al.* 1980), of La Pampa and southwest Buenos Aires provinces (central-southern Argentina; Fig. 1) over the course of 20 years has yielded more than 20 000 remains of continental vertebrates. Most of these are mammals (Goin & Montalvo 1988, Montalvo *et al.* 1996, 2008, Verzi *et al.* 1999, 2003, Goin *et al.* 2000, Cerdeño & Montalvo 2002, Urrutia *et al.* 2008, Verzi & Montalvo 2008), although reptiles have also been reported (Albino *et al.* 2006, Albino & Montalvo 2006). In contrast, until very recently, birds had only been recorded at the locality Salinas Grandes de Hidalgo, classically assigned to the Epecuén 'Formation' and later included in the Cerro Azul Formation (Goin *et al.* 2000). This locality has yielded few but interesting remains; one of the best known of these is the holotype of the giant teratorn *Argentavis magnificens* Campbell & Tonni, 1980. Another, less elegant specimen is a coracoid referred to a tinamid related to *Eudromia* (Tambussi & Tonni 1985a, Tambussi 1987), although this element has never been illustrated or exhaustively described.

This study describes and illustrates birds previously reported from the Cerro Azul Formation, and documents new avian remains that have been located recently in palaeontological collections. The specimens are referred to nine taxa representing at least six families, four of which have living representatives; the remaining two are extinct.

## Geological setting

The specimens studied here were collected from several localities, at which the Cerro Azul Formation (Linares *et al.* 1980; Fig. 1) is partially exposed, in the provinces of La Pampa (Salinas Grandes de Hidalgo, Laguna Guatraché, Quehué, Bajo Giuliani, El Guanaco and Caleufú) and Buenos Aires (Carhué).

The Cerro Azul Formation is characterized by its lithological homogeneity; it mostly consists of silts, sandy silts and very fine silty sands that are pinkish to reddish brown, homogeneous and massive in appearance, and with common carbonate nodules and evidence of pedogenesis (Folguera & Zárate 2009). Within this unit, Goin *et al.* (2000) recognized three sedimentary facies associations, two of which are represented in the localities whose faunal associations include bird remains. These facies consist

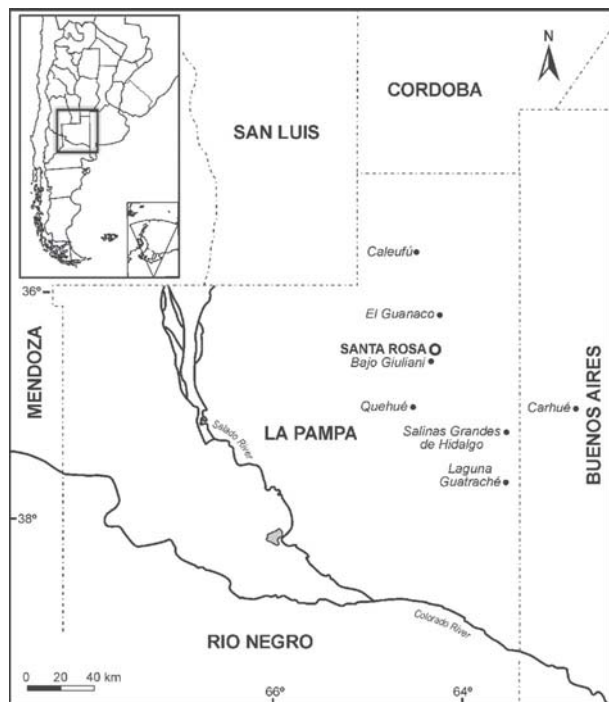


Fig. 1. Geographic location of the Argentine palaeontological sites mentioned in this work.

of lacustrine sediments overlain by aeolian deposits with abundant pedogenic features (Goin *et al.* 2000).

This formation is widely distributed; in its original definition, it only represented deposits exposed within La Pampa province. Recently, based on lithological similarities and lateral tracing of strata, Folguera & Zárate (2009) redefined it to also include deposits exposed in the west and southwest of Buenos Aires province, including the Epecuén 'Formation' (Pascual 1961), in agreement with a proposal by Goin *et al.* (2000). In addition, these authors pointed out that the deposits of the Cerro Azul Formation comprise a sedimentary blanket extending over various morphostructural units (Macachín Basin, Colorado Basin, Bonaerian Positive and Chadileuvú Block), a fact that would explain the temporal differences evident between some faunal associations (Verzi *et al.* 2008).

The localities Salinas Grandes de Hidalgo and Laguna Guatraché are within the Macachín Basin. The first has been studied extensively (e.g. Pascual *et al.* 1965, Campbell & Tonni 1980, Verzi *et al.* 1994, Goin *et al.* 2000, Cerdeño & Montalvo 2001, Urrutia *et al.* 2008) and assigned to the Huayquerian land mammal age (late Miocene). The second has been assigned the same age, but its associations have been less studied (Cerdeño & Montalvo 2001). The remaining localities analyzed here are located in the eastern sector of the Chadileuvú Block. The latter,

slightly inclined eastwards, is dissected by the Transversal Valleys of La Pampa, on whose margins and floor the Cerro Azul Formation is exposed. Classically, the faunal associations recovered from the latter exposures have been assigned to the Huayquerian faunal stage (Verzi *et al.* 2008, Verzi & Montalvo 2008, and literature cited therein).

## Materials and methods

Osteological terminology follows Baumel & Witmer (1993). Some references to ligament insertions in Tinamidae used by Bertelli (2002) and Bertelli & Chiappe (2005) have been modified following Baumel & Witmer (1993).

The systematic criteria for the Tinamidae follow the proposals of Bertelli (2002) and Bertelli & Chiappe (2005); the descriptions include the characters used by these authors and additional ones derived from our own observations; the latter are denoted by an asterisk in the corresponding section. We include Phorusrhacidae and Cariamidae within the Cariamiformes (instead of Gruiformes) according to Remsen *et al.* (2010, SACC of AOU, proposal 290) and literature cited therein. Within the Phorusrhacidae, we follow the taxonomical proposal of Alvarenga & Höfling (2003); however, the taxa recognized as subfamilies by those authors are used here as morphological types. Additionally, the exclusion of *Brontornis burmeisteri* Moreno & Mercerat, 1891 from Phorusrhacidae (Agnolin 2007) is not followed in this work. The Falconidae are described according to the systematic scheme of Griffiths *et al.* (2004).

*Institutional abbreviations.* (AMNH) American Museum of Natural History, New York, USA; (DGM) Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil; (FMNH) Field Museum of History Natural, Chicago, USA; (GHUNLPam) Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina; (MACN) Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; (MLP) Museo de La Plata, La Plata, Argentina; (MMCN) Museo Municipal de Ciencias Naturales y Tradicional, Mar del Plata, Argentina; (MNHN) Museo Nacional de Historia Natural, Montevideo, Uruguay; (MPM-PV) Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina; (NHM) Natural History Museum, London, Great Britain; (YPM-PU) Yale Peabody Museum, Princeton University Collection, New Haven, USA.

*Metric descriptors and measurements.* D–dist, depth of distal end; D–prox, depth of proximal end;

D–TIII, depth of trochlea metatarsi III; L–c, length of sulcus articularis coracoideus; L–TIII length of trochlea metatarsi III; TL, total length; W–dist, width of distal end; W–fa, width of facies articularis sternalis; W–prox, width of proximal end; W–shaft, width of shaft; W–sp, transverse width of spina interna; W–TIII, width of trochlea metatarsi III. Measurements (in mm) were taken with a digital vernier caliper to the nearest 0.01 mm and are expressed (e.g. in Table 1) as follows: max–min, mean (N).

*Comparative material.* Comparisons were undertaken with specimens of the following extant species, which are deposited in MLP and MACN: *Pterocnemia pennata*, *Rhea americana*, *Crypturellus parvirostris*, *C. tataupa*, *C. undulatus*, *Eudromia elegans*, *E. formosa*, *Nothoprocta cinerascens*, *N. ornata*, *N. pentlandii*, *Nothura boraquira*, *N. darwini*, *N. maculosa*, *Rhynchotus rufescens*, *Tinamotis ingoufi*, *T. pentlandii*, *Tinamus solitarius*, *Milvago chimango*, *M. chimachima*, *Polyborus plancus*, *Falco femoralis*, *F. peregrinus*, *F. sparverius*, *F. fusco-caerulescens*, *F. columbarius*, *F. tinunculus*, *Herpetotheres cachinnans*, *Spizopteryx circumcinctus*, *Elanoides forficatus*, *Polihierax semitorquatus*, *Buteo jamaicensis*, *B. magnirostris*, *B. erythro-notus*, *B. buteo*, *B. polyosoma*, *Accipiter striatus*, *A. nisus*, *A. cooperii*, *Rostrhamus sociabilis*, *Geranoaetus melanoleucus*, *Buteogallus urubitinga*, *Ictinia plumbea*, *Circus cinereus*, *C. buffoni*, *Elanus leucurus*, *Heterospizias meridionalis*, *Busarellus nigricollis*, *Harpyhaliaetus coronatus*, *Haliaeetus leucocephalus*, *Harpia harpyja*, *Gypaetus barbatus*, *Neophron percnopterus*, *Pandion haliaetus*, *Cathartes aura*, *Coragyps atratus*, *Vultur gryphus*, *Sarcorhamphus papa*, *Chunga burmeisteri*, *Cariama cristata*, *Colaptes campestris*, *C. melanolaimus*, *Drymornis bridgesii*, *Upucerthia certhioides*, *Cinclodes fuscus*, *Furnarius rufus*, *Pseudoseisura lophotes*, *P. gutturalis*, *Phytotoma rutila*, *Pitangus sulphuratus*, *Tyrannus savana*, *Progne modesta*, *Cyanocorax chrysops*, *Troglodytes aedon*, *Mimus saturninus*, *Turdus rufiventris*, *Polioptila dumicola*. The following fossil specimens were used for comparison: Tinamidae indet. (Bertelli & Chiappe 2005; MACN SC–3610, 3613, 3609, 3611, 3612, 1449, 360, 1399, 1440), *Eudromia olsoni* (MACN 16597), *Eudromia* sp. (MLP 52-X-5-33, 63-VII-30-1), *Nothura parvula* (MACN 16596), *Hinasuri nehuensis* (MLP 86-VI-20-1), *Psilopterus colzecus* (MLP 76-VI-12-2), ‘*Devincenzia pozzii*’ (MACN 6681, 17749, 13243), *Brontornis burmeisteri* (MLP 20-88, 566-II), *Phorusrhacos longissimus* (MLP 22-130, = *Mesembriornis studeri*; 22-137, = *Mesembriornis quatrefagesi*; 20-572), ‘*Patagornis marshi*’ (MLP 20-85, 20-154, 84-III-9-2), ‘*Hermosior-*

*nis*’ *milneedwardsi* (MACN 5944, MLP 84-III-9-2, 20-154; MLP 20-141), ‘*Hermosiornis*’ *incertus* (MACN 6934), *Procarium simplex* (MACN 8225, 6939); ‘*Psilopterus australis*’ (MLP 20-162); ‘*Psilopterus delicatus*’ (MLP 20-167), ‘*Andalgalornis steulleti*’ (MLP 88-IX-20-16), *Chunga incerta* (MLP 71-VII-5-1, 71-VII-5-2, 71-VII-5-4), *Paleopsilopterus itaboraiensis* (MACN 19163, cast), *Phorusrhacidae* indet. (MACN 18602).

## Systematic palaeontology

Class AVES Linnaeus, 1758

Order STRUTHIONIFORMES Latham, 1790

Family RHEIDAE Bonaparte, 1849

**Pterocnemia** Gray, 1871

**Pterocnemia** sp. (Fig. 2A–H)

*Referred material and geographical provenance.* GHUNLPam 6231, trochlea metatarsi III of left tarsometatarsus (Salinas Grandes de Hidalgo); GHUNLPam 6232, pedal phalanx I of left digit 2 with proximal end missing (Salinas Grandes de Hidalgo; Fig. 1).

*Measurements.* GHUNLPam 6231, W–TIII: 19.43 (*Pterocnemia pennata*: 18.58–16.06, 17.63 [16]; *Rhea americana*: 20.14–19.60, 19.87 [5]); D–TIII: 18.10 (*P. pennata*: 22.70–17.97, 21.22 [16]; *R. americana*: 23.71–22.63, 23.17 [5]); L–TIII: 30.13 (*P. pennata*: 28.57–24.04, 26.68 [16]; *R. americana*: 33.89–31.65, 32.77 [5]). GHUNLPam 6232; W–dist: 13.15; D–dist: 11.21.

*Description and comparisons.* GHUNLPam 6231 (Fig. 2A–D) differs from *Rhea* and can be referred to *Pterocnemia* by the following combination of characters (Tambussi & Tonni 1985b): (1) lesser relative length; (2) trochlear ridges convergent proximally and dorsally delimiting the fossa defined by the proximal portion of the mesial longitudinal groove; (3) in distal view, the medial trochlear ridge is less projected dorsally; (4) in plantar view, the basis trochlearis is wider and shorter; (5) in plantar view, the lateral trochlear ridge emerges more proximally than its medial counterpart.

Some of the dimensions of GHUNLPam 6231 are greater than those observed in modern specimens of *P. pennata* (see Measurements). Apart from this, the phalanx GHUNLPam 6232 (Fig. 2E–H) differs from those of *Rhea* and is similar to those of *Pterocnemia* by the following characteristics: (1) in dorsal view, the

	Sternum		Coracoideum		Humerus		Carpometacarpus		Femur		Tibiotarsus		Tarsometatarsus	
	L-c	W-sp	TL	W-fa	W-dist	D-dist	W-prox	D-prox	W-dist	D-dist	W-prox	D-prox	W-dist	D-dist
<i>Eudromia elegans</i>	10.07-9.38	6.53-4.68	38.71-35.45	10.27-8.78	14.28-12.28	8.22-7.07	11.06-10.40	7.04-6.20	13.75-11.49	11.25-9.71	9.39-7.82	10.10-8.29	11.68-10.17	7.42-6.03
	9.87(7)	5.83(5)	37.56(8)	9.63(8)	12.95(9)	7.63(8)	10.66(7)	6.60(8)	12.59(9)	10.36(8)	8.65(9)	8.84(10)	10.83(10)	6.69(10)
<i>Eudromia formosa</i>			39.74	9.87	13.42-13.07	7.92-7.85	11.87		13.05					
					13.24(2)	7.88(2)								
<i>Eudromia obscur*</i> Holotype MACN 16597					12.94		11.35	6.10	13.70	10.55				
cf. <i>Eudromia</i> sp.* GHUNLPam 21566/22														
<i>Eudromia</i> sp.* MLP 87-XI-20-3														
<i>Rhynchotus rufescens</i>	10.64-7.57	7.38-4.50	40.83-33.84	10.87-7.65	14.06-10.23	8.55-6.40	12.89-8.30	7.63-5.05	12.94-10.47	11.50-9.77	9.96-7.85	10.28-8.07	12.46-9.77	8.00-6.55
	9.15(6)	5.55(6)	38.38(6)	9.31(6)	12.48(9)	7.55(9)	10.85(8)	6.42(8)	12.23(9)	10.60(9)	9.03(14)	9.33(13)	11.24(13)	7.36(13)
	11.9-10.53	8.57-8.37	37.58-36.27	11.72-10.46	12.64-12.29	7.33-7.32	10.53-10.45	7.01-6.33	13.28-12.46	10.42-10.33	8.95-8.59	8.93	12.05	7.65
	11.21	8.47	36.80	11.22	12.48	7.32	10.49	6.67	12.75	10.37	8.77			
<i>Tinaamatis inguifi</i>			41.73	10.74	13.67		13.2		13.37		11.09	10.27	14.12	9.24
			52.06	13.48	16.96		15.10		14.26		11.52		13.69	
<i>Tinaamatis pentlandi</i>			35.08	9.38	11.50	6.58	10.16	5.87	9.83	8.28	6.90	7.59	8.69	5.92
<i>Tinaamatis solitaria</i>	8.33	3.68												
<i>Crypturellus undulatus</i>	6.22	2.62	23.30-22.93	6.75-6.32	8.05-7.04	4.83-4.60	6.36	3.23	6.90-6.82	5.50-5.10	5.15-4.66	5.33-4.51	6.30-5.88	4.02-3.79
<i>Crypturellus tatapua</i>			23.11(2)	6.53(2)	7.38(3)	4.68(3)			6.86(2)	5.30(2)	4.90(2)	4.92(2)	6.09(2)	3.90(2)
<i>Crypturellus parvisirostris</i>	6.18	3.49	24.43	6.77	7.68	4.63	6.62	3.57	7.29	5.82	5.05	4.43	6.05	4.31
<i>Notioprocta cinerascens</i>	9.25-7.59	4.76-2.85	34.62-30.09	9.13-8.10	11.43-9.84	7.04-5.81	10.03-8.52	6.08-5.22	10.89-9.34	9.05-7.59	7.93-6.48	8.45-6.90	10.29-8.50	8.89-5.37
	8.36(13)	3.84(13)	32.27(16)	8.37(17)	10.57(18)	6.44(17)	9.16(16)	5.89(12)	10.16(18)	8.29(14)	7.14(18)	7.47(14)	9.01(16)	6.01(16)
	8.00-7.38	6.99-6.49	32.71-32.20	7.73-7.72	11.57-11.06	6.35-6.20	8.83-8.66	5.83-5.60	11.51-10.08	9.48-8.94	7.48-7.12	7.75-7.18	8.35-8.02	6.74-6.11
	7.69(2)	6.72(2)	32.45(2)	7.72(2)	11.31(2)	6.27(2)	8.74(2)	5.71(2)	10.84(3)	9.17(3)	7.32(3)	7.49(3)	8.24(3)	6.35(3)
<i>Notioprocta penilamdi</i>	7.19-4.91	6.17-4.08	26.03-25.42	6.88-5.50	8.94-8.54	5.13-4.64	7.26-6.71	4.60-4.12	8.75-8.08	7.04-6.62	6.00-5.46	6.15-5.72	6.65-6.26	5.24-4.67
	6.27(5)	4.97(5)	25.01(5)	6.15(5)	8.79(5)	4.90(5)	7.07(4)	4.34(4)	8.39(5)	6.77(5)	5.77(5)	6.19(5)	6.39(5)	4.94(5)
	6.64	2.22	28.10	6.56	8.92	5.31	8.32		8.32	7.14				
<i>Nothura borinquira</i>	7.00-5.27	4.76-3.54	26.85-23.32	7.34-5.41	8.67-7.38	5.22-4.66	7.74-6.69	4.40-3.83	8.61-7.32	6.75-5.91	6.50-5.15	6.53-5.21	7.76-6.45	5.16-4.05
<i>Nothura darwini</i>	6.19(10)	4.05(10)	24.62(10)	6.25(10)	7.78(10)	4.79(10)	7.03(9)	4.17(9)	7.71(10)	6.15(10)	5.41(10)	5.69(10)	6.99(10)	4.53(10)
	7.07-5.22	4.62-2.81	27.61-22.63	7.84-5.40	8.80-6.98	5.19-4.44	8.40-6.50	4.35-3.53	8.74-7.47	7.09-5.57	6.32-4.88	6.33-5.28	7.90-6.30	5.32-4.06
<i>Nothura maculosa</i>	5.95(18)	3.65(17)	25.08(22)	6.23(22)	7.80(16)	4.73(16)	6.77(13)	4.00(13)	7.95(20)	6.37(19)	5.67(19)	5.76(17)	7.24(16)	4.65(16)
			24.42	6.85	8.61	5.40	7.18	4.64	8.75**				7.92	5.40
<i>Nothura parvula*</i> Holotype MACN 16596					7.55	4.81					5.29	5.39		
<i>Nothura</i> sp.* GHUNLPam 27042													5.54	
<i>Nothura</i> sp.* GHUNLPam 14861/1														3.80**
<i>Nothura</i> sp.* GHUNLPam 5901/1														
<i>Nothura</i> sp.* GHUNLPam 5901/2														
<i>Nothura</i> sp.* GHUNLPam 8070/1														
cf. <i>Nothura</i> sp.* GHUNLPam 6233														
Tinaamidae indet.* MACN-PV SC-36009	5.81	3.80	27.59	6.54					7.99	6.12				
Tinaamidae indet.* MACN-PV SC-1399														
Tinaamidae indet.* MACN-PV SC-1440					9.30	6.30					6.77	6.47		
Tinaamidae indet.* MACN-PV SC-360					9.51	6.94					6.20	7.08		
Tinaamidae indet.* MACN-PV SC-1449														

Table 1. Measurements for the Tinaamidae from the Cerro Azul Formation compared with living and fossil representatives of the family. \*Fossil specimens; \*\*measurements estimated for incomplete specimens.

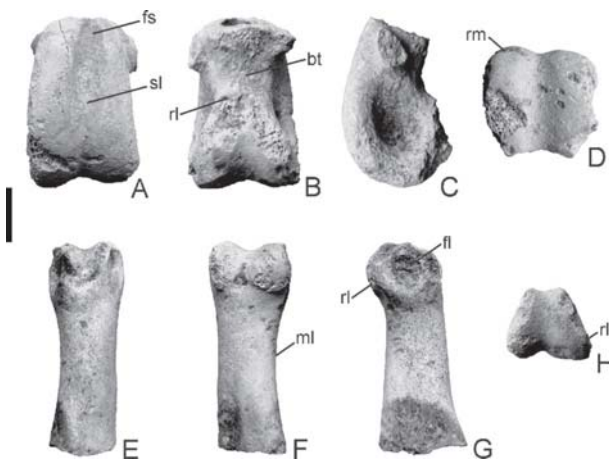


Fig. 2. Fossil Rheidae from the Cerro Azul Formation. A–D, *Pterocnemia* sp., left trochlea metatarsi III (GHUNLPam 6231) in dorsal (A), plantar (B), lateral (C) and distal view (D). E–H, *Pterocnemia* sp., left tarsal phalanx I of digit 2 (GHUNLPam 6232) in dorsal (E), plantar (F), medial (G) and distal view (H). Abbreviations: bt, basis trochlearis; fl, fossa ligamentaria lateralis; fs, fossa; ml, margo lateralis; sl, longitudinal sulcus mesialis; rl, lateral trochlear ridge; rm, medial trochlear ridge. Scale bar = 10 mm.

latero-plantar ridge of the articular facet projects more laterally; (2) in lateral view, the lateral ring of the articular facet is larger and projects somewhat more caudally; (3) its wider fossa ligamentaria lateralis; (4) in caudal view, the margo lateralis is strongly curved.

**Comments.** The lesser rhea, *P. pennata*, is one of the two living allopatric species of Rheidae, a family of flightless cursorial palaeognathous birds endemic to South America. The fossil record of the family extends back to the Paleocene. Pedal phalanges from the middle Paleocene of Las Flores locality, Río Chico Formation (Chubut Province), represent their earliest record (Tambussi 1995). Much better represented is *Diogenornis fragilis* Alvarenga, 1983 from the late Paleocene of Itaboraí, Brazil, a species smaller and more slender than the living representatives and indeed more so than all the extinct species assigned to this family, including GHUNLPam 6231 described in this paper (see Measurements).

According to measurements reported by Ameghino (1895), the extinct species *Opisthodactylus patagonicus* Ameghino, 1895 (early–middle Miocene of Patagonia) was similar in size to the living *P. pennata*. The material GHUNLPam 6231 from the Cerro Azul Formation can not be assigned to *O. patagonicus* because its trochlea metatarsi III is more slender and elongated.

Additionally, two extinct taxa have been recorded from the early Pliocene Monte Hermoso Formation

(southwestern Buenos Aires Province): *Heterorhea dabbenei* Rovereto, 1914 and *Hinasuri nehuensis* Tambussi, 1995. The first is slightly larger than the Greater Rhea, *Rhea americana*, but is otherwise difficult to differentiate from the latter. Because the holotype of the species is missing (Tambussi 1989), its taxonomic status can not be reassessed. Judging from the description, measurements and figures provided by Rovereto (1914), the trochlea metatarsi of GHUNLPam 6231 is wider and shorter; thus, the specimen could not be assigned to *H. dabbenei*. The second taxon, *H. nehuensis*, was erected on the basis of a fragmentary femur, thus precluding direct comparison with the material from the Cerro Azul Formation. However, Tambussi (1995) suggested that *H. nehuensis* corresponds to a much more robust morphotype than any other known Rheidae. Finally, it is worth noting that Noriega & Agnolin (2008) reported the presence of *Pterocnemia* sp. in the basal section of the Ituzaingó Formation ('Ossiferous Conglomerate' or 'Mesopotamian' of Entre Ríos province, Argentina), a unit also assigned to the Huayquerian (see Cione *et al.* 2000).

Order TINAMIFORMES (Huxley, 1872)  
Family TINAMIDAE Gray, 1840

**Eudromia** Geoffroy Saint-Hilaire, 1832

**Eudromia** sp. (Fig. 3A–D)

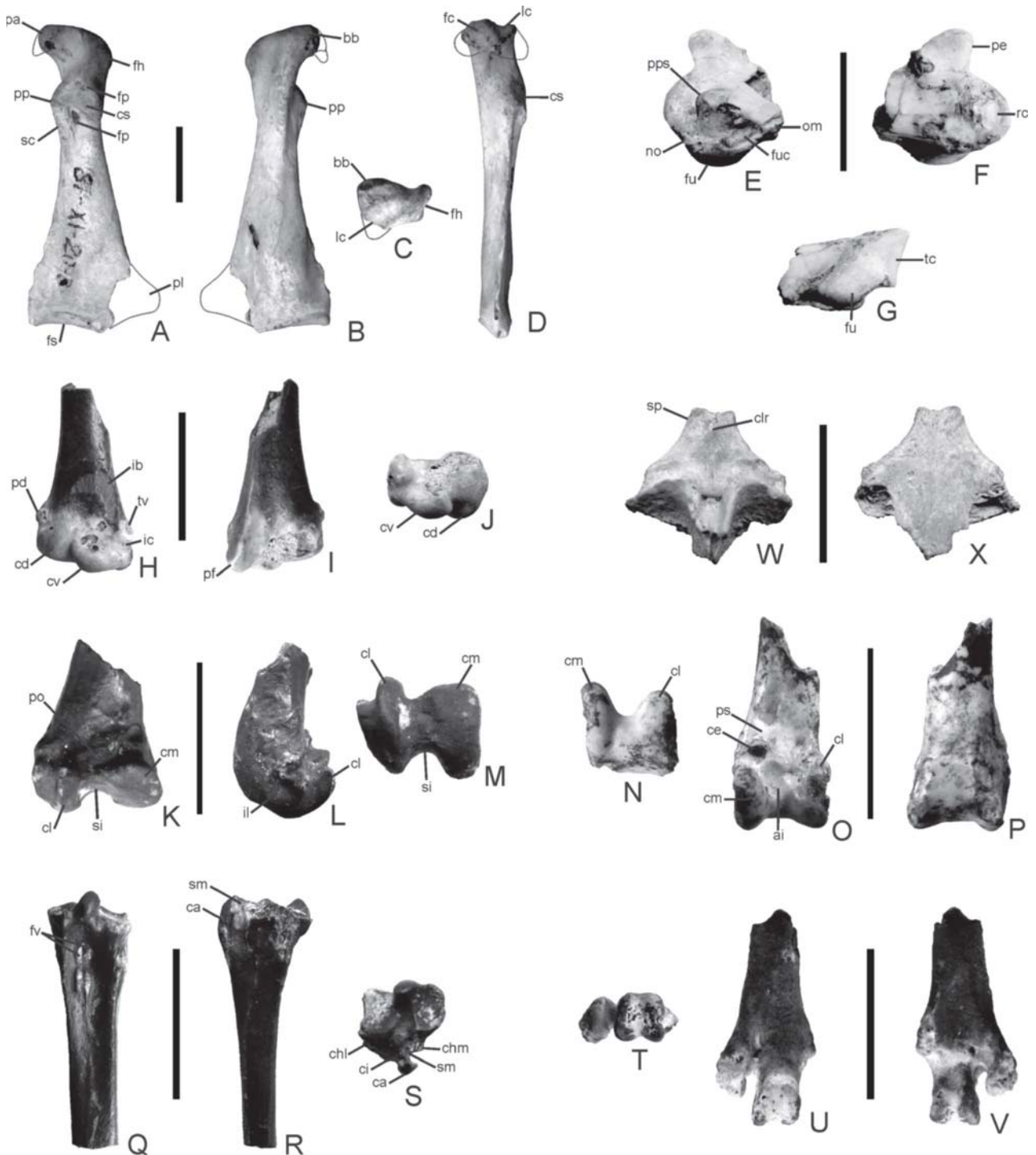
**Referred material and geographic provenance.** MLP 87-XI-20-3, right coracoid with missing processus lateralis and partially eroded facies articularis clavicularis (Salinas Grandes de Hidalgo, Fig. 1).

**Measurements.** See Table 1.

**Description and comparisons.** The following characters allow the assignation of MLP 87-XI-20-3 to *Eudromia* (Bertelli 2002, Bertelli & Chiappe 2005): (1) the foramen pneumaticum is well developed on the dorsal surface of the coracoid, adjacent to the processus procoracoideus and proximal to the cotyla scapularis (reduced in *Taoniscus* and *Nothura*; a synapomorphy for Tinamidae, see also Parker 1866, Ericson 1997); (2) even though the facies articularis clavicularis is partially fragmented at its dorsal and ventral ends, in medial view it appears to have been crescentic, with a well-developed tuberculum brachiale (circular to oval and with reduced tuberculum brachiale in *Nothocercus*, *Taoniscus*, *Nothura*, *Nothoprocta*, *Rhynchotus* and *Tinamotis*); (3) the impressio ligamenti acrocoracohumeralis converges distally with the facies

articularis clavicularis (being separated and contacting the dorsal margin of the sulcus m. supracoracoidei in *Nothocercus*, *Taoniscus*, *Nothura*, *Nothoprocta* and *Rhynchotus*); (4) the processus acrocoracoideus is at the same level or slightly more distally projected than the facies articularis humeralis (there is a conspicuous distal projection in *Tinamus*, *Nothocercus*, *Taoniscus*,

*Nothura*, *Nothoprocta* and *Rhynchotus*); (5) the impressio musculi biceps brachii forms a distinctive scar on the dorsal surface of the processus acrocoracoideus (which is absent in *Tinamus*, *Nothocercus* and *Crypturellus*); (6) the wide processus acrocoracoideus (it is narrow in *Tinamus*, *Crypturellus*, *Taoniscus*, *Nothura*, *Nothoprocta* and *Rhynchotus*);



(7) the foramen pneumaticum is positioned on the distal margin of the cotyla scapularis (it is absent in *Tinamus*, *Nothocercus*, *Taoniscus*, *Nothura*, some *Nothoprocta* and *Tinamotis pentlandi*); (8) the long, narrow, medial ridge projecting proximally from the base of the processus procoracoideus (vs not projecting in *Tinamus*, *Nothocercus*; short and thin in *Crypturellus*); (9) although the processus lateralis is fragmented laterally, the projection of its margins allows inference with certainty that it was prominent, as long as or longer than the facies articularis sternalis (vs poorly developed in *Nothocercus*, and well developed but shorter than the facies articularis sternalis in *Tinamus*, *Taoniscus* and *Crypturellus undulatus* and *Crypturellus noctivagus*); (10) the absence of the foramina pneumatica on the dorsal surface at the level of impressio m. sternocoracoidei (present in *Nothoprocta*, *Nothura* and some specimens of *Rhynchotus*).

On the other hand, characters (3), (4), (6) and (8) allow the Cerro Azul Formation specimens to be distinguished from the morphotypes assigned to Tinamidae indet. exhumed from the Santa Cruz Formation (Bertelli & Chiappe 2005). In addition, the size of the preserved specimens is smaller than that of the representatives of *Tinamus* and greater than that of the species of *Taoniscus*, *Nothoprocta*, *Nothura*, *Crypturellus* and the specimens from the Miocene of Santa Cruz; their size falls within the range observed for the genera *Eudromia*, *Rhynchotus* and *Tinamotis* (Table 1).

**Comments.** The fossil species *Eudromia olsoni* Tambussi & Tonni, 1985a was described from the early Pliocene of southwestern Buenos Aires province (Monte Hermoso Formation, although originally referred to *Tinamisornis* Rovereto, 1914, see Tonni 1977, Tambussi 1987). Unfortunately, neither the holotype nor the paratypes of this species include

coracoids, precluding a direct comparison. Nevertheless, all preserved elements of *E. olsoni* have proportions similar to those of extant *Eudromia* species (Tonni 1977; see also Table 1) and to the material described here. Tonni (1977) assigned two coracoids to *Eudromia* sp. cf. *E. olsoni*: MLP 52-X-5-33 (Chapadmalal Formation, middle Pliocene, Miramar) and MLP 63-VII-30-1 ('Irenense', early Pliocene, Quequén Salado River, in part referred to the late Miocene, see Verzi *et al.* 2008). The specimen MLP 63-VII-30-1 was later ascribed to *Eudromia* sp. (Tonni 1980, Tambussi 1989), although Tambussi (1987) directly assigned it to *E. olsoni* without giving reasons for this decision; the same assignment was adopted by Tambussi & Noriega (1996). According to a preliminary analysis of MLP 52-X-5-33 and MLP 63-VII-30-1, we consider it appropriate to refer these materials to *Eudromia* sp., since the lack of coracoids in the type materials of *E. olsoni* makes the link between these taxa merely conjectural.

cf. **Eudromia** sp. (Fig. 3E–G)

*Referred material and geographic provenance.* GHUNLPam 21566/22, proximal end of left carpo-metacarpus (Caleufú, Fig. 1).

*Measurements.* See Table 1.

*Description and comparisons.* The material GHUNLPam 21566/22 shares the following characteristics with *Eudromia* (Bertelli 2002, Bertelli & Chiappe 2005): (1) on its ventral surface, there is a deep well-defined fossa for the ligamentum ulnocarpometacarpale ventralis between the processus pisiformis and the os metacarpale minor (barely insinuated and shallower in *Nothocercus*; a possible autapomorphy for the Tinamidae, Bertelli 2002); (2) the outline of the ventral ring of the trochlea carpalis is interrupted

*Fig. 3.* Fossil Tinamidae from the Cerro Azul Formation. **A–D**, *Eudromia* sp., right coracoideum (MLP 87-XI-20-3) in dorsal (**A**), ventral (**B**), proximal (**C**) and medial view (**D**). **E–G**, cf. *Eudromia* sp., proximal end of left carpo-metacarpus (GHUNLPam 21566/22) in ventral (**E**), dorsal (**F**) and caudal view (**G**). **H–J**, *Nothura* sp., distal end of right humerus (GHUNLPam 27042) in cranial (**H**), caudal (**I**) and distal view (**J**). **K–M**, *Nothura* sp., distal end of left femur (GHUNLPam 8070/1) in caudal (**K**), lateral (**L**) and distal view (**M**). **N–P**, *Nothura* sp., distal end of left tibiotarsus (GHUNLPam 14861/1) in distal (**N**), cranial (**O**) and caudal view (**P**). **Q–S**, *Nothura* sp., proximal end of left tarsometatarsus (GHUNLPam 5901/1) in dorsal (**Q**), lateral (**R**) and proximal view (**S**). **T–V**, *Nothura* sp., distal end of right tarsometatarsus (GHUNLPam 5901/2) in distal (**T**), dorsal (**U**) and plantar view (**V**). **W–X**, cf. *Nothura* sp., cranial fragment of sternum (GHUNLPam 6233) in ventral (**W**) and dorsal view (**X**). *Abbreviations:* ai, area intercondylaris; bb, impressio m. biceps brachii; ca, crista hypotarsi intermedia major; cd, condylus dorsalis; ce, canalis extensorius; chl, crista hypotarsi lateralis; chm, crista hypotarsi medialis; ci, crista hypotarsi intermedia minor; cl, condylus lateralis; clr, central longitudinal ridge; cm, condylus medialis; cs, cotyla scapularis; cv, condylus ventralis; fc, facies articularis clavicularis; fh, facies articularis humeralis; fp, foramen pneumaticum; fs, facies articularis sternalis; fu, facies articularis ulnocarpalis; fuc, fossa lig. ulnocarpometacarpale ventralis; fv, foramina vascularia proximalia; ib, impressio m. brachialis; ic, impressio lig. articulare craniale; il, impressio lig. collateralis lateralis; lc, impressio lig. acrocoracohumeralis; no, notch; om, os metacarpale minor; pa, processus acrocoracoideus; pd, processus supracondylaris dorsalis; pe, processus extensorius; pf, processus flexorius; pl, processus lateralis; po, fossa poplitea; pp, processus procoracoideus; pps, processus pisiformis; ps, pons supratendineus; rc, impressio lig. radiocarpometacarpale dorsalis; sc, impressio lig. sternoprocoracoideum; si, sulcus intercondylaris; sm, sulcus hypotarsi medialis; sp, spina interna; tc, trochlea carpalis; tv, tuberculum supracondylaris ventralis. Scale bars = 10 mm.



by a notch dividing it into caudal and proximal halves (it is continuous from the facies articularis ulnocarpalis to processus extensorius in *Nothura*, *Nothoprocta cinerascens*, *Nothoprocta taczanowskii*, *Nothoprocta pentlandii*, *Rhynchotus* and *Tinamotis ingoufi*); (3) absence of the foramen pneumaticum in the area of insertion of the ligamentum radiocarpometacarpale ventrale (it is present in *Crypturellus*, *Nothura*, *Taoniscus* and *Nothoprocta*); (4\*) in ventral view, the facies articularis ulnocarpalis is robust with a broadly elliptical outline in caudal aspect (being more slender in *Rhynchotus* and *Tinamotis*). The dimensions of the material are smaller than that of *Tinamus*, greater than *Crypturellus*, *Taoniscus*, *Nothoprocta* and *Nothura*, and only broadly similar to those of *Eudromia*, *Rhynchotus* and *Tinamotis* (Table 1).

*Comments.* The material from the Cerro Azul Formation can be assigned to the subfamily Nothurinae and referred with some certainty to the clade formed by *Rhynchotus* + *Eudromia* + *Tinamotis* (Bertelli 2002, Bertelli *et al.* 2002, Bertelli & Chiappe 2005). Although the fossil has a mosaic of characters previously observed in various species of this clade (Tambussi 1989), it shows greatest affinity with members of *Eudromia*. Nevertheless, some features, perhaps autapomorphic, differ from the condition in established *Eudromia* species (e.g. more caudal position of, and larger and deeper area for the insertion of, the ligamentum radiocarpometacarpale dorsalis). There are no records of the carpometacarpus in the known fossil specimens with the exception of *Nothura parvula* (Rovereto, 1914; see above), from which it differs by its much larger size, and by characters (2) and (3) mentioned above.

**Nothura** Wagler, 1827

**Nothura** sp. (Fig. 3H–V)

*Referred material and geographical provenance.* GHUNLPam 27042, distal portion of right humerus (Quehué, Fig. 1); GHUNLPam 8070/1, distal portion of left femur (Bajo Giuliani); GHUNLPam 14861/1, distal portion of left tibiotarsus (El Guanaco); GHUNLPam 5901/1, proximal portion of left tarsometatarsus (Quehué); GHUNLPam 5901/2, distal portion of right tarsometatarsus (Quehué).

*Measurements.* See Table 1.

*Description and comparisons.* All the materials fall within the range of variation observed for *Nothura*

and *Crypturellus* species; they are larger than specimens of *Taoniscus* and smaller than those of the remaining tinamids (Table 1). Likewise, the referred materials can be assigned to *Nothura* on the basis of the characters outlined below (Bertelli 2002, Bertelli & Chiappe 2005).

*Humerus* GHUNLPam 27042 (Fig. 3H–J): (1) the major axis of the condylus ventralis is larger than that of the condylus dorsalis (condyli similar in *Tinamotis*); (2) the impressio musculi brachialis is shallow (vs deep in *Taoniscus*); (3) the impressio musculi brachialis is markedly crescentic (vs oblique with respect to the diaphysial axis and oval in *Tinamus*, *Eudromia*, *Tinamotis*, *Rhynchotus* and most species of *Nothocercus*); (4) the impressio musculi brachialis is narrow, with ventral and proximal margins forming a marked angle to each other (only shared with *Nothoprocta pentlandii*); (5) the processus flexorius is not extended beyond the condylus ventralis (compared with well elongated distally in *Nothocercus*, *Taoniscus*, *Nothoprocta* and *Rhynchotus*); (6) the tuberculum supracondylare ventrale (impressio musculi pronator superficialis) located on the cranioventral margin (but further toward the cranial surface in *Tinamotis* and *Eudromia*); (7) the processus supracondylaris dorsalis (impressio musculi extensor metacarpi radialis) is developed as a rounded compact tuberosity (scarcely developed in *Taoniscus*, *Eudromia*, *Tinamotis* and *Nothocercus bonapartei*; with a second small tuberosity on the proximal margin in *Tinamus* and some species of *Crypturellus*); (8) there are two fossae distales on the ventral side, below the processus supracondylaris dorsalis (vs three fossae in *Tinamus*, *Nothocercus* and *Crypturellus*); (9) the condylus ventralis is well defined proximally (less defined in *Tinamus*, *Nothocercus*, *Crypturellus* and *Taoniscus*); (10) the impressio ligamenti articulare craniale is moderately deep, forming a distinct circular depression (vs very shallow to absent in *Tinamus*, *Nothocercus* and *Crypturellus*). Characters (3), (7) and (10) allow differentiation of this material from the fossil morphotypes described by Bertelli & Chiappe (2005).

*Femur* GHUNLPam 8070/1 (Fig. 3K–M): (1) in medial view, the caudal articular surface of the condylus medialis is extended more proximally than its cranial counterpart (extending to the same level in *Tinamus*, *Nothoprocta ornata*, *Nothoprocta perdicaria*, *Eudromia* and *Tinamotis*); (2) in cranial view, the sulcus intercondylaris is moderately excavated and relatively wide (vs deeper and narrower in *Rhynchotus*, *Eudromia* and *Tinamotis*, and very narrow in *Crypturellus*); (3\*) the condylus medialis is little projected in the medial and proximal direction (but

more projected in *Rhynchotus rufescens*); (4\*) in distal view, the condylus lateralis is relatively more robust (more slender in *Eudromia*, *Nothocercus* and *Crypturellus*); (5\*) the impressio ligamenti collateralis lateralis is slightly marked (vs quite conspicuous and craniocaudally extended in *Eudromia* and *Tinamotis*); (6\*) the fossa poplitea is shallow (vs deep in *Rhynchotus* and *Eudromia*).

*Tibiotarsus* GHUNLPam 14861/1 (Fig. 3N–P): (1) the condylus lateralis is elongated with proximal and distal margins subequal (vs pointed and broadening towards its distal margin in *Tinamus*, *Nothocercus* and *Eudromia formosa*; and rounded in *Tinamotis*); (2) the condylus lateralis is wider than the condylus medialis (the condyli are similar in size in *Nothoprocta perdicaria*, *N. ornata* and *N. taczanowskii*); (3) the condylus medialis is slightly shorter than the condylus lateralis (vs much shorter in *Tinamus*, *Nothocercus*, *Rhynchotus*, *E. formosa*, *Crypturellus undulatus* and *Crypturellus noctivagus*; the condyli are subequal in *Tinamotis*); (4) on the depressio epicondylaris medialis, a groove extending along its caudal margin is delimited by a ridge (the depressio is deep on the cranial margin in *Crypturellus* and *Nothocercus*; reduced or poorly developed in *Tinamus* and *Tinamotis*); (5) there is no groove along proximal margin of area intercondylaris (a groove is present with various degrees of development in *Tinamus*, *Crypturellus* and *Nothocercus*); (6) the distal margin of the pons supratendineus is at the same level as the proximal margin of the condylus lateralis (but located distally in *Tinamus* and *Nothocercus*; and proximally in *Tinamotis*); (7) the proximal margin of the condylus medialis is slightly curved and adjacent to the distal opening of the canalis extensorius (vs strongly curved and separated from the distal opening of the canalis extensorius by a conspicuous depression in *Nothocercus*, *Rhynchotus*, *Eudromia* and *Tinamotis*). Additionally, character (4) allows differentiation of GHUNLPam 14861/1 from the Miocene fossil specimens MACN SC-1399 and MACN SC-1440 of Santa Cruz.

*Tarsometatarsi* GHUNLPam 5901/1 (Fig. 3Q–S) and GHUNLPam 5901/2 (Fig. 3T–V): (1) the crista hypotarsi medialis is present and the sulcus hypotarsi medialis has a circular outline and opens medially (the crista medialis is absent and the sulcus opens caudally in *Eudromia*); (2) the opening of the sulcus hypotarsi medialis is greater than or equal to the width of the sulcus (but smaller than the width of the sulcus in *Tinamus*, *Nothocercus*, *Crypturellus*, *Taoniscus* and *Eudromia*); (3) the hypotarsus is triangular in cross-section, with the distal margin gradually expanding and ending distal to the foramina vascu-

laris proximalia (in contrast to rectangular in cross-section and with a truncated distal margin that never surpasses the foramina in *Nothocercus*); (4) the two cristae intermediae hypotarsi (cristae intermediae minor et major) are present (only a single crista intermedia is present in *Tinamotis*).

*Comments.* Two fossil species of *Nothura* have been described, both from Buenos Aires province: *Nothura paludosa* Mercerat, 1897 (middle–late Pleistocene, Arrecifes; Tonni 1980, Tambussi 1987, 1989) and *N. parvula* (early Pliocene, near Pehuén-Có; Tambussi 1987, 1989). The first of these was based on a right femur, which was inadequately described, never illustrated, and is apparently lost (Tonni 1980). Moreover, both the measurements and the brief description provided by Mercerat (1897) cast doubts on the validity of this species and its assignation to *Nothura*. In contrast, *N. parvula* is based on better materials but its discrimination from the extant species of the genus is difficult and based mainly on the possession of a more robust tarsometatarsus (Tonni 1977, Tambussi 1989). Both quantitatively (see Table 1) and qualitatively, the materials from the Cerro Azul Formation are referable to *Nothura*. However, distinguishing them from the extant and extinct species of the genus is difficult due to their fragmentary nature. Nevertheless, these remains show some differences from the extant species of the genus (e.g. the processus flexorius of the humerus is more prolonged distally; in lateral view, they reveal a wider condylus lateralis femoralis; in distal view, the impressio ligamenti cruciati cranialis is deeper and limited cranially by a ridge; they have a narrower condylus lateralis femoralis) that suggests the presence of one (or several) new taxa of small nothurines.

cf. *Nothura* sp. (Fig. 3W–X)

*Referred material and geographic provenance.* GHUNLPam 6233, cranial fragment of sternum, represented by middle portion of sternal manubrium (Salinas Grandes de Hidalgo, Fig. 1).

*Measurements.* See Table 1.

*Description and comparisons.* Although the material is very fragmentary, a central longitudinal ridge is evident on the ventral surface of the spina interna (Fig. 3W, clr). This character can be verified in *Crypturellus* (except in *C. undulatus*), *Nothura* and some subspecies of *Rhynchotus* (in the remaining tinamids the above-mentioned ridge is very small or

No.	Taxon	Specimen	W-shaft	W-dist
1	<i>Chunga burmeisteri</i> (a)	MLP 52	5.80	12.65
2	<i>Chunga burmeisteri</i> (a)	MLP 535	5.80	11.70
3	<i>Cariama cristata</i> (a)	MLP 533	7.78	15.03
4	<i>Chunga incerta</i> (a)	MLP 71-VII-5-1	7.97	12.26
5	<i>Chunga incerta</i> (a)	MLP 71-VII-5-2	7.90	13.45
6	<i>Chunga incerta</i> (a)	MLP 71-VII-5-4	7.00	12.10
7	Cariaminae indet. (a)	MPM-PV 3512	7.50	12.55
8	Cariaminae indet. (a)	MPM-PV 3510	8.70	15.25
9	<i>Psilopterus bachmanni</i> (b)	YPM-PU 15904	13.00	18.50
10	<i>Psilopterus lemoinei</i> (b)	YPM-PU 15402	15.00	23.00
11	<i>Psilopterus lemoinei</i> (b)	AMNH 9257	15.00	22.50
12	<i>Procarriama simplex</i>	MACN 8225	17.17	31.81
<b>13</b>	<b>Phorusrhacidae indet. 1</b>	<b>GHUNLPam 6325</b>	<b>25.67</b>	<b>47.35</b>
14	' <i>Andalgalornis steulleti</i> ' (c)	MLP 88-IX-20-16	22.00	36.00
15	' <i>Patagornis marshi</i> '	MLP 20-154	22.84	37.75
16	<i>Patagornis marshi</i> (d)	BMHN A516	27.00	43.00
17	<i>Patagornis marshi</i>	MLP 84-III-9-2	28.83	49.51
18	<i>Hermosiorinis incertus</i> (e)	FMHN-P 14422	26.00	39.00
19	' <i>Hermosiorinis rapax</i> ' (e)	MMCN S-155	32.00	57.00
20	<i>Hermosiorinis milneedwardsi</i> (f)	MACN 5944	32.00	52.00
21	<i>Phorusrhacos longissimus</i> (e)	AMHN 9146	39.00	62.00
22	<i>Phorusrhacos longissimus</i>	MLP 22-130	44.32	57.50
23	<i>Phorusrhacos longissimus</i>	MLP 22-137	42.56	59.30
24	<i>Paraphysornis brasiliensis</i> (g)	DGM-1418-R	54.00	91.00
25	' <i>Devincenzia pozzii</i> '	MACN 17749	53.00	92.81
26	' <i>Devincenzia pozzii</i> '	MACN 13243	52.78	111.78
27	'Phorusrhacinae' indet. (f)	MNHN 1563	58.00	103.6
28	<i>Brontornis burmeisteri</i> (f)	MLP 20-88	69.96	116.66

Table 2. Comparative measurements of tibiotarsus for the Phorusrhacidae indet. 1 (GHUNLPam 6325) from the Cerro Azul Formation and other phorusrhacoid birds. In parentheses, measurements taken from: (a) Noriega *et al.* 2009, (b) Sinclair & Farr 1932, (c) Noriega & Agnolin 2008, (d) Andrews 1899, (e) Alvarenga & Höfling 2003, (f) Tambussi *et al.* 1999, (g) Alvarenga 1993.

absent; see Bertelli 2002). The combination of dimensions falls within the range observed exclusively for species of *Nothura* (Table 1).

Order CARIAMIFORMES Verheyen, 1957  
Family PHORUSRHACIDAE Ameghino, 1889

Phorusrhacidae indet. 1 (Fig. 4A–D)

*Referred material and geographic provenance.* GHUNLPam 6325, shaft and distal end of left tibiotarsus (Laguna Guatraché, Fig. 1).

*Measurements.* See Table 2 and Fig. 5.

*Description and comparisons.* The material can be clearly distinguished from other large-bodied taxa occurring in the continental Cenozoic of South America (e.g. Teratornithidae, Rheidae) on the basis of the following characteristics: (1) the pons supratendineus is ossified; (2) the opening of the canalis extensorius is on the medial side of the shaft; (3) a

tuberculum is located lateral to the distal opening of the canalis extensorius, with varying development but always present; (4) the area intercondylaris is large and rounded; (5) the condylus medialis is not oriented medially. It can be referred to the Phorusrhacidae and differs from the Cariamidae (*Chunga* and *Cariama*) by: (1) having a much larger size (Table 2); (2) the incisura intercondylaris being narrower and deeper; (3) in distal view, the condylus medialis being well extended cranially; (4) the condyli having their major axes parallel to the shaft (except in some *Psilopterus* sp.; see Sinclair & Farr 1932, pl. 29, Fig. 4); (5) in lateral view, the condylus lateralis being more rounded (vs craniocaudally elongated in Cariamidae). Among the Phorusrhacidae, the measurements of this specimen fall within the range observed for the Patagornithinae (i.e. '*Andalgalornis steulleti*' [Kraglievich, 1931], *Patagornis marshi* Moreno & Mercerat, 1891; see Table 2 and Fig. 5) and Hermosiornithinae (*Hermosiorinis*), and are much larger than those of the Psilopterinae (*Psilopterus*, *Procarriama simplex* Rovereto, 1914) and much smaller than in the

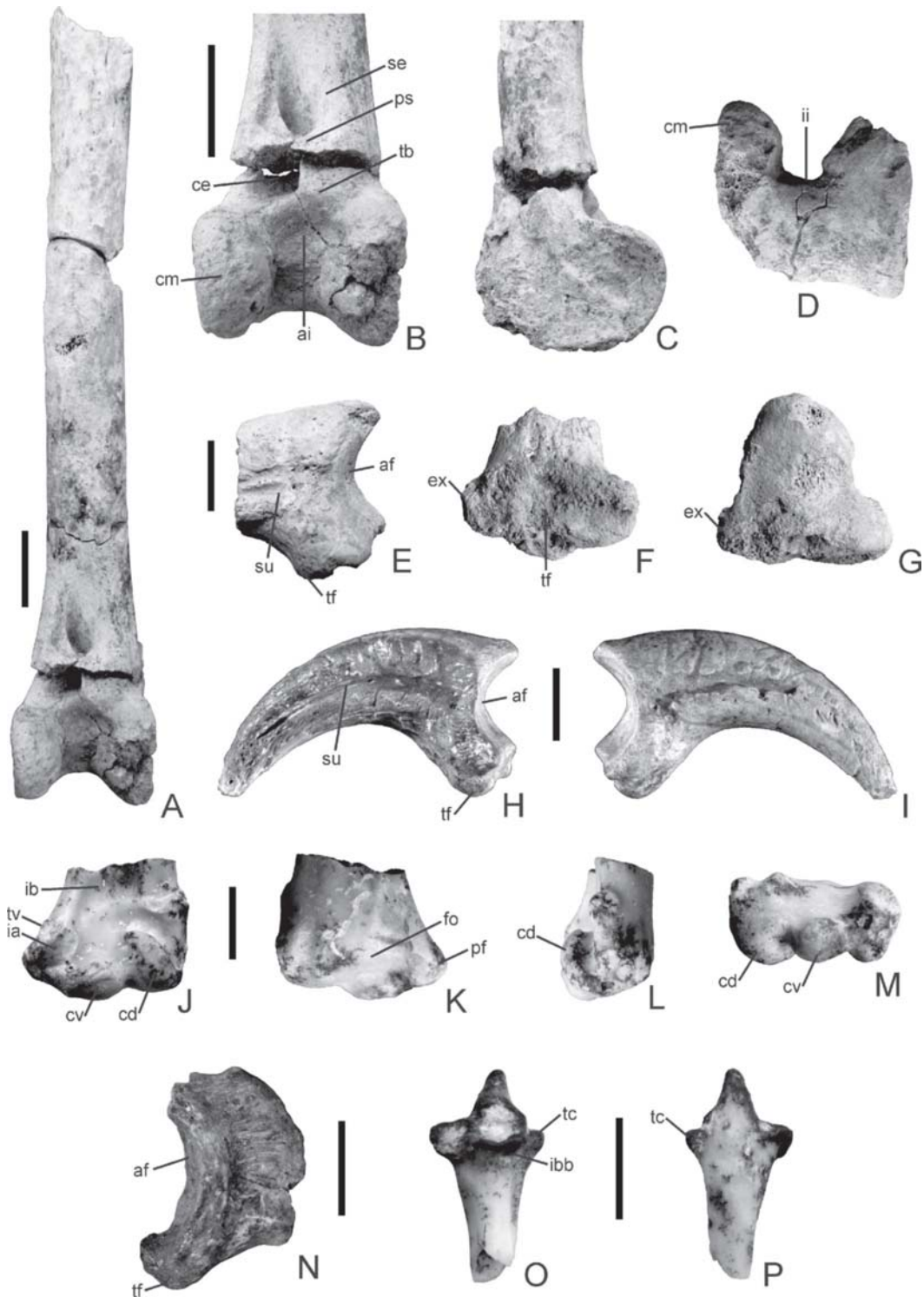


Fig. 4. Phorusrhacidae, Falconidae, Teratornithidae and Tyrannidae from the Cerro Azul Formation. A–D, Phorusrhacidae indet. 1, shaft and distal end of left tibiotarsus (GHUNLPam 6325) in complete cranial view (A), detail of cranial (B), medial (C) and distal view (D). E–G, Phorusrhacidae indet. 2, ungual phalanx of right digit IV? (GHUNLPam 6234) in medial (E), plantar (F) and proximal view (G). H–I, Phorusrhacidae indet. 3, ungual phalanx of digit II (MMCN s/n<sup>o</sup>) in lateral (H) and medial view (I). J–M, *Milvago* sp. (GHUNLPam 19867/16), distal end of left humerus in cranial (J), caudal (K), dorsal (L) and distal view (M). N, *Argentavis magnificens* holotype (MLP 65-VII-29-49), proximal end of undetermined ungual phalanx. O–P, Tyrannidae indet., proximal end of right ulna (GHUNLPam 19865/15) in cranial (O) and caudal view (P). Abbreviations: ai, area intercondylaris; af, articular facet; cd, condylus dorsalis; ce, canalis extensorius; cm, condylus medialis; cv, condylus ventralis; ex, expansiones latero-mediales; fo, fossa olecrani; ia, impressio lig. articularis cranialis; ib, impressio m. brachialis; ibb, impressio m. biceps brachii; ii, incisura intercondylaris; pf, processus flexorius; ps, pons supratendineus; tb, tuberculum; tc, tuberculum ligamenti collateralis ventralis; tf, tuberculum flexorius; tv, tuberculum supracondylaris ventralis; se, sulcus extensorius; su, surcos lateromediales. Scale bars = 30 mm (A–D), 10 mm (E–I, N), 5 mm (J–M, O–P).

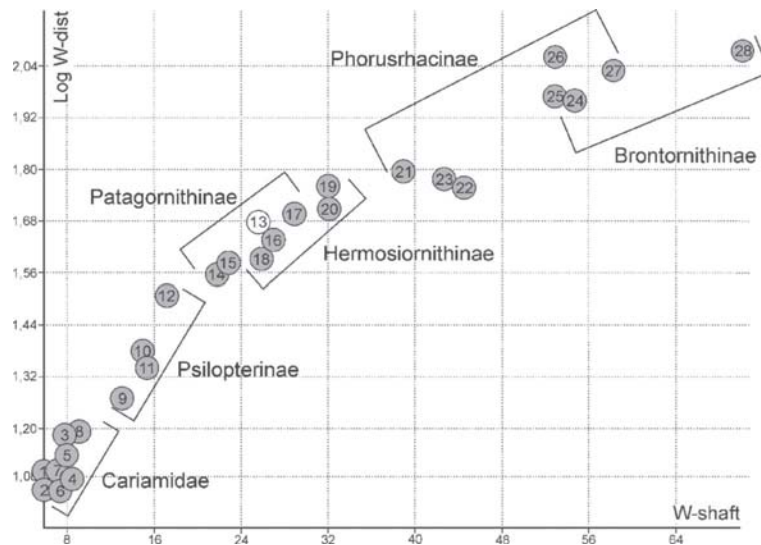


Fig. 5. Bi-plot showing relationship between the measurements W-shaft and log-transformed W-distal of tibiotarsus for the Phorusrhacidae specimens listed in Table 2.

Phorusrhacinae (*Phorusrhacos*, *Devincenzia*) and Brontornithinae [*Brontornis burmeisteri*, *Paraphysornis brasiliensis* (Alvarenga, 1982)].

In addition, GHUNLPam 6325 is characterized by the following features: (1) the distal end (at the level of the condyli) is expanded latero-medially with respect to the shaft (compared with more continuous with the shaft in *Psilopterus*, *P. marshi*, *Hermosiornis milneedwardsi* Rovereto, 1914); (2) there is slight development of a tuberculum located laterally to the distal opening of canalis extensorius (vs well developed in Psilopterinae, *Devincenzia* and *Phorusrhacos*); (3) the pons supratendineus is proximodistally narrow (but broad in *Psilopterus*); (4) the pons supratendineus is oblique with respect to the diaphysal axis (more transverse in *Hermosiornis* and *Phorusrhacos*); (5) the ridge on the pons supratendineus is slightly developed (strongly developed in *Devincenzia* and *Phorusrhacos*, but less so in Psilopterinae); (6) in distal view, the incisura intercondylaris is narrow (wider in Psilopterinae); (7) the condylus medialis is elongated proximodistally (vs much more robust in *Devincenzia*, more elongate in *Psilopterus*); (8) the sulcus extensorius is narrow and shallow (wider and deeper in Phorusrhacinae and *Hermosiornis*); (9) the groove between the opening of the canalis extensorius and proximal end of the condylus medialis is narrower and shallower (vs wider and deeper in 'Phorusrhacinae' and *Hermosiornis*); (10) in distal view, the condylus medialis slightly protrudes cranially (more protruding in *Devincenzia* and

*Paraphysornis*).

*Comments.* *Paleopsilopterus itaboraiensis* Alvarenga, 1985 (late Paleocene of Brazil) was considered the oldest record for the family; however, it has recently been excluded from the Phorusrhacidae (Phororhacoidae *sensu* Agnolin 2009). Some putative Phorusrhacidae remains have been recorded from the early-late Eocene of Patagonia and northeastern Argentina (Pascual *et al.* 1981, Acosta-Hospitaleche & Tambussi 2005); however, additional materials are necessary to confirm these records. Unquestionable Phorusrhacidae initiate in the late Oligocene of Argentina and Brazil (e.g. Ameghino 1895, Alvarenga 1982, 1993). Their greatest diversity seems to have developed during the early-middle Miocene (Tonni 1980), subsequently decreasing during the Mio-Pliocene (Tambussi 1989) and ending with their last record in the late Pleistocene of Uruguay (Alvarenga *et al.* 2010).

Recently, Agnolin (2009) performed the first phylogenetic analysis of the Phorusrhacidae, including both living (e.g. Cariamidae, Psophidae) and extinct (e.g. Bathornithidae, Idiornithidae, Ameghinornithidae) cariamae. The material described here can not be included in any of the groups of Phorusrhacidae defined by that author, because the synapomorphies that define these groups do not include characters from the distal tibiotarsus. Alvarenga & Höfling (2003) made a complete revision of the group, but, unfortunately, the infrafamilial taxa recognized in that work were diagnosed fundamentally on the basis of relative proportions of the lower limbs and morphology of the tarsometarsus. Thus, the isolated and

fragmentary nature of the tibiotarsus from the Cerro Azul Formation does not allow a reliable assignation of this material to any of the subfamilies recognized by previous authors. The evaluation of quantitative parameters indicates that this element seems to be quite conservative among the Phorusrhacidae, with a presumably more derived morphology in the Phorusrhacinae–Brontornithinae group.

Vezzosi (2006) reported the presence of a specimen of *P. simplex* (MMCN 990, a taxon previously recognized for the Huayquerian of Catamarca; see Rovereto 1914) from Salinas Grandes de Hidalgo, and represented by a large portion of the skeleton. Unfortunately, this specimen could not be examined for this study.

Phorusrhacidae indet. 2 (Fig. 4E–G)

*Referred material and geographic provenance.* GHUNLPam 6234, ungual phalanx of right digit IV? with distal end missing (Salinas Grandes de Hidalgo; Fig. 1).

*Measurements.* W–prox: 21.11, D–prox: 20.35. For other Phorusrhacidae, the values for these measurements are: *P. simplex* = 5.8, 8.6; *P. marshi* 12, 13; ‘*Brontornis platyonyx*’ Ameghino, 1895 = 15, 16; *P. brasiliensis* = 20, 26.8.

*Description and comparisons.* The material can be referred to Phorusrhacidae on the basis of the following combination of characters: (1) large size, great robustness and high bone density; (2) the presence of lateral and medial grooves (except *P. brasiliensis*); (3) in distal view, the outline is elliptical and the plantar surface convex; (4) in lateral view, the tuberculum flexorius is flat and projecting slightly in the plantar direction (not protuberant); (5) in plantar view, the tuberculum flexorius is expanded lateromedially (lateromedial expansions or ‘basilar apophyses’ of Moreno & Mercerat 1891) with the insertion area concave and well extended transverse to the greater axis; (6) the dorsal lip of the articular facet slightly projects proximally; (7) in proximal view, the articular facets are wide and barely demarcated.

*Comments.* According to Patterson & Kraglievich (1960), the lower limb of the Phorusrhacidae may incorporate two morphological types of ungual phalanges: those of digits I and II are strongly arched and lateromedially compressed, with a rounded tuberculum flexorius that is strongly projected in the plantar direction (especially in digit II); in turn, those of digits III and IV are straighter and broader, with the tuberculum flexorius elongated lateromedially, flat-

tened and concave. This specialization in the phalanges of the lower limb is most accentuated in the Phorusrhacidae, but also slightly reflected in the Bathornitidae and Cariamoidea (*sensu* Agnolin 2009; see also Patterson & Kraglievich 1960). The characteristics cited for the second type of ungual phalanges in the Phorusrhacidae agree with those present in specimen GHUNLPam 6234. Furthermore, the elliptical transverse outline of the preserved distal portion, together with the presence of a tuberculum flexorius whose medial expansion is more projected than its lateral counterpart, permits its referral to an ungual phalanx of digit IV. If this assignation is correct, the size of this material is only similar to that of the corresponding element in the large Phorusrhacinae (mainly in *Phorusrhacos longissimus* Ameghino, 1887) or Brontornithinae (see measurements reported by Ameghino 1895).

Phorusrhacidae indet. 3 (Fig. 4H–I)

*Referred material and geographic provenance.* MMCN s/n°, ungual phalanx of digit II (near Carhué, Fig. 1).

*Measurements.* TL:  $41.70 \pm 20$ , W–prox: 13.00, D–prox: 22.10. The same measurements in other Phorusrhacidae are, respectively: *Psilopterus australis* Moreno & Mercerat, 1891 = 27, 7, 13; *P. marshi* = 43, 12, 20; *P. longissimus* =  $\pm 70$ , 20, 31; ‘*Devincenzia*’ *pozzii* (Kraglievich, 1931) = 90, 23.5, 38.5; *B. burmeisteri* = 54, 50, 26, ‘*B. platyonyx*’ = 60, 31, 25; *P. brasiliensis* = 74.4, 27, 33.8.

*Description and comparisons.* The material can be referred to the ungual phalanx of digit II of a Phorusrhacidae on the basis of the combination of characters mentioned for GHUNLPam 6234 (characters 1, 3, 6 and 7) and the following: the strongly curved longitudinal axis; in lateral view, the inflated tuberculum flexorius; and the strongly compressed mediolateral profile. It is worth noting that all these characters are already inferred to characterize basal Cariamoidea and Bathornithidae (*sensu* Agnolin 2009), which are distinguished from the Phorusrhacidae by their smaller size and less specialization.

The characteristics observed in MMCN s/n° correspond to the first morphological type of ungual phalanges as described by Patterson & Kraglievich (1960). More precisely, the morphology corresponds to the ungual phalanx of digit II, differing from that of digit I by its greater curvature and relative length, stronger lateromedial compression, and more developed tuberculum flexorius. The material is indistinguishable in its shape from the corresponding element in all the compared Cariamidae and Phorusrhacidae, except for the Brontornithinae (e.g. *P. brasiliensis*,

Brontornithinae indet. MACN A52-193), in which the features described are weaker, possibly as a derived condition. A noteworthy characteristic of MMCN s/n° is the presence of medial and lateral longitudinal grooves; these characters constitute the generalized condition for bird phalanges. However, in most Phorusrhacidae for which the ungual phalanx of digit II is known (e.g. *Psilopterus colzecus* Tonni & Tambussi, 1988 MLP 76-VI-12-2; *P. simplex* MACN 8225; *P. longissimus*, 'D.' *pozzii* MACN 6681 3-II), the above-mentioned grooves are closed and show a simple opening along their proximal portion (not homologous to the medial and lateral foramina present on the tuberculum flexorius in Strigiformes and Accipitriformes). In contrast, and similar to the Carhué specimen, other Phorusrhacidae studied have quite visible grooves (e.g. *Patagornis* sp. MLP 20-164, *Phorusrhacos* sp. AMHN 9497 and AMHN 15557 published by Sinclair & Farr 1932). Another remarkable feature within the Cariamidae is the presence of the above-mentioned character in *Chunga* and its absence in *Cariama*. Additionally, its proportions agree with those recorded for the Patagornithinae, especially with the measurements known for *Patagornis marshi*, whereas they are larger than those recorded for Psilopterines and smaller than those of the large Phorusrhacinae and Brontornithinae. Unfortunately, no ungual phalanges of Hermosiornithinae were available for comparison in this work and, therefore, the comparative analysis is pending.

*Comments.* This material was originally reported by Campbell (1995) as additional material for *Argentavis magnificens* and referred to the latter taxon by the presence of only two characters: great development of the tuberculum flexorius and prominent grooves on the lateral and medial surfaces. First, we contend that such an assignation to species level is not supported on the basis of only two characters in a bone as little diagnostic as an ungual phalanx. Moreover, before Campbell (1995) made this description, no ungual phalanges were known for *A. magnificens* and, therefore, that author based his assignation on non-overlapping elements of the holotype. The recent study of the *A. magnificens* holotype (MLP 65-VII-29-49) has allowed recognition of a proximal fragment of ungual phalanx corresponding to an undetermined digit (see Fig. 4N) that was not reported in the original description (Campbell & Tonni 1980). This material lacks the only two characteristics cited by Campbell (1995) and differs from MMCN s/n° by having: (1) prominent lateral and medial ridges in the articular facet, (2) the tuberculum flexorius minimally or not developed, (3)

the proximal absence of marked grooves on its lateral and medial surfaces. On the other hand, MMCN s/n° can be differentiated from the Cathartidae and *Teratornis merriami* Miller, 1909 by its: (1) strongly curved longitudinal axis (2) phalangeal body more compressed lateromedially, (3) convex plantar surface (flat in *T. merriami*), (4) articular facet deep and more extended dorsoplantarly, (5) dorsal lip of the articular facet more extended proximally.

Order ACCIPITRIFORMES (Vieillot, 1816)  
Family FALCONIDAE Vigors, 1824

**Milvago** Spix, 1824  
**Milvago** sp. (Fig. 4J–M)

*Referred material and geographic provenance.* GHUNLPam 19867/16, distal end of left humerus (Caleufú, Fig. 1).

*Measurements.* W–dist: 11.07 (*Caracara plancus*: 20.77–19.02, 19.78 [7]; *Caracara cheriway*: 18.50–16.80, 17.70 [7]; *Milvago chimango*: 12.53–11.48, 12.04 [7]; *Milvago chimachima*: 12.03–11.90, 11.96 [2]; *Milvago brodkorbi*: 14.60–13.60, 14.00 [6]).

*Description and comparisons.* The material can be assigned to the Falconinae Caracarini (*Phalcoboenus*, *Milvago*, *Daptrius* and *Caracara*) and distinguished from the Falconini (*Microhierax*, *Polihierax*, *Falco* and *Spizapteryx*) and Herpetotherinae (*Micrastur* and *Herpetotheres*) by the presence of a shallow fossa olecrani and less-developed processus flexorius. Additionally, the material GHUNLPam 19867/16 shares with the Caracarinae a condylus ventralis with elliptical outline (rounded in *Herpetotheres cachinnans* and *Falco* spp.) and a well-marked impressio musculi brachialis distally delimited by a ridge (impressio diffuse in *Polihierax semitorquatus* and *Spizapteryx circumcinctus*; continuous, without a ridge in *H. cachinnans*).

The fossil species *Pediohierax ramenta* (Wetmore, 1936) from the middle Miocene of Nebraska, USA, was considered by Becker (1987) as the primitive sister group of the Falconinae, but that author pointed out that the presence of a shallow fossa olecrani and the lesser development of the processus flexorius would place it phylogenetically closer to the Caracarinae. However, in *P. ramenta*, the impressio musculi brachialis is oriented parallel to the diaphysial axis, a unique character among the falconids and is, thus, different from the Cerro Azul Formation material.

The species of *Phalcoboenus*, *Daptrius* and *Caracara* are considerably larger in size than the

specimen studied here (see measurements). Specimen GHUNLPam 19867/16 differs from the two extant species of the genus, *M. chimango* (Vieillot, 1816) and *M. chimachima* (Vieillot, 1816), by the following characteristics: (1) in dorsal view, the profile is more compressed cranio-caudally; (2) in distal view, the condylus ventralis is less projected cranially; (3) in caudal view, the processus flexorius is less elongate and more ventrally oriented (similar to that of *M. chimachima*); (4) the presence of a wide area on the condylus ventralis, between the condylus dorsalis and impressio ligamenti articulare craniale; (5) the tuberculum supracondylaris ventralis at the same level as the proximal margin of the condylus dorsalis (as in *M. chimachima*, slightly more proximal in *M. chimango*).

Three fossil *Milvago* species have been recognized, namely *Milvago alexandri* Olson, 1976 (Pleistocene, Haiti), *Milvago carbo* Suárez & Olson, 2003 (late Pleistocene–early Holocene, Cuba) and *Milvago brodkorbi* Campbell, 1979 (late Pleistocene, Perú). Unfortunately, the first two of these species were erected on the basis of non-comparable elements with the material described here. However, the insular nature of the first species (possibly derived from *M. chimachima*, see Olson 1976) and the large size of the elements preserved in the case of the second one (Suárez & Olson 2003) allows us to dismiss a direct relationship between these species and GHUNLPam 19867/16. *Milvago brodkorbi*, is closely related to *M. chimango* (Campbell 1979), and its dimensions are somewhat larger than those of the living species of the genus. The material from La Pampa differs from the latter palaeospecies by having a longer and wider impressio musculi brachialis and the processus flexorius being more strongly projected ventrally.

If the synonymy proposed by Emslie (1998) is correct and the palaeospecies *Milvago readei* (Brodkorb, 1959) from the late Pleistocene of Florida (Campbell 1980) actually corresponds to the living species *M. chimachima*, then this latter taxon would have had a wider geographical range in the past. Remains of undetermined *Milvago* species have been recorded from the late Pleistocene of Cuba (Suárez & Arredondo 1997) and Ecuador (Campbell 1976).

*Comments.* With the exception of an undetermined species assigned to *Milvago* from the late Pliocene of Chile (Emslie & Guerra 2003), until the present, all fossil remains assigned to living and extinct species of this genus have come exclusively from deposits dated as late Pleistocene–early Holocene. *Milvago chimango* has been reported from Luján (Buenos Aires province, Argentina; Ameghino 1891) and in sympatry

with *M. chimachima* in Minas Gerais, Brazil (Brodkorb 1964).

The oldest known remains of Falconids in South America are of *Badiostes patagonicus* Ameghino, 1895 from the Santa Cruz Formation (early–middle Miocene), included by Olson (1985) within the Caracarinae. A possible member of this subfamily has been reported from upper Eocene deposits of Seymour Island, Antarctic Peninsula (Tambussi *et al.* 1995, Noriega & Tambussi 1996, Tambussi & Acosta-Hospitaleche 2007), which would represent the oldest record of the subfamily. Finally, two undetermined Falconidae have been reported from the Friasian of Neuquén province (late Miocene; Tonni 1980) and from the Pinturas Formation in Santa Cruz province (early–middle Miocene, Chiappe 1991), but to date, neither of these remains has been described.

#### Order INCERTAE SEDIS

Family TERATORNITHIDAE Miller, 1909

**Argentavis** Campbell & Tonni, 1980

**Argentavis magnificens** Campbell & Tonni, 1980

*Holotype.* MLP 65-VII-29-49, associated partial skeleton consisting of portions of skull, right quadrate, humeral end and shaft of right coracoid, left humerus with eroded proximal and distal ends, fragmentary shaft of possible left ulna, portion of shaft of right radius, distal end of left metacarpal II, midportion of left metacarpal III, shaft of right tibiotarsus, shaft of right tarsometatarsus, fragmentary proximal end of an undetermined ungual phalanx (Salinas Grandes de Hidalgo; Fig. 1).

*Measurements.* See Campbell & Tonni (1980; Table 1).

*Description and comparisons.* See Campbell & Tonni (1980, 1981, 1983).

*Comments.* Additional *Argentavis magnificens* specimens were reported by Campbell (1995) from diverse localities of Argentina, comprising a fragmentary left coracoideum and the eroded distal end of a left tibiotarsus (Chiquimil and Río Añacos localities respectively, Andalhualá Formation, upper Miocene, Santa María Valley, Catamarca province). A third specimen represented by an undetermined ungual phalanx has been reassigned here to Phorusrhacidae indet. As previously noted, re-examination of the holotype has allowed adding a proximal fragment of the ungual phalanx (Fig. 4N) that had not been reported in the original description; this element was



	Salinas Grandes de Hidalgo	Carhué	Laguna Guatraché	Bajo Giuliani	Quehué	El Guanaco	Caleufú
Rheidae							
<i>Pterocnemia</i> sp.	GHUNLPam 6231 GHUNLPam 6232						
Tinamidae							
<i>Eudromia</i> sp. cf. <i>Eudromia</i> sp. <i>Nothura</i> sp.	MLP 87-XI-20-3			GHUNLPam 8070/1	GHUNLPam 27042 GHUNLPam 5901/1 GHUNLPam 5901/2	GHUNLPam 14861/1	GHUNLPam 21566/22
cf. <i>Nothura</i> sp.	GHUNLPam 6233						
Phorusrhacidae							
Phorusrhacidae indet. 1			GHUNLPam 6325				
Phorusrhacidae indet. 2	GHUNLPam 6234						
Phorusrhacidae indet. 3		MMCN s/n°					
<i>Procarriama simplex</i>	MMCN 990						
Falconidae							
<i>Mitvago</i> sp.							GHUNLPam 19867/16
Teratornithidae							
<i>Argentavis magnificens</i>	MLP 65-VII-29-49						
Passeriformes							
cf. Tyrannidae indet.							GHUNLPam 19865/15

Table 3. Synthesis of fossil birds recovered from sites of the Cerro Azul Formation.

hitherto unknown for this taxon. It was also possible to establish that the fragment of an os maxillare that Campbell & Tonni (1980, fig. 1) had placed laterally on the rostrum of *A. magnificens* is in fact part of the ventral portion of the rostrum (the apparent processus nasalis corresponds more closely to the processus maxillopalatinus), thus being more parsimonious with respect to the condition evident in *T. merriami*. Additionally, mid-dorsal fragments of the os maxillare have been identified for the first time.

Teratorns were among the largest flying birds that ever existed, only rivalled by the giant pelagornithids (see e.g. Mayr & Rubilar-Rogers 2010). *Argentavis magnificens* is certainly the largest flying bird known to date (in terms of mass). This has led to prolific speculation on its palaeobiology and that of other teratorns (e.g. Campbell & Tonni 1981, 1983, Vizcaino & Fariña 2000, Palmqvist & Vizcaino 2003, Chatterjee *et al.* 2007). This contrasts strongly with the currently available studies on the comparative anatomy (Campbell & Tonni 1981, 1983) and phylogenetic relationships of the group (Emslie 1988). Moreover, some, including *A. magnificens*, are known from very fragmentary remains, and have traditionally been interpreted only by comparison with *T. merriami*. Although practically the entire skeleton of the latter species is indeed well known through at least a hundred individuals, as noted by Suárez & Olson (2009), its osteology has still not been described completely. Available descriptions have usually emphasized the postcranial similarities between teratorns and the Cathartidae vultures, although remarkable similarities to other bird groups, such as the ciconiidae, 'pelecaniformes' and procellariiformes (Jollie 1976, 1977, Olson 1979, Campbell & Tonni 1980, 1981, 1983) have also been noted.

Order PASSERIFORMES (Linnaeus, 1758)  
Suborder TYRANNI Wetmore & Miller, 1926  
Family TYRANNIDAE Vigors, 1825

cf. Tyrannidae indet. (Fig. 40–P)

*Referred material and geographic provenance.* GHUNLPam 19865/15, proximal epiphysis of right ulna (Caleufú, Fig. 1).

*Measurements.* W-prox: 5.64.

*Description and comparisons.* The presence of the following characters allows differentiation of GHUNLPam 19865/15 from the Passeri and its referral to the Tyranni (Ballmann 1969, Mayr & Manegold 2006): (1) a well-developed tuberculum

ligament collateralis ventralis, (2) a shallow pit at the insertion area of the musculus biceps brachii, (3) the cotyla dorsalis proximodistally being shorter than the cotyla ventralis, (4) the proximal rim of the cotyla ventralis is rounded (proximal notch absent). Additionally, based on the materials available for comparison, among the Tyranni, the material from Caleufú resembles the Tyrannidae by having: (1) the tuberculum ligamenti collateralis ventralis well developed and conspicuously projecting ventrally, (2) the cotyla dorsalis slightly projected dorsally, (3) a well-marked proximal notch between the cotylae ventralis et dorsalis. The dimensions of this material are similar to those of *Pitangus sulphuratus* (Linnaeus, 1766).

*Comments.* The fossil record of Passeriformes in Argentina is extremely poor. The oldest record for South America corresponds to an undetermined Passeriformes (probably belonging to Tyranni) that was described by Noriega & Chiappe (1993) from the Pinturas Formation (lower–middle Miocene) in Santa Cruz province. Remains attributable to Tyranni become abundant in Argentina from the Pliocene (see Noriega 1998, Tonni & Noriega 2001).

## Discussion and conclusions

From an actualistic perspective, the records of taxa with living representatives are the most relevant for making palaeoenvironmental inferences. However, some precautions need to be taken. The absence of diagnostic characters at species level in the records presented here has allowed only assignment to genus level in most cases; thus, we can not exclude the possibility that these could be new species with ecological requirements different from those of living species. Likewise, these records evidently come from stratigraphic sections that span a wide chronological interval and, therefore, they can not be considered a synchronous faunal association. However, an understanding of all the Huayquerian assemblages and the contrast of this information with the evidence provided by the diverse faunal suites exhumed from the Cerro Azul Formation permits some commentary on the avifaunal composition for this land mammal age in central-southern Argentina.

Until now, the fossil record of birds in the Cerro Azul Formation comprises at least nine taxa, including four families with living representatives (Rheidae, Tinamidae, Falconidae and Tyrannidae) and two extinct ones (Phorusrhacidae and Teratornithidae, see Table 3). Of these nine taxa, three are carnivorous (Falconidae, Phorusrhacidae and Teratornithidae), two are flightless (Rheidae, Phorusrhacidae), and

three comprise giant forms (Rheidae, Phorusrhacidae and Teratornithidae) with body masses greater than 20 kg.

Currently, the area incorporating the studied localities is part of the Espinal biogeographic province within the Chacoan Domain (*sensu* Cabrera & Willink 1973). Typical extant representatives of the above-mentioned taxa for this area are *Eudromia elegans*, *Nothura maculosa*, *Nothura darwini* and *Milvago chimango*, together with very common and numerous tyrannid species (Cabot 1992, Narosky & Yzurieta 2003, Echarri *et al.* 2008). On the other hand, the distributional limit of *Pterocnemia pennata* (the only living species of the genus) is located somewhat further southwards (north of the Negro River, in southwestern La Pampa province; see Handford & Mares 1982). In this sense, it is noteworthy that the current distributions of the species of *Pterocnemia*, *Eudromia*, *Nothura* and *Milvago* share a sympatric area located only about 150 km southwest of the southernmost locality studied here. However, this distributional pattern could be recent (since the last glacial maximum), given that remains of *P. pennata* from the late Pleistocene–early Holocene have been recorded outside its current distribution area (Tonni & Laza 1980, Tambussi & Acosta-Hospitaleche 2002). Fossil *Eudromia* species also occur beyond this genus current distribution, in deposits dated as early and middle Pliocene (see comments in the description of *Eudromia* sp.).

According to phylogenetic reconstructions made by Bertelli *et al.* (2002) and Bertelli & Chiappe (2005), the ‘plesiomorphic’ habitat of tinamids is represented by tropical forests, and this habitat is occupied by most species belonging to the paraphyletic group ‘Tinaminae’ (e.g. *Nothocercus*, *Tinamus*, *Crypturellus*). In contrast, *Eudromia* and *Nothura* are representatives of the clade Nothurinae, which comprises tinamids that inhabit open areas and display a tendency toward the cursorial habit; the utmost specialization of this group is represented by the Chacoan–Patagonian genera: *Eudromia* and *Tinamotis*. Convergently with *R. americana* and *P. pennata*, these tinamids are characterized by the loss of digit I and secondary reduction of flight, a condition that is possibly associated with their stronger cursorial habit (Sick 1984). Acquisition of the cursorial habit would be correlated with the advent of more open environments in South America, possibly since the early Miocene (Sick 1984, Bertelli *et al.* 2002, Bertelli & Chiappe 2005). Using a bioclimatic analysis, Echarri *et al.* (2008) have indicated that the current distribution of *Eudromia* spp. is highly correlated with variables related to precipitation; *E. elegans* occupy-

ing areas with less precipitation than *E. formosa*. Similar conclusions were reached by Tambussi & Acosta-Hospitaleche (2002) for *P. pennata* with respect to *R. americana*.

Thus, it is evident that all taxa in the fossil assemblages with living representatives currently inhabit open environments that range from xerophyllous shrub steppe to xerophyllous semi-desert and are highly tolerant of arid and cold conditions. With some restrictions, open habitats have also been inferred for the extinct taxa Phorusrhacidae (Tambussi *et al.* 1999) and Teratornithidae (Campbell & Tonni 1983, Chatterjee *et al.* 2007). This agrees with the palaeoenvironmental inferences made from mammalian faunas (e.g. Verzi *et al.* 1999, Vucetich *et al.* 1999, Goin *et al.* 2000) that indicate an increase in aridity at the end of the late Miocene compared with earlier times, and the consequent development of open environments in central Argentina, following a gradual trend that began in the Chasicuan (‘Age of the Southern Plains’; see Pascual & Bondesio 1982, Pascual & Ortiz-Jaureguizar 1990, Tonni & Carlini 2008). According to Verzi & Montalvo (2008), this cold arid pulse represents a marked change recorded globally (e.g. MacFadden & Cerling 1996, Cerling *et al.* 1997, Bobe 2006) possibly correlative with polar glacial expansion in the latest Miocene, ca 5.7–5.8 Ma (Opdyke 1995, OIS TG20–TG22 of Shackleton 1995).

The oldest tinamids from the early–middle Miocene of Patagonia are more primitive than the Nothurines described here and undoubtedly represent extinct taxa (their synapomorphic characters indicate an intermediate position between the ‘Tinaminae’ and the Nothurinae; see Bertelli & Chiappe 2005). Similarly, the pre-Huayquerian records of Rheids comprise extinct forms (i.e. *D. fragilis*, *O. patagonicus*). In turn, the modern taxa *Eudromia*, *Nothura*, *Milvago* and Tyrannidae have their oldest records represented here, with only *Pterocnemia* having been previously recorded from coeval Huayquerian sequences of Entre Ríos province (Noriega & Agnolin 2008). This shows that during the late Miocene, the avifaunal association in central Argentina already had modern characteristics, with the first records of typical Pampean–Patagonian elements such as the rheids and nothurine tinamids.

## Acknowledgements

This work was partially funded by Project grants from Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de La Pampa. The authors thank K.E. Campbell for sending photographs of the materials referred to *A. magnificens* deposited at

Instituto Miguel Lillo, M.A. Zárate for the critical revision of the section on geological aspects, E.P. Tonni for providing photographs of *T. merriami*, F. Agnolin and F. Novas for collecting part of the materials studied here and graciously permitting their study.

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