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New fossil birds from the Miocene of Patagonia, Argentina
Nuevas aves fósiles del mioceno de Patagonia, Argentina

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Abstract: The present contribution aims to describe new fossil bird remains coming from early-middle Miocene beds (Pinturas and Santa Cruz Formations) in Santa Cruz province, Patagonia, Argentina. These include a new tinamid, a basal anseriform, one anhimid, two new tadornine ducks, possible gruid, psophiid, and parvigruid cranes, an uncertain falconid, a new species of the falconid genus *Thegornis*, a possible sophiornithid, a coraciid, and remains of innominate rallids, phoenicopterids and passeriforms of the clade Tyranni. If correctly identified, the gruid represents the oldest record for the clade in South America and one of the few findings of the group in the entire continent. The sophiornithid and parvigruid may constitute the first record for each clade in South America. The psophiid may constitute the first fossil record for the clade worldwide. The coraciid represents the first record for the family in South America and both the youngest and second record for coraciiforms in the continent. This, together with the gruid, constitute members of bird clades that were geographically widespread by Paleogene and early Neogene times, but now are restricted as relicts to the Old Word and North America. Their extinction from the Neotropical Region is still uncertain. The presence of at least three different members of Tyranni, reinforces previous thoughts sustaining a long and complex history of the subclade, and passeriforms as a whole, in South America.
Keywords: Birds, early Miocene, Santa Cruz province, Patagonia, Argentina.

Resumen: La finalidad de la presente contribución es la de describir nuevos restos de aves fósiles procedentes de capas del Mioceno temprano-medio (Formaciones Punturas y Santa Cruz) en la provincia de Santa Cruz, Argentina. Estos incluyen un nuevo tinámido, un anhímido, dos nuevos patos tadorninos, posibles gruídos, psófidos y parvigruidos, un falcónido incierto, una nueva especie de falcónido del género *Thegornis*, un posible sofiornítido, un corácido, y restos de rállidos, foenicoptéridos y paseriformes del clado Tyranni innominados. Si la identificación es correcta el gruido representa el registro más antiguo para América del Sur y uno de los escasos hallazgos para el grupo en el continente entero. Por otro lado, el sofiornítido y el parvigruido constituirían los primeros registros para cada clado en Sudamérica. El psófido podría constituir el primer registro fósil certero para el clado a nivel mundial. El corácido constituye el primer registro para la familia en América del Sur y el más joven y segundo registro para los Coraciiformes en el continente. Este, junto al gruido, constituyen miembros de clados de aves que estaban ampliamente distribuidos durante el Paleógeno y Neógeno, pero que hoy en día se restringen a modo de relicto en el Viejo Mundo y en Norteamérica. Su extinción de la región Neotropical es aún incierta. La presencia de al menos tres miembros diferentes de Tyranni, refuerza las hipótesis previas que sostienen una larga y compleja historia no solo para el subclado, sino para los Passeriformes en general en América del Sur.
Palabras clave: Aves, Mioceno temprano, provincia de Santa Cruz, Patagonia, Argentina.

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INTRODUCTION

The documentation of fossil birds in South America is still very poor and several clades entirely lack a single fossil record (Agnolín, 2016; Tonni, 1980; Tambussi and Degrange, 2013). Florentino Ameghino was the first paleontologist that systematically described fossil birds from South America, including Oligocene, Miocene, Pliocene, and Pleistocene birds (Ameghino, 1891, 1894, 1895, 1898, 1899). Particularly, from early Miocene Santa Cruz beds, Ameghino described a large number of taxa belonging to tinamids, rheids, anatids, anhimids, falconids, cathartids, gruiforms, cariamids, basal anseriforms, anhingids, and giant flightless phororhacoid and brontornithid birds (see the following and references therein: Agnolín, 2016; Degrange, 2022; Degrange *et al.*, 2012; Diederle and Noriega, 2020; Tambussi and Degrange, 2013; Tambussi and Noriega, 1996; Tonni, 1980). The Santacrucian birds, without any doubt, represent the most well-known paleornithological assemblage from the early-middle Miocene of the South American continent. However, most of the Cenozoic record of terrestrial birds in South America rests on the finding of very large birds that have hard and thick bones, such as anhingids, phororhacoids, and rheids, whereas other bird lineages which have more fragile bones are frequently known by isolated and incomplete specimens (Agnolín, 2016).

This paper aims to describe several remains of fossil birds coming from early-middle Miocene beds in Santa Cruz province, Argentina (Table 1; Figure 1).

These birds were collected during joint paleontological expeditions of the Museo Argentino de Ciencias Naturales and the State University of New York (Stony Brook) during the decade of the 1980s. The expeditions had the main goal of finding mammalian specimens, particularly primates (Bown and Fleagle, 1993; Bown and Larriestra, 1990; Bown *et al.*, 1988). The fossil bird collection described here was preliminarily (and partially) presented in a conference paper by Chiappe (1991), and later, the distal end of a passeriform humerus and a distal end of a tinamid tibiotarsus were described by Noriega and Chiappe (1993) and Bertelli and Chiappe (2005), respectively.

MATERIALS AND METHODS

The material reported here originates from two main fossiliferous sites. The first one is the "Monte Observación locality" at Monte León National Park, northwestern Santa Cruz province, Argentina. Monte Observación is a well-known fossiliferous locality, from which several fossil birds were previously described (Tonni, 1980; see Vizcaíno *et al.*, 2012). The specimens reported here come from beds of the Santa Cruz Formation (early-middle Miocene; see details in Fleagle *et al.*, 1995; Tauber 1997a,b; 1999).

Table 1. Bird specimens described here and their stratigraphical distribution.
Tabla 1. Especímenes aquí descriptos y su distribución estratigráfica.

Taxon/Stratigraphical unit	Pinturas Formation	Santa Cruz Formation
Mininothura talenki **nov. sp.**	X	
Peioa australis **nov. sp.**		X
Chainkanas koshon **nov. sp.**	X	
Kaikenia mourerchauvirea **nov. sp.**		X
Tamtamia yzurietai **nov. sp.**	X	
Phoenicopteriformes indet.	X	
Rallidae indet.	X	
Patagogrus olsoni **nov. sp.**	X	
Archaeopsophia aoni **nov. sp.**		X
Alhuenia eduardotonnii **nov. sp.**	X	
Caroohierax rapoporti **nov. sp.**	X	
Thegornis spivacowi **nov. sp.**	X	
Enskenia galeanoi **nov. sp.**	X	
Chehuenia facongrandei **nov. sp.**		X

The Loma de la Lluvia and Portezuelo Sumich fossil sites are located very close to the Río Pinturas, in northeastern Santa Cruz province (Bown and Larriestra, 1990). The fossil bird specimens reported here come from beds of the Pinturas Formation that outcrop on the site, and that are thought to be early-middle Miocene in age (Bown and Larriestra, 1990; Fleagle *et al.*, 1995). Despite some authors suggesting that the Pinturas Formation was coeval with the Santa Cruz Formation, radiometric dates suggest that Pinturas is definitively older (Ré *et al.*, 2010). As indicated by Fleagle *et al.* (2012) the lower and middle beds of Pinturas are certainly older than 16.9 Ma (perhaps 18.5 Ma at its base), whereas several localities further out from Pinturas lack a clear age constraint. The age of the Santa Cruz Formation base is debated, but the top of the unit extends up to 12.1 Ma (Fleagle *et al.*, 2012).

The environmental conditions prevailing during the deposition of the Pinturas and Santa Cruz Formations indicate a relatively warm, and humid climate with periodically drier conditions and open areas (see Vizcaíno *et al.*, 2012).

The osteological nomenclature employed by Baumel and Witmer (1993) is used here, but with terms in Latin translated to the English language. In the case of Anseriformes, the anatomical terminology of the humerus follows that employed by Hiroshige and Yoshikazu (2007), with modifications by Worthy (2009) and De Pietri *et al.* (2016). The Romerian terminology of "anterior" instead of dorsal or cranial and "posterior" instead of plantar or caudal is employed. In the case of the humerus, the margo dorsalis and margo ventralis (sensu Baumel and Witmer, 1993) these are regarded here as lateral and medial, respectively.

Institutional abbreviations. BMNH, Ameghino Collection, British Museum of Natural History, London, UK; MACN SC, Santa Cruz Collection, Vertebrate Paleontology Collection, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

SYSTEMATIC PALEONTOLOGY

PALAEOGNATHAE PYCRAFT, 1900

Tinamidae Huxley, 1872

Genus *Mininothura* **nov. gen.**

Diagnosis. Very small tinamid, smaller than members of the genus *Nothura* and diagnosable on the basis of the following unique combination of characters: 1- relatively wide and well-defined brachial fossa; 2- anterior articular ligament not raised and subcircular in contour; 3- ectepicondylar process not raised, forming a prominent and thickened lateral edge; and 4- ventral condyle distally extended and subequal in size to dorsal condyle.

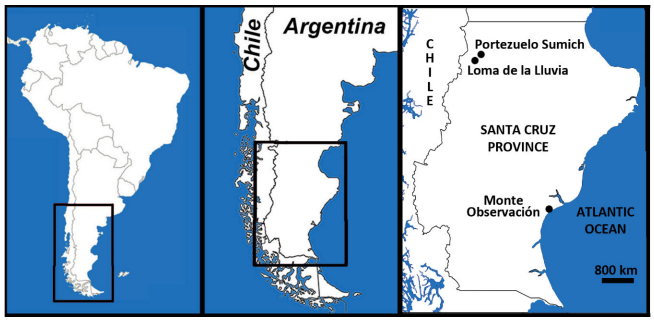

FIGURE 1. Map of southern Argentina Santa Cruz province, with the location of fossil sites mentioned in the text.

FIGURA 1. Mapa de la provincia de Santa Cruz, Argentina, con la ubicación de las localidades fosilíferas mencionadas en el texto.

Etymology. Mini, meaning small in Latin, *Nothura*, a tinamid genus.

Type and only known species. *Mininothura talenki* **nov. sp.**

Mininothura talenki **nov. sp**.

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 1429, incomplete distal end of left humerus (Figure 2 A-J).

Paratypes. MACN SC 1612, incomplete distal end of right humerus (Figure 2 K-O); MACN SC 1427, incomplete distal end of left humerus (Figure 2 P-R).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimens come from beds belonging to the Early-Middle Miocene Pinturas Formation.

Etymology. From the Aonikenk language, talen meaning small.

Description. The distal end of the humerus is notably transversely wide and anteroposteriorly flattened (17 milimeters of maximum transverse width).

The brachial fossa is nearly flat, with its lateral margin delimited by a narrow ridge and medially by a relatively low, rounded, and longitudinally extended shaft ridge. The fossa is relatively wide and ovoidal in contour. The flattened anterior surface of the humerus shows a wide and ovoidal-shaped flat surface proximal to the dorsal condyle, and a wide, flattened, and subcircular-shaped surface separating the ventral condyle from the dorsal condyle and from the facet of the anterior articular ligament.

The entepicondylar process is anteromedially oriented. It is proximally delimited by a small and well-defined pit for the *m. pronator superficialis*. Distal to this tubercle, the attachment of the anterior articular ligament is represented by a slightly raised and subcircular-shaped surface. The

surface for attachment of the *m. carpi ulnaris* is cup-shaped and relatively deep.

The ectepicondylar process is not prominent. It forms part of a thickened lateral ridge that delimits the distal margin of the humerus. This process is proximally placed with respect to the dorsal condyle.

The main axis of the ventral condyle is subequal to that of the dorsal condyle. A deep and wide intercondylar groove separates both condyles. The distal margin of the dorsal condyle is convex. The ventral condyle is strongly distally extended, it is rounded in shape and shows a laterally extended articular surface. The flexor process is subvertically oriented, it projects distally as far as the ventral condyle does.

In posterior view, the humerotricipital groove is excavated but with faintly defined margins. The olecranon fossa is deep but poorly defined.

Remarks. *Mininothura* shows a combination of characters present in tinamids, including the distal end of the humerus being transversely wide and anteroposteriorly flat, dorsal and ventral condyles subequal in size, poorly excavated brachial fossa, a wide and ovoidal-shaped flat surface proximal to the dorsal condyle, a wide, flattened, and subcircular-shaped surface separating the ventral condyle from the dorsal condyle and from the facet of the anterior articular ligament (see Bertelli, 2002, 2017; Bertelli and Chiappe, 2005; Bertelli *et al.*, 2014).

Extant tinamids are distributed in two main clades: Nothurinae or open-area tinamous, and Tinaminae or forest-dweeling tinamous (Bertelli, 2017; Bertelli and Chiappe, 2005; Bertelli *et al.*, 2014).

Mininothura shares with tinamines a rounded ectepicondylar process, a character that is synapomorphic of the clade (Bertelli and Chiappe, 2005). However, *Mininothura* is unique in the shape of the ectepicondylar process, which is represented by a poorly defined intumescense that is continuous with the lateral margin of the bone. Whether this condition is homologous to that of tinamines is far from certain, and thus, *Mininothura* is not assigned to any particular tinamid subclade.

The small size of the material may fall within the range of the genera *Nothura, Crypturellus, Nothoprocta* or *Taoniscus*, being much smaller than other tinamids (Cenizo *et al.*, 2012; Chandler, 2012). Comparisons with other tinamids reinforces the distinctiveness of *Mininothura*. In *Mininothura* the brachial fossa is obliquely oriented with respect to the axis of the bone shaft and is oval in contour, a morphology shared with *Tinamus*, *Eudromia*, *Tinamotis*, *Rhynchotus* and *Nothocercus*, and different from the crescent-shape observed in *Nothura, Nothoprocta* and *Peioa* (Bertelli *et al.*, 2014). The brachial fossa is more excavated than in other small tinamids, such as *Nothura* and *Nothoprocta*, resembling *Toaniscus* in this aspect (Bertelli *et al.*, 2014). The flexor process is relatively short, not extended beyond the ventral condyle, and very different from the elongate condition present in *Nothocercus, Taoniscus, Nothoprocta* and *Rhynchotus* (Bertelli *et al.*, 2014). *Mininothura* lacks the secondary process close to the supracondylar dorsal process observed in *Tinamus* and some *Crypturellus* species (Bertelli, 2002). The ventral condyle is proximally undercut, whereas in *Tinamus, Nothocercus, Crypturellus* and *Taoniscus* it is poorly delimited proximally (Cenizo *et al.*, 2012). The dorsal condyle is subequal in size to the ventral one, a condition shared with *Tinamotis* (Bertelli and Chiappe, 2005). The facet for the anterior articular ligament forms a shallow and well-differentiated subcircular concavity that differs from the less defined and shallower condition observed in *Tinamus, Nothocercus* and *Crypturellus* (Cenizo *et al.*, 2012).

Bertelli and Chiappe (2005) reported the distal end of tinamid humeri as coming from early-middle Miocene beds of the Santa Cruz Formation, in Santa Cruz province. The two specimens described by Bertelli and Chiappe (2005) belong to two closely related, but different species. These specimens can be clearly distinguished from *Mininothura* by having ventral condyle notably larger than the dorsal one, by the much smaller and shallow brachial fossa, and by a prominent ectepicondylar process. On this basis, it can be affirmed that at least three different small-sized and one large tinamid were present in Santa Cruz province during early-middle Miocene times.

Anseriformes Wagler, 1831

Genus *Peioa* **nov. gen.**

Diagnosis. Medium-sized anseriform, having the following unique combination of characters: 1- brachial fossa crescent-shaped, well-defined, and notably narrow; 2- brachial fossa obliquely oriented, with its distal third subvertically oriented, very close and subparallel to the medial edge of the shaft; 3- surface for the anterior articular ligament anteriorly protrudent and distally facing; 4- ectepicondylar process prominent, but located distal to the proximal level of the dorsal condyle; and 5- humerotricipital groove well-defined and delimited by relatively sharp ridges.

Etymology. Peio, from the Aonikenk language, meaning hen.

Type and only known species. *Peioa australis* **nov. sp.**

Peioa australis **nov. sp.**

Diagnosis. The same as for genus by monotypy.

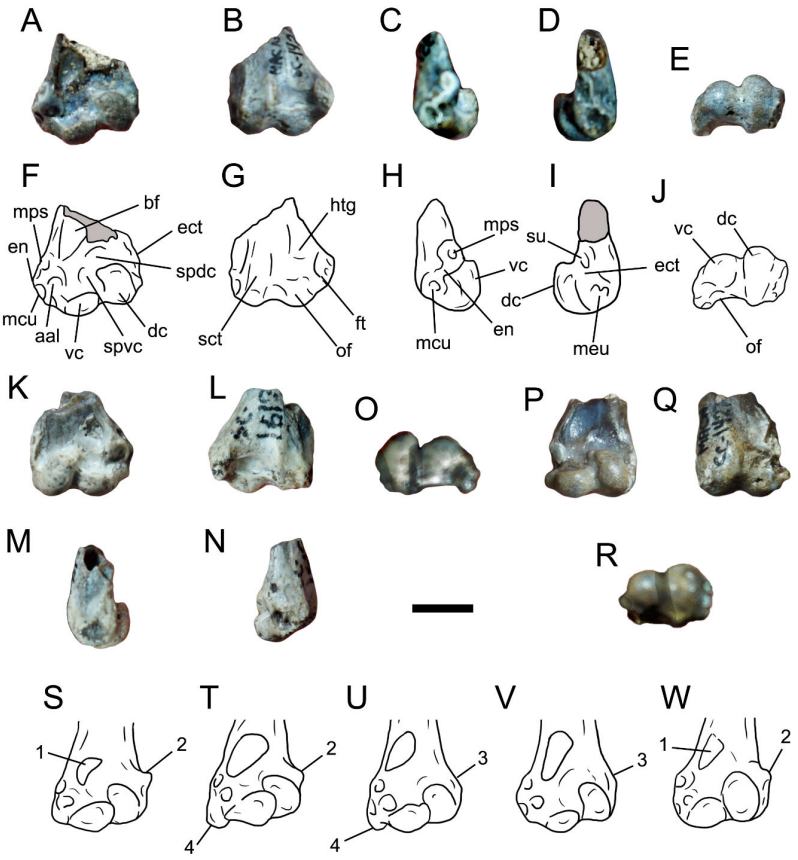

FIGURE 2. *Mininothura talenki* A-J, incomplete distal end of left humerus (MACN SC 1429, holotype) in A,F, anterior; B,G, posterior; C,H, medial; D,I, lateral; and E,J, distal views; K-O, incomplete distal end of right humerus (MACN SC 1612, paratype) in K, anterior; L, posterior; M, lateral; N, medial; and O, lateral views; P-R, incomplete distal end of left humerus (MACN SC 1427, paratype) in P, anterior; Q, posterior; and R, distal views. S-W, distal end of left humerus of selected tinamids in anterior view; S, *Crypturellus tataupa*; T, *Nothoprocta cinerascens*; U, *Tinamotis pentlandii*; V, *Mininothura talenki*; and W, *Eudromia elegans*. Abbreviations. aal, attachment for the anterior articular ligament; bf, brachial fossa; dc, dorsal condyle; ect, ectepicondylar process; en, entepicondylar process; ft, flexor tubercle; htg, humerotricipital groove; mcu, attachment of the *m. carpi ulnaris*; meu, surface for the *m. ectepicondyloulnaris*; mps, pit for the *m. pronator superficialis*; of, olecranal fossa; sct, scapulotricipital groove; spdc, flat surface proximal to the dorsal condyle; spvc, flat surface proximal to the ventral condyle; su, surface for the *m. supinator*; vc, ventral condyle. Remarkable diagnostic features of selected tinamids: 1, small and crescent-shaped brachial fossa; 2, well-developed and prominent ectepicondylar process; 3, small and rounded ectepicondylar process; 4, distally extended and prominent flexor process. Scale bar: A-R, 5 mm; S-W, not to scale.

FIGURA 2. *Mininothura talenki* A-J, extremo distal incompleto de húmero izquierdo (MACN SC 1429, holotipo) en vistas A,F, anterior; B,G, posterior; C,H, medial; D,I, lateral; y E,J, distal; K-O, extremo distal incompleto de húmero derecho (MACN SC 1612, paratipo) en vistas K, anterior; L, posterior; M, lateral; N, medial; y O, lateral; P-R, extremo distal incompleto de húmero izquierdo (MACN SC 1427, paratipo) en vistas P, anterior; Q, posterior; y R, distal. S-W, extremo distal del húmero izquierdo de algunos tinámidos en vista anterior; S, *Crypturellus tataupa*; T, *Nothoprocta cinerascens*; U, *Tinamotis pentlandii*; V, *Mininothura talenki*; and W, *Eudromia elegans*. Abreviaturas. aal, superficie para el ligamento articular anterior; bf, fosa braquial; dc, cóndilo dorsal; ect, proceso ectepicondilar; en, proceso entepicondilar; ft, tubérculo flexor; htg, surco húmerotricipital; mcu, superficie para el *m. carpi ulnaris*; meu, superficie para el *m. ectepicondyloulnaris*; mps, excavación para el *m. pronator superficialis*; of, fosa olecraneana; sct, surco escápulotricipital; spdc, superficie plana proximal al cóndilo dorsal; spvc, superficie plana proximal al cóndilo ventral; su, superficie para el *m. supinator*; vc, cóndilo ventral. Características remarcables de algunos tinámidos: 1, fosa braquial pequeña y en forma de media luna; 2, proceso ectepicondilar bien desarrollado y prominente; 3, proceso ectepicondilar pequeño y redondeado; 4, proceso flexor extendido distalmente y prominente. Escala: A-R, 5 mm; S-W, No a escala.

Holotype. MACN SC 1452, distal half of right humerus (Figure 3).

Locality and horizon. The specimen comes from the Santa Cruz Formation (Early-Middle Miocene), at the well-known fossiliferous locality of Monte Observación (the label indicates "Estaca 29"), Monte León National Park, Santa Cruz province, Argentina.

Etymology. Australis, from the Latin language, meaning southern.

Description. The distal end of the humerus is notably transversely wide and anteroposteriorly flattened (13 milimeters of maximum transverse width).

The fossa for the *musculus brachialis* is relatively shallow, but well-defined. The fossa is crescent-shaped in contour and obliquely oriented, with its distal third oriented subparallel to the medial margin of the bone shaft. The anterior surface of the humerus shows a wide and ovoidal-shaped flat surface proximal to the dorsal condyle, and a wide, flattened, and subcircular-shaped surface separating ventral condyle from dorsal condyle and from the facet of the anterior articular ligament.

The entepicondylar process is medially oriented and proximally delimited by a relatively shallow *m. pronator superficialis*. Distally, it shows a well defined and deep fossa for the *m. carpi ulnaris*. Anterodistal to this tubercle, the attachment of the anterior articular ligament is represented by a well-raised, subcircular-shaped, and distally oriented surface.

The ectepicondylar process is not prominent and is rounded. It is distally located, close to the mid-height of the dorsal condyle.

The main axis of the ventral condyle is shorter than that of the dorsal one. A deep and wide intercondylar groove separates both condyles. The distal margin of the dorsal condyle is convex. The flexor process is subvertically oriented, it projects distally as far as the ventral condyle.

In the posterior view, the humerotricipital groove is well-defined, excavated and delimited by subvertically oriented ridges. It is notably proximally extended. The olecranon fossa is deep and well-defined. The scapulotricipital groove is wide, relatively deep and well-defined, delimited by narrow longitudinal ridges.

Remarks. *Peioa australis* **nov. sp.** shows a combination of characters that indicate anseriform affinities: a low ectepicondylar process, a flattened entepicondyle with subparallel, well-defined, and oval pits for the *m. carpi ulnaris* and *m. pronator superficial*, and an ectepicondylar process with subparallel, well-defined, and oval pits for the *m. carpi radialis* and *lig. collateral* fossa (Worthy *et al.*, 2022). In spite of being clearly anseriform, the morphology of *Peioa* is very different from most ducks and geese.

The distal end of the humerus in *Peioa* **nov. gen.** is remarkable in being transversely expanded, anteroposteriorly compressed, with a very small and poorly excavated *musculus brachialis antiquus* impression, and the shaft poorly differentiated from the distal end of the bone (Woolfenden 1961, Olson 1999; Cenizo and Agnolín, 2010), similar to the condition observed in the basal anseriforms *Conflicto*, *Anseranas* and *Anatalavis* (Olson 1999; Tambussi *et al.*, 2019; Worthy *et al.*, 2022). However, *Peioa* clearly differs from the later taxa in some anatomical details. In *Peioa* the surface for the anterior articular ligament is anteriorly protrudent and distally facing, it is transversely wide and proximodistally low. In contrast, in *Conflicto, Anatalavis* and *Anseranas,* this surface is not prominent and ovoidal in contour, being more proximodistally tall than transversely wide. The flexor process in *Peioa* is much more distally extended than in *Anatalavis* and *Anseranas,* and the brachial fossa is smaller. In *Peioa* the ectepicondylar process is prominent, but is located distal to the proximal level of the dorsal condyle, whereas in *Anatalavis* and *Anseranas* it is located more proximally (Olson, 1999). In contrast to *Anseranas* and reminiscent to *Anatalavis*, in *Peioa* the olecranal and humerotricipital fossae are deep and well-defined (Olson, 1999). The shape of the brachial fossa in *Peioa* clearly differs from that of *Anatalavis* and *Anseranas*.

Eutelornis patagonicus was described by Ameghino (1894) based on associated distal radius, distal humerus and partial tibiotarsus from the Santa Cruz Formation, in Santa Cruz province, Argentina. Ameghino regarded *Eutelornis* as an anseriform of uncertain affinities. Later, because of its plesiomorphic-looking aspect, Cenizo and Agnolín (2010) indicated that it was a very basal anseriform of uncertain affinities, probably related to Anseranatidae.

Eutelornis is somewhat reminiscent to *Peioa* in having the distal end notably flattened, the brachial fossa not strongly excavated and crescent-shaped, and its distal end subvertically oriented and subparallel to the medial margin of the humeral shaft. Furthermore, it shows a very large ventral condyle, a condition similar to that of palaeognathous tinamids (Bertelli and Chiappe, 2005). *Peioa* differs from *Eutelornis* in having a smaller ventral condyle, in having a rounded and not prominent supracondylar process that is more distally positioned, and in having well-defined humerotricipital groove and ridges.

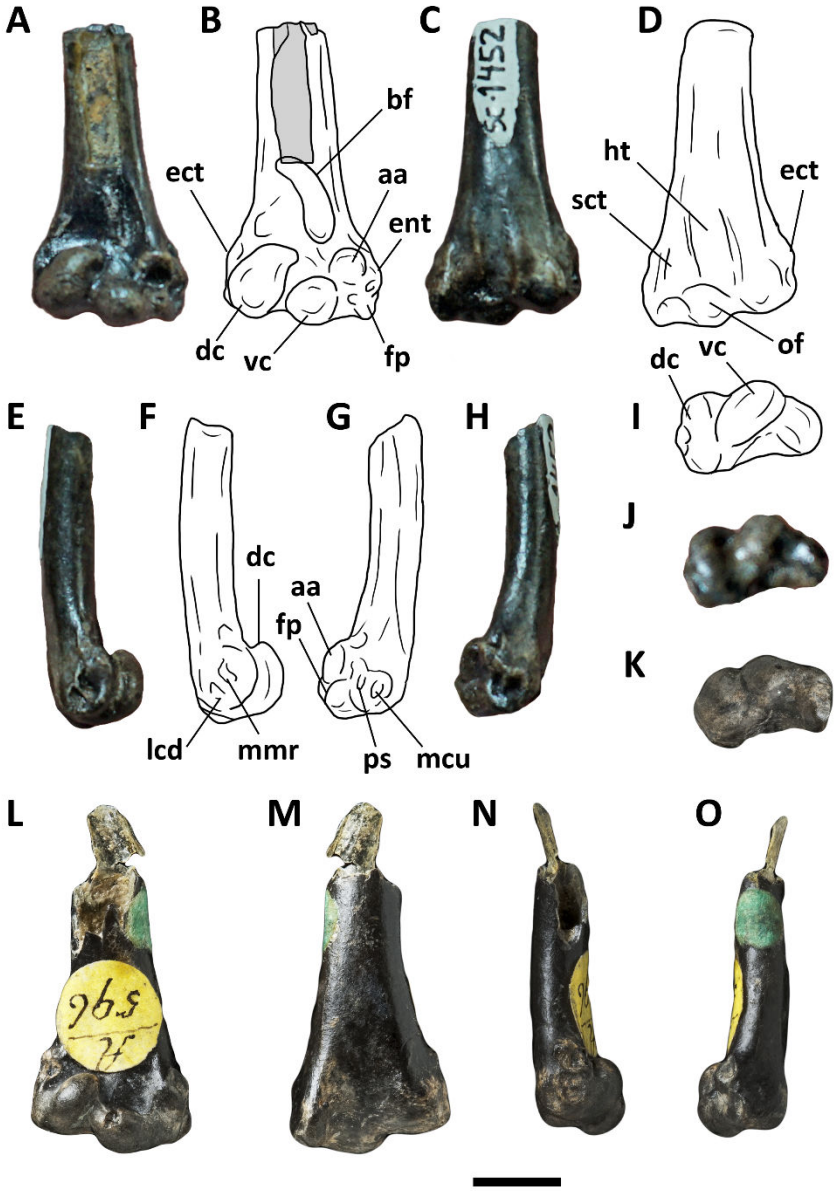

FIGURE 3. A-J, *Peioa australis*, distal half of right humerus (MACN SC 1452, holotype) in A-B, anterior; C-D, posterior; E-F, medial; G-H, lateral; and I-J, distal views. K-O, *Eutelornis patagonicus*, distal half of right humerus (BMNH A-596, holotype) in K, distal; L, anterior; M, posterior; N, medial; and O, lateral views. Abbreviations. aa, surface for the anterior articular ligament; bf, brachial fossa; ect, ectepicondylar process; ent, entepicondylar process; fp, flexor process; ht, humerotricipital groove; lcd, scar of the dorsal collateral ligament; mcu, scar for the m. carpi ulnaris; mmr, scar for the m. metacarpi radialis; of, olecranon fossa; ps, scar for the pronator superficial; sct, scapulotricipital groove. Eroded areas shaded in grey. Scale bar 1 cm. Photographs K-O, courtesy of Sandra Chapman (BMNH) and Jorge Noriega. Scale bar 5 mm.

FIGURA 3. A-J, *Peioa australis*, extremo distal de húmero derecho (MACN SC 1452, holotipo) em vistas A-B, anterior; C-D, posterior; E-F, medial; G-H, lateral; y I-J, distal. K-O, *Eutelornis patagonicus*, mitad distal de húmero derecho (BMNH A-596, holotipo) en vistas K, distal; L, anterior; M, posterior; N, medial; y O, lateral. Abreviaturas. aa, superficie para el ligamento articular anterior; bf, fosa braquial; dc, cóndilo dorsal; ect, proceso ectepicondilar; en, proceso entepicondilar; fp, tubérculo flexor; ht, surco húmerotricipital; lcd, cicariz para el ligamento colateral dorsal; mcu, superficie para el *m. carpi ulnaris*; mmr, superficie para el *m. metacarpi radialis*; of, fosa olecraneana; ps, excavación para el *m. pronator superficialis*; sct, surco escápulotricipital. Áreas deterioradas sombreadas en gris. Fotografías K-O, cortesía de Sandra Chapman (BMNH) y Jorge Noriega. Barra de escala 5 mm.

Based on the presence of a large number of common morphological attributes, it is probable that *Peioa* and *Eutelornis* may form a clade of basal anseriforms.

Anhimidae Stejneger, 1885

Genus *Chainkanas* **nov. gen.**

Diagnosis. Large anseriform diagnosed on the basis of the following combination of characters: 1- procoracoid extensive and dorsally hooked (shorter and not dorsally tilted in *Chauna, Anhima* and *Chaunoides*); 2- humeral facet strongly medially tilted (not tilted in *Chauna, Anhima* and *Chaunoides*); 3- humeral facet nearly reaching the level of the distal end of the scapular facet (more proximally placed in *Chauna, Anhima* and *Chaunoides*); 4- scapular facet subcircular in contour and deeply excavated, and slightly distally oriented (strongly laterally oriented in *Chauna, Chaunoides* and *Anhima*); and 5- acrocoracoid process elongated (shared with *Chaunoides*; much wider and stouter in *Chauna* and *Anhima*).

Etymology. Chaink, meaning large in Aonikenk language; anas, meaning duck in Latin.

Type and only known species. *Chainkanas koshon* **nov. sp.**

Chainkanas koshon **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 3306, right coracoid with incomplete distal end (Figure 4).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Etymology. Koshon, from the Aonikenk language meaning scream; members of the family Anhimidae are popularly known as "screamers" in English language.

Description. Relatively elongate coracoid, especially the acrocoracoid process (68 millimeters of maximum preserved length). Poorly excavated triosseal concavity, with well-defined margins. Ventral fossa deep and well-defined. The scapular facet is deeply excavated, subcircular in contour, and with well-raised margins. It is distolaterally oriented, and is connected with the acrocoracoid by menas of a thick and rounded ridge. The humeral facet is roughly ovoidal in contour. It distally extends for almost three quarters the proximodistal height of the scapular facet. It is strongly medially tilted and, consequently, its lateral exposure is relatively narrow. Its margins are delimited by a very narrow, but well-raised minute ridge. Procoracoid process prominent and thick, strongly proximally curved and hook-like. The base of this process shows an ellipsoidal-shaped and relatively wide procoracoid foramen.

The coracoid body is transversely wide and shows a nearly flat lateral surface that is only interrupted by obliquely oriented muscle scars. The distal end preserves the margin that delimited a very large distal pneumatic foramen.

Remarks. *Chainkanas* **nov. gen.** can be included among anhimids by having very large size, robust coracoid with a large procoracoid process, procoracoid foramen extensive and ellipsoidal in contour, and the presence of a large pneumatic foramen at its distal end (Alvarenga, 1999). As indicated in the diagnosis, *Chainkanas* can be clearly distinguished by other extant and extinct anhimids, especially by its procoracoid shape. Among anhimids, it is more similar to the Oligocene genus *Chaunoides* from Brazil than to extant genera *Anhima* and *Chauna*, by having a relatively elongate coracoid, narrow acrocoracoid process, and very wide and deep scapular fossa (Alvarenga, 1999).

Loxornis clivus is a bird species based on a distal tibiotarsus with eroded distal condyles coming from the Deseadan beds (Oligocene) of Santa Cruz province. The only known specimen. It was originally described by Ameghino (1895) as an uncertain anseriform (Tonni, 1980), and more recently it was regarded as a possible anhimid by Alvarenga (1999; see Cenizo and Agnolín, 2010). Because *Loxornis* and *Chainkanas* are based on different materials, a direct comparison between them is not possible. However, it should be pointed out, that both come from distant stratigraphical units that show strong faunal differences. Furthermore, as pointed out by Alvarenga (1999) the phylogenetic position of *Loxornis* is not clear, and it is not entirely certain that it belongs to Anhimidae.

Anatidae Leach, 1820

Tadorninae Reichenbach, 1850

Genus *Kaikenia* **nov. gen.**

Diagnosis. Relatively large anatid, very similar in size and shape to *Miotadorna*, having the following unique combination of characters: 1- lateral margin of the shaft nearly straight; 2- attachment of the pronator muscle distally located with respect to the proximal margin of the anterior articular ligamental facet (at the same level in remaining tadornines; Worthy *et al.*, 2009); 3- scapulotricipital groove deep, but does not extend around the distal end of the bone (in contrast to remaining tadornines; Worthy *et al.*, 2009); 4- flexor process poorly extended distally; and 5- olecranal fossa in distal view, laterally delimited by a thick ridge.

Etymology. Kaiken, meaning members of the goose genus *Chloephaga* in Aonikenk language.

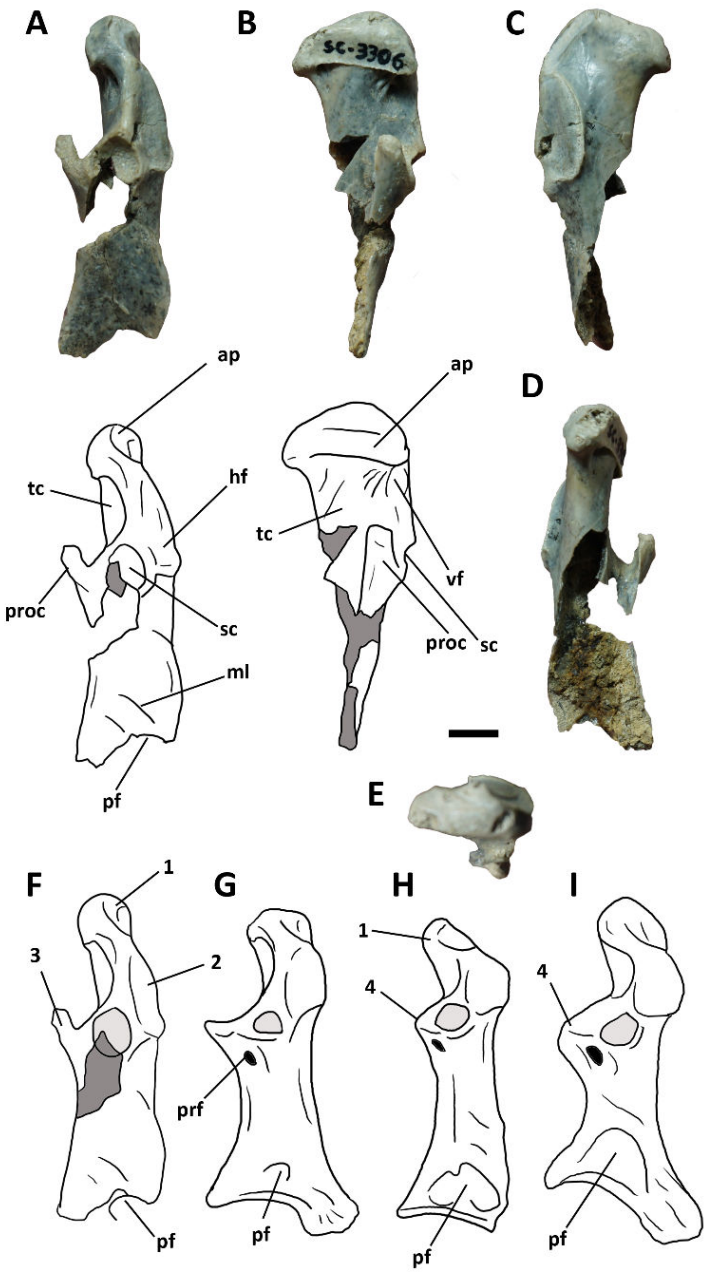

FIGURE 4. *Chainkanas koshon* (MACN SC 3306, holotype), right coracoid lacking distal end in A, dorsal; B, medial; C, lateral; D, ventral; and E, proximal views. F-I, coracoid of selected anhimids in dorsal view: F, *Chainkanas koshon*; G, *Anhima cornuta*; H, *Chaunoides antiquus*; I, *Chauna torquata*. Abbreviations. ap, acrocoracoid process; hf, humeral facet; ml, muscular line; pf, pneumatic foramen; prf, procoracoid foramen; proc, procoracoid process; sc, scapular facet; tc, triosseal canal; vf, ventral fossa. 1, relatively narrow acrocoracoid; 2, medially tilted humeral facet; 3, hooked procoracoid process; 4, thickened and short procoracoid process. Scale bar: A-E, 1 cm; F-I, not to scale. G-I, redrawn from Alvarenga (1999) and personal inspection of specimens.

FIGURA 4. *Chainkanas koshon* (MACN SC 3306, holotipo), coracoides derecho carente del extremo distal en vistas A, dorsal; B, medial; C, lateral; D, ventral; y E, proximal. F-I, coracoides de algunos anhímidos en vista dorsal: F, *Chainkanas koshon*; G, *Anhima cornuta*; H, *Chaunoides antiquus*; I, *Chauna torquata*. Abreviaturas. ap, proceso acrocoracoideo; hf, faceta humeral; ml, línea muscular; pf, foramen neumático; prf, foramen procoracoideo; proc, proceso procoracoideo; sc, faceta escapular; tc, canal trióseo; vf, fosa ventral. 1, acrocoracoides relativamente estrecho; 2, faceta humeral inclinada medialmente; 3, proceso procoracoideo en forma de gancho; 4, proceso procoracoideo corto y grueso. Barra de escala: A-E, 1 cm; F-I, no a escala. F-I, redibujado de Alvarenga (1999) e inspección personal de los especímenes.

Type and only included species. *Kaikenia mourerchauvirea* **nov. sp.**

Kaikenia mourerchauvirea **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 4506, right humerus lacking its proximal third (Figure 5).

Locality and horizon. The specimen comes from the Santa Cruz Formation (Early-Middle Miocene), at the well-known fossiliferous locality of Monte Observación (the label of the specimen indicates "Estaca 7"), Monte León National Park, Santa Cruz province, Argentina. Collected in 1991.

Referred material. MACN SC 3431, proximal end of left carpometacarpus (Figure 6).

Locality and horizon. The referred specimen comes from the Santa Cruz Formation (Early-Middle Miocene), Monte Observación locality, Monte León National Park, Santa Cruz province, Argentina.

Etymology. The specific epithet honors Cécile Mourer-Chauviré, a leading paleontologist from France, who greatly contributed to our current knowledge on palaeornithology.

Description. Kaikenia nov. gen. is a relatively large anatid, the size of *Chloephaga*, but having more gracile proportions (20 millimeters of maximum distal width). The preserved shaft indicates that the humerus was narrow and with nearly straight lateral and medial margins, lacking the remarkable sigmoid curvature present in some genera such as *Anabernicula* and *Tadorna* (Howard, 1964).

The anterior surface of the shaft is nearly flat, with an ellipsoidal-shaped but shallow and poorly defined brachial fossa. This fossa is proximally placed, and its distal end does not reach the level of the proximal end of the ectepicondylar prominence. This latter prominence is well-defined but proximodistally low and shows a well defined concavity for attachment of the dorsal collateral ligament. The facet of the attachment for the anterior articular ligament is very wide and not well-raised from the surface surrounding it. The surface for the attachment of the *m. carpi ulnaris* is very deep, prominent, and distally located. The flexor process is poorly distally extended and is level with the distal margin of the dorsal condyle.

Dorsal and ventral condyles are prominent and well-defined, the latter being smaller than the former, and ovoidal in contour.

In posterior view the olecranal fossa is shallow and is not dorsally delimited by a subhorizontally oriented ridge. The scapulotricipital groove is well defined but shallow and does not extend around the distal end of the bone.

In distal view the olecranal fossa is delimited along its lateral margin by a thick ridge. This ridge is continuous with the distal edge of the dorsal condyle extending posteriorly and ending in a subtriangular bump.

The proximal end of the carpometacarpus is referred to *Kaikenia* because of its size and corresponding characteristics. It shows a shallow infratrochlear fossa and relatively deep anterior and cuneiform fossae. The posterior fossa is notably deep and forms a strong notch at the base of the carpal trochlea. The proximal synostosis is proximodistally short. The minor metacarpal is medially grooved.

Remarks. *Kaikenia* **nov. gen.** may be referred to Tadorninae on the basis of the following combination of characteristics: tendence to narrowing of the humeral shaft, distinct ectepicondylar prominence and scapulotricipital groove, distal margin of flexor process level with distal margin of dorsal condyle, and shallow brachial fossa (Worthy, 2009; Worthy *et al.*, 2007).

Its large size easily distinguishes *Kaikenia* from several small tadornines, such as *Nannonetta, Pleistoanser* and *Anabernicula*. The North America Pleistocene genus *Brantadorna* lacks overlaping material with *Kaikenia*, and thus, comparisons are not possible (Howard, 1963).

Kaikenia differs from members of the genera *Chloephaga, Neochen, Anabernicula, Australotadorna, Pleistoanser* and *Alopochen* in having a straight shafted and narrow humerus, with poorly developed flexor tubercle, and much less prominent ectepicondylar prominence (see Agnolín, 2006a; Howard, 1964; Worthy, 2009). In these features, *Kaikenia* resembles tadorninines of the genera *Tadorna* and *Miotadorna*. However, it differs from both by having a prominent entepicondylar process and the attachment for the *m. carpi ulnaris* very deep and medially oriented (Worthy *et al.*, 2007). Particularly, *Kaikenia* is similar in shape and development of the ectepicondylar process, flexor process, and facet for the anterior articular attachment to the extinct Miocene genus *Miotadorna* (Worthy and Lee, 2008; Worthy *et al.*, 2007). However, it differs in several important anatomical features (as indicated above), including a shallower brachial fossa (distally very deep in *Miotadorna*, *Alopochen* and *Australotadorna*; Worthy, 2009) and having a poorly distally oriented flexor process (Worthy *et al.*, 2007). A feature that occurs in *Kaikenia*, that is unknown in other tardornines, is the presence in distal view of a ridge that delimits the olecranal fossa. This feature may be regarded as autapomorphic of *Kaikenia*.

Teleornis impressus is an anatid named by Ameghino 1899 on the basis of an incomplete forelimb coming from Deseadan Oligocene beds at Santa Cruz province. *Teleornis* was later considered as belonging to Tadorninae (Agnolín, 2004). *Kaikenia* differs from *Teleornis* in being much larger and in having the distal end of the bone transversely wider and more anteroposteriorly flattened.

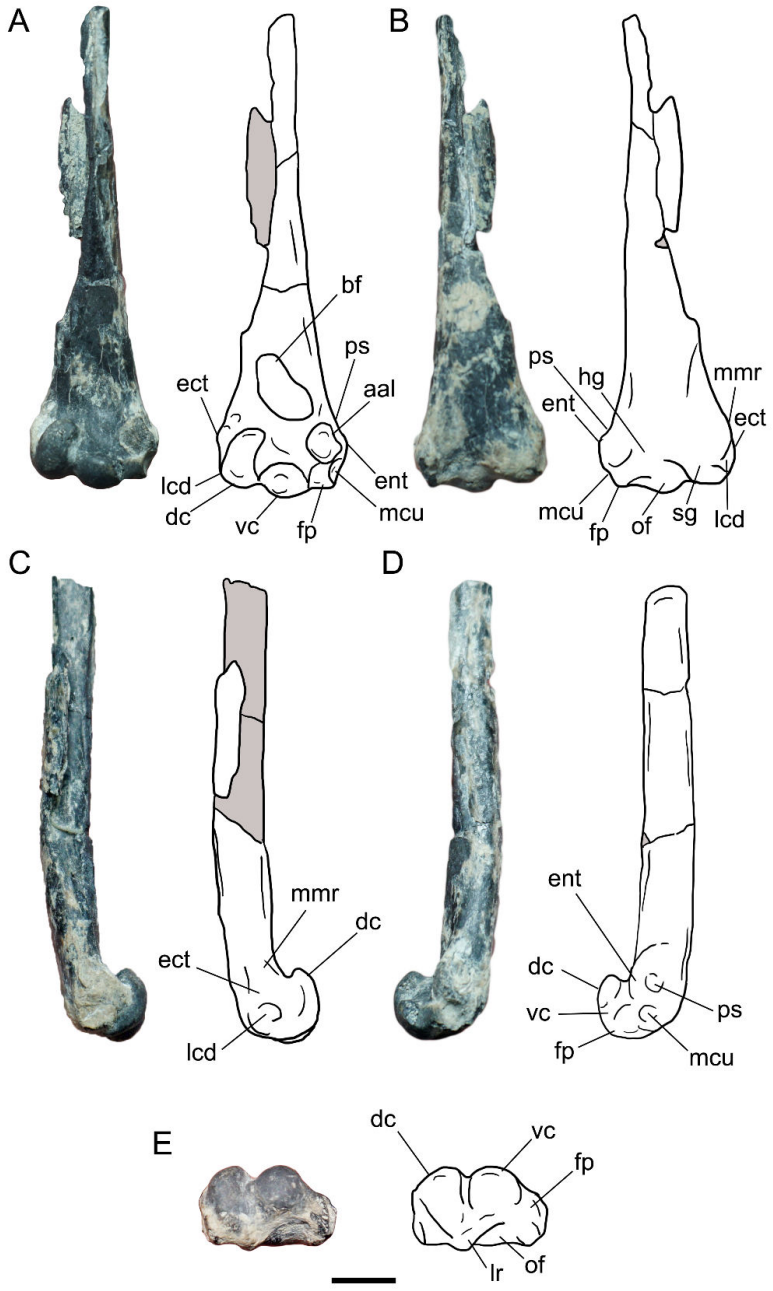

FIGURE 5. *Kaikenia mourerchauvirea* A-E, right humerus lacking proximal end (MACN SC 4506, holotype) in A, anterior; B, posterior; C, lateral; D, medial; and E, distal views. Abbreviations. aal, surface for the anterior articular ligament; bf, brachial fossa; ect, ectepicondylar process; ent, entepicondylar process; fp, flexor process; hg, humerotricipital groove; lcd, scar of the dorsal collateral ligament; lr, lateral ridge; mcu, scar for the m. carpi ulnaris; mmr, scar for the m. metacarpi radialis; of, olecranon fossa; ps, scar for the pronator superficial; sg, scapulotricipital groove. Scale bar 1 cm.

FIGURA 5. *Kaikenia mourerchauvirea* A-E, húmero derecho sin el extremo proximal (MACN SC 4506, holotipo) en vistas A, anterior; B, posterior; C, lateral; D, medial; y E, distal. Abreviaturas. aal, superficie para el ligamento articular anterior; bf, fosa braquial; ect, proceso ectepicondilar; ent, proceso entepicondilar; fp, proceso flexor; hg, surco humerotricipital; lcd, superficie para el ligamento colateral dorsal; lr, cresta lateral; mcu, superficie para el m. carpi ulnaris; mmr, superficie para el m. metacarpi radialis; of, fosa olecraneana; ps, superficie para el pronador superficial; sg, surco escápulotricipital. Barra de escala: 1 cm.

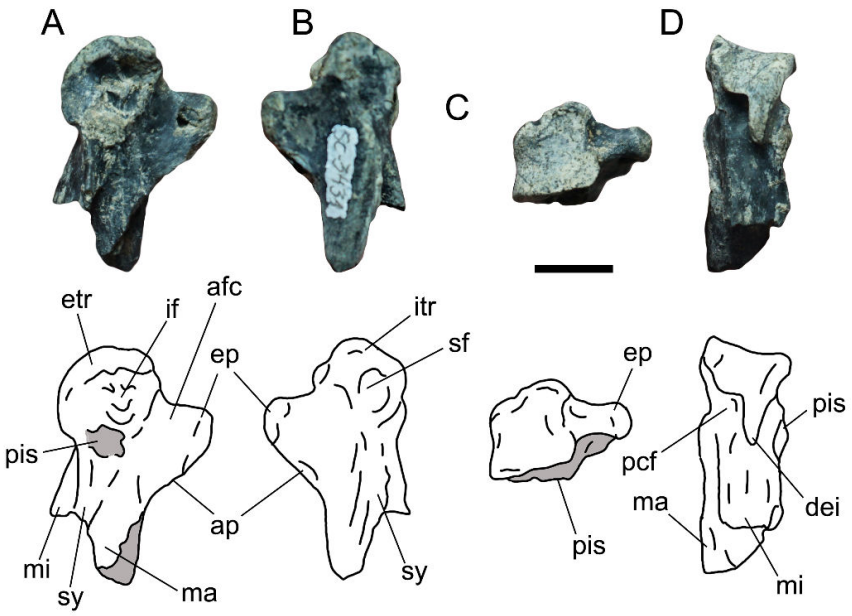

Figure 6. *Kaikenia mourerchauvirea* A-D, proximal end of left carpometacarpus (MACN SC 3431, referred material), A, medial; B, lateral; C, proximal; and D, posterior views. Eroded areas shaded in grey. Abbreviations. afc, anterior carpal fossa; ap, alular process; dei, distal extension of medial rim of carpal trochlea; ep, extensor process; etr, external carpal trochlea; if, infratrochlear fossa; ma, major metacarpal; mi, minor metacarpal; pcf, posterior carpal fossa; pis, pisiform process; sf, supratrochlear fossa; sy, proximal synostosis. Scale bar: 1 cm.

Figura 6. *Kaikenia mourerchauvirea* A-D, extremo proximal de carpometacarpo izquierdo (MACN SC 3431, material referido), en vistas A, medial; B, lateral; C, proximal; y D, posterior. Areas deterioradas sombreadas en gris. Abreviaturas. afc, fosa carpal anterior; ap, proceso alular; dei, extensión distal del anillo medial de la tróclea carpal; ep, proceso extensor; etr, tróclea carpal externa; if, fosa infratroclear; ma, metacarpal mayor; mi, metacarpal menor; pcf, fosa carpal posterior; pis, proceso pisiformes; sf, fosa supratroclear; sy, sinostosos proximal. Barra de escala: 1 cm.

Furthermore, *Kaikenia* differs in having a much thicker and less distally extended flexor process, and by the shallower humerotricipital groove.

Genus *Tamtamia* **nov. gen.**

Diagnosis. Mid-sized and relatively gracile tadornine diagnosable on the basis of the following combination of characteristics: distal end of humerus: 1- very low ectepicondylar prominence that is distally located level with the dorsal margin of the dorsal condyle; 2- very prominent and large attachment for the anterior articular ligament, which is very prominent and medially displaced; 3- attachment for the anterior articular ligament ventrally delimited by a strongly concave fossa for the *m. carpi ulnaris*; 4- small flexor process that is not distally extended and is located close to the dorsal margin of the ventral condyle; proximal end of humerus: 5- transversely expanded and anteroposteriorly flattened; 6- shallow pneumotricipital fossa; 7- ventral pneumotricipital fossa pneumatic, and delimited by lateral and well-raised ridge (dorsal crus commune); 8- bicipital crest extensive and strongly flared; and 9- capital ridge located between the humeral head and the dorsal tubercle.

Etymology. Támtam, meaning female members of the goose genus *Chloephaga* in Aonikenk language.

Type and only included species. *Tamtamia yzurietai* **nov. sp.**

Tamtamia yzurietai **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 4507, distal end of right humerus and proximal end of left humerus from the same individual (Figure 7 A-E, I-M).

Paratypes. MACN SC, 4508, distal end of left humerus (Figure 7 N-R); MACN SC 3309, proximal end of right humerus (Figure 7 F-H).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Etymology. Yzurietai, honouring the naturalist, birdwatcher and artist Dario Yzurieta (1931-1996). Together with "Tito" Narosky they published the most useful Bird Guide Identification of the Neotropics. Due to their conjoined efforts, hundreds

of young people become birdwatchers (including the author of the present contribution).

Description. *Tamtamia* **nov. gen.** is a relatively gracile tadornine (maximum transverse width of proximal end 14 milimeters; maximum transverse width of distal end 12 milimeters). The preserved shaft of humerus indicates that it was narrow and with nearly straight lateral and medial margins, lacking the strong sigmoid curvature present in some genera such as *Anabernicula, Australotadorna* and *Tadorna* (Howard, 1964; Worthy, 2009).

The ventral pneumotricipital fossa is relatively wide and deep. Despite being partially covered by matrix, it is clear that it was pneumatized. It is strongly medially extended along a flat surface formed by the bicipital crest. It is laterally delimited by the dorsal crus commune which extends distally as a ridge. The ventral tubercle is subtriangular in contour and relatively low. It is laterally delimited by a very wide and deeply excavated capital groove. The dorsal pneumotricipital fossa is wide and deep. The humeral head is relatively low and not very prominent; it is well-separated from the dorsal tubercle by a concavity. The capital ridge is prominent and is located between the humeral head and the dorsal tubercle. The dorsal tubercle is very wide, proximally extended and notably prominent. The deltopectoral crest is incomplete, but its surface is notably concave in posterior view.

In anterior view, the transverse ligamental groove is represented by a shallow and poorly defined excavation that distally delimits the humeral head.

The anterior surface of the shaft shows a well-defined and ellipsoidal shaped brachial fossa which deepens towards its disto-medial margin. This fossa is proximally placed, and its distal end does not reach the level of the proximal end of the ectepicondylar prominence. This prominence is well-defined, distally located (at the same level as the dorsal margin of the dorsal condyle) and is mound-shaped in anterior view. It shows a well-defined concavity for the attachment of the *m. pronator superficialis*. The facet for the attachment of the anterior articular ligament is very wide and very well-raised from the surface surrounding it. It is anterodistally oriented. It is strongly medially located and is far from the medial margin of the ventral condyle. It is ventrally delimited by a very deep and wide *m. carpi ulnaris* fossa. The flexor process is poorly developed and slightly extended distally, being close to the proximal margin of the ventral condyle.

Dorsal and ventral condyles are prominent and well-defined. The latter is much smaller than the former, ovoidal in contour, and is subhorizontally oriented.

In posterior view the olecranal fossa is well-excavated and dorsally delimited by a subhorizontally oriented ridge. The scapulotricipital and humerotricipital grooves are relatively wide and shallow.

Remarks. The distal end of the humerus of *Tamtamia* **nov. gen.** is very different from basal forms such as anseranatids, anhimids, dendrocygnines and romainvilliines by being anteroposteriorly thicker and transversely narrow, and by the poorly excavated distal end of the bone proximal to the ventral and dorsal condyles (Agnolín and Tomassini, 2012; Mayr, 2008).

Tamtamia is assigned to Tadorninae on the basis of the following combination of characteristics: prominent capital shaft ridge located close to the level of the dorsal tubercle, elevated and elongate dorsal tubercle, dorsal pneumotricipital fossa narrow and not strongly excavated under the humeral head, large ventral pneumotricipital fossa, deltoid crest concave in posterior view, and strongly raised and distally oriented facet for the anterior articular ligament (Woolfenden, 1961; Worthy, 2009).

Tamtamia differs from *Chloephaga* in that it lacks the very weak capital ridge and the shaft compression adjacent to the angle of the deltoid crest, but well rounded from there, a condition unique to this genus (Worthy, 2009). It also differs in the more proximodistally narrow and less prominent humeral head. It differs from Pleistocene *Anabernicula, Pleistoanser* and *Nannonetta* in the poorly distally extended flexor process and in the distally positioned ectepicondylar prominence, among several other anatomical details (Agnolín, 2006a; Howard, 1964). From *Neochen*, *Alopochen* and *Brantadorna* it differs in the much more gracile proportions, narrower shaft, and smaller and less prominent humeral head (see Howard, 1963; Short, 1970). It differs from *Australotadorna* in having a more gracile construction, with a less prominent humeral head, ventral pneumotricipital fossa delimited by a ridge, and rounded and relatively low ventral tubercle, among several other anatomical traits (see Worthy, 2009).

In size and proportions, *Tamtamia* is reminiscent to the extant genus *Tadorna* and extinct Miocene genus *Miotadorna* (see Worthy and Lee, 2008; Worthy *et al.*, 2007). It differs from *Tadorna* in having a much wider and excavated ventral pneumotricipital fossa that is laterally delimited by a subvertical ridge, by having a more prominent but distally located ectepicondylar prominence, and a proximally positioned flexor process. It differs from *Miotadorna* in having a notably wider and more excavated ventral pneumotricipital fossa, and a prominent and distally located ectepicondylar prominence (Worthy and Lee, 2008; Worthy *et al.*, 2007).

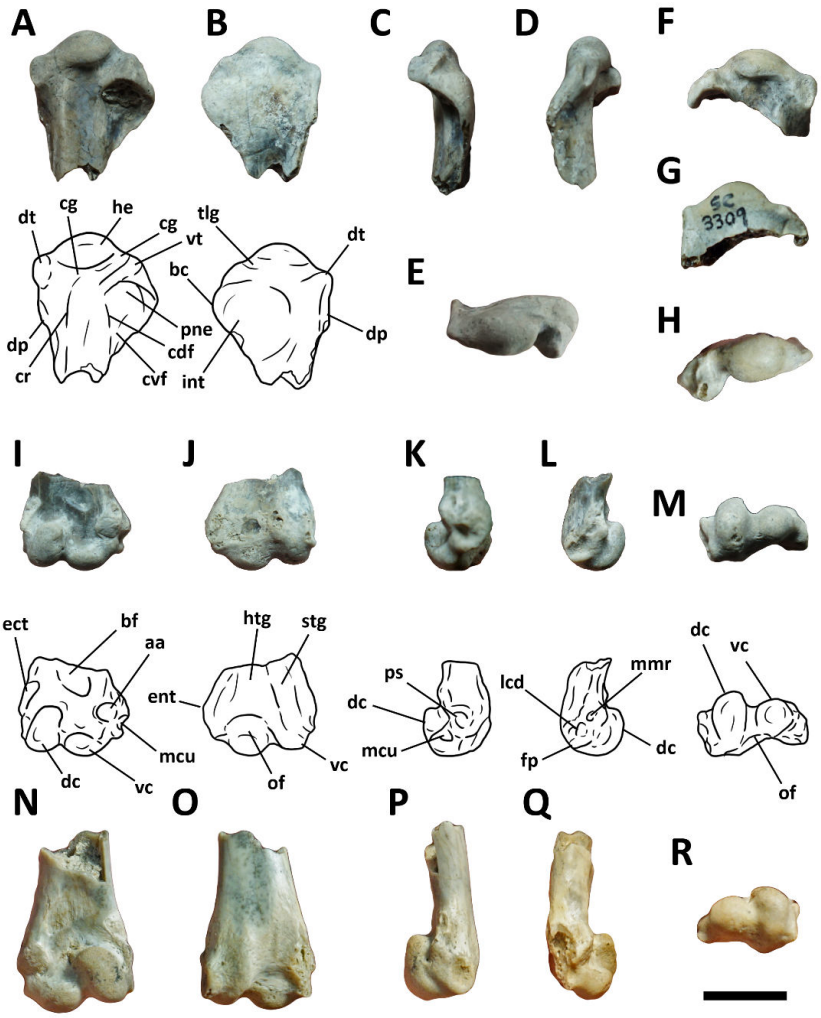

Figure 7. *Tamtamia yzurietai*. A-E, I-M, distal end of right humerus and proximal end of left humerus (MACN SC 4507, holotype) in A, J, posterior; B,I, anterior; C,K, medial; D,L, lateral; and E,M, distal views. F-H, proximal end of right humerus (MACN SC 3309, paratype) in F, posterior; G, anterior; and H, proximal views. N-R, distal end of left humerus (MACN SC, 4508, paratype) in N, anterior; O, posterior; P, lateral; Q, medial; and R, distal views. Abbreviations. aa, surface for the anterior articular ligament; bc, bicipital crest; bf, brachial fossa; cdf, crus dorsale fossae; cg, capital groove; cr, capital ridge; cvf, crus ventrale fossae; dt, dorsal tubercle; dp, deltopectoral crest; ect, ectepycondyle; ent, entepicondylar process; fp, flexor process; he, humeral head; htg, humerotricipital groove; int, intumescencia; lcd, scar of the dorsal collateral ligament; mcu, scar for the m. carpi ulnaris; mmr, scar for the m. metacarpi radialis; of, olecranon fossa; pne, pneumotricipital fossa; ps, scar for the pronator superficial; stg, scapulotricipital groove; vt, ventral tubercle. Scale bar 1 cm.

Figura 7. *Tamtamia yzurietai*. A-E, I-M, extremo distal de húmero derecho y proximal de húmero izquierdo (MACN SC 4507, holotipo) en vistas A, J, posterior; B,I, anterior; C,K, medial; D,L, lateral; y E,M, distal. F-H, extremo proximal de húmero derecho (MACN SC 3309, paratipo) em vistas F, posterior; G, anterior; y H, proximal. N-R, extremo distal de húmero izquierdo (MACN SC, 4508, paratipo) en vistas N, anterior; O, posterior; P, lateral; Q, medial; y R, distal. Abreviaturas. aa, superficie para el ligamento articular anterior; bc, cresta bicipital; bf, fosa braquial; cdf, crus dorsale; cg, surco capital; cr, cresta capital; cvf, crus ventrale; dt, tubérculo dorsal; dp, cresta deltopectoral; ect, ectepicóndilo; ent, proceso entepicondilar; fp, proceso flexor; he, cabeza humeral; htg, surco húmerotricipital; int, intumescencia; lcd, superficie del ligamento colateral dorsal; mcu, superficie para el m. carpi ulnaris; mmr, superficie para el m. metacarpi radialis; of, fosa olecraneana; pne, fossa neumotricipital; ps, superficie para el pronador superficial; stg, surco escápulotricipital; vt, tubérculo ventral. Barra de escala: 1 cm.

Tamtamia differs from *Kaikenia* (described above) in several features, including a deeper and more extensive humerotricipital groove, a well-raised facet for the anterior articular ligament, a deep brachial fossa, and different development of the ectepicondylar process and flexor process. *Tamtamia* differs from *Teleornis* (Ameghino, 1899; Agnolín, 2004) in that the latter has a prominent and distally extended flexor process, whereas in *Tamtamia* it is much shorter and more proximally positioned with respect to the distal end of the ventral condyle. The ventral condyle in *Tamtamia* is subhorizontally oriented, whereas in *Teleornis* it is strongly oblique, forming an angle of about 90° with the main axis of the dorsal condyle (see Agnolín, 2004).

Tamtamia comes from beds that are probably coeval with those that yielded the basal anatid *Ankonetta larriestrai* (Cenizo and Agnolín, 2010). Regrettably, *Ankonetta* is based on an incomplete tarsometatarsus, and thus, there is no overlapping material with *Tamtamia*. As described by Cenizo and Agnolín (2010), *Ankonetta* is a basal dendrocygnine-like anatid, and in all probability larger in size than that inferred for *Tamtamia*. It is not improbable that after the finding of new materials, *Tamtamia* may result in being a junior synonym for *Ankonetta*.

PHOENICOPTERIFORMES SHARPE, 1891

Indeterminate genus and species

Referred material. MACN SC 1401, distal end of left humerus (Figure 8A-E); MACN SC 4509, distal end of right tarsometatarsus lacking II metatarsal trochlea (Figure 8 F-N).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Description. The distal end of the humerus is anteroposteriorly flattened and transversely wide. The distal condyles are not very prominent, the ventral one being subequal in size to the dorsal one.

There is no prominent ectepicondylar process, and the surface for the attachment of the *m. carpi radialis* and the collateral ligament is nearly continuous. The ectepicondylar prominence is notably thick and forms a continuous and convex ridge that is more proximally extended than the facet of the anterior articular ligament.

In posterior view, the olecranal fossa is well defined and subhorizontally oriented. The humerotricipital and scapulotricipital grooves are not evident. The flexor process is prominent, bump-like, and distally extended.

The distal end of the tarsometatarsus is strongly eroded and poorly preserved. The bone is remarkable because of its strong transverse compression. The shaft is transversely compressed but anteroposteriorly long. The distal vascular foramen is not preserved, but it was proximally placed. The groove separating distal trochleae IV and III is well-defined, narrow and deep. The base of trochlea II has been preserved, and it is much more proximally located than trochlea IV. Trochlea IV is strongly posteriorly oriented and shows a very wide and posteriorly extended posterolateral wing. The base of trochlea IV indicates that it was laterally tilted.

Remarks. The specimens described here can be referred to Phoenicopteriformes on the basis of the following combination of characteristics: high and flattened ventral supracondylar tubercle, flexor process not posteriorly extended, well-defined olecranal fossa, tarsometatarsus strongly transversely compressed, trochlea IV with very wide and expanded posterior wing, and proximally positioned vascular foramen (Ericson, 1999; Feduccia, 1976; Zelenkov, 2021).

Among phoenicopteriforms, MACN SC 1401 and MACN SC 4509 are reminiscent to stem-phoenicopteriforms, such as *Juncitarsus,* in being relatively small in size, having strong distal compression of the tarsometatarsus, and in having a small and obliquely oriented ectepicondylar process on the humerus (Ericson, 1999). These features distinguish them from modern phonicopteriforms, such as *Phoenicopterus, Phoeniconaias* and *Palaelodus* (Vickers Rich *et al.*, 1987). In this way, we regard these specimens as probably being related to stem-phoenicopteriforms like *Juncitarsus*.

GRUIFORMES (BONAPARTE, 1854)

Rallidae Vigors, 1825

Indeterminate genus and species

Referred material. MACN SC 1431, incomplete distal end of right tarsometatarsus (Figure 9 I-O); MACN SC 1433, proximal end of left tarsometatarsus (Figure 9 A-H).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Description. The specimens reported here match the size, shape and characteristics of the extant genus *Rallus*. It is possible that both belong to the same taxon.

The proximal end of the bone is poorly preserved. The proximal intercotylar eminence is relatively low, anteriorly projected and prominent. The medial cotyle is more excavated and more proximally placed than the lateral one. It shows an acute and very well-raised medial margin. The hypotarsus shows a well-developed lateral crest and a reduced medial one. The hypotarsus ends in a well-defined distal notch.

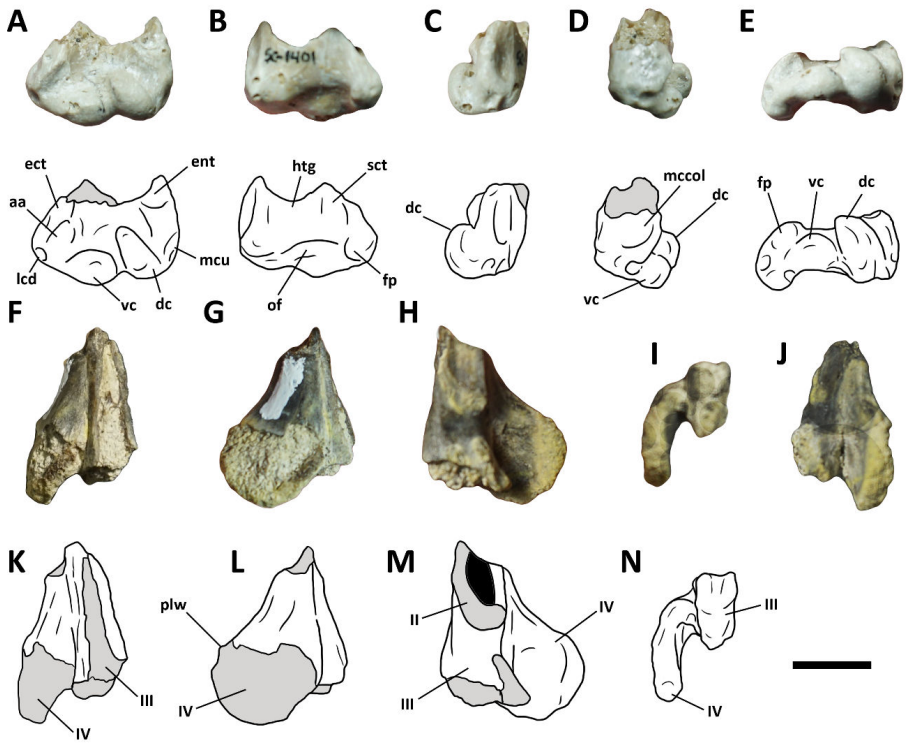

Figure 8. Indeterminate Phoenicopteriformes. A-E, distal end of left humerus (MACN SC 1401) in A, anterior; B, posterior; C, lateral; D, medial; and E, distal views; F-N, distal end of right tarsometatarsus lacking II metatarsal trochlea (MACN SC 4509) in F, anterior; G, lateral; H, medial; I, distal; and J, posterior views. Abbreviations. aa, anterior articular ligament; dc, dorsal condyle; ect, ectepicondylar process; ent, entepicondylar process; fp, flexor process; htg, humerotricipital groove; lcd, scar of the dorsal collateral ligament; mccol, surface for attachment of the *m. carpi radialis* and the collateral ligament; mcu, scar for the m. carpi ulnaris; of, olecranal fossa; plw, posterolateral wing; scg, scapulotricipital groove; vc, ventral condyle. II-IV, distal metatarsal trochleae. Eroded areas shaded in grey. Scale bar: 1 cm.

Figura 8. Phoenicopteriformes indeterminados. A-E, extremo distal de húmero izquierdo (MACN SC 1401) en vistas A, anterior; B, posterior; C, lateral; D, medial; y E, distal; F-N, extremo distal de tarsometatarso derecho sin la tróclea II (MACN SC 4509) en vistas F, anterior; G, lateral; H, medial; I, distal; y J, posterior. Abreviaturas. aa, superficie para el ligamento articular anterior; dc, cóndilo dorsal; ect, proceso ectepicondilar; ent, proceso entepicondilar; fp, proceso flexor; htg, surco húmerotricipital; lcd, superficie para el ligamento colateral dorsal; mccol, superficie para el *m. carpi radialis*; mcu, superficie para el m. carpi ulnaris; of, fosa olecraneana; plw, ala posterolateral; scg, surco escápulotricipital; vc, cóndilo ventral. II-IV, trócleas distales. Áreas deterioradas sombreadas en gris. Barra de escala: 1 cm.

The distal end of the tarsometatarsus is gracile and shows subparallel lateral and medial margins of the shaft. It shows a subrectangular cross-section.

Distal trochleae are disposed nearly on the same plane when viewed distally. The articular surfaces of the trochleae are wide and proximally extended. In anterior view the III metatarsal trochlea is more distally extended than trochlea II and shows a well excavated surface. It is highly asymmetrical, with the external rim much more prominent and proximally extended than the inner rim. Its proximal margin is subtriangular in contour.

Trochlea IV is subrectangular in contour and is poorly excavated. It is separated by a wide and proximally extended intertrochlear groove. The distal vascular foramen is wide and deep, and is obliquely oriented. In spite of not being preserved, the base of trochlea II is separated from the rest of the shaft and is posteriorly oriented.

In posterior view the distal trochleae are poroximally delimited by a wide concave surface. A large and well-defined scar is present proximal to the articular surface of trochlea III. The articular surface of trochlea III is subtriangular in contour.

Remarks. The specimens reported here can be referred to Rallidae on the basis of a unique combination of characteristics, including a hypotarsus with a prominent lateral crest and a reduced medial one, intercotylar eminence relatively low and well-defined, and anteriorly projected, distal

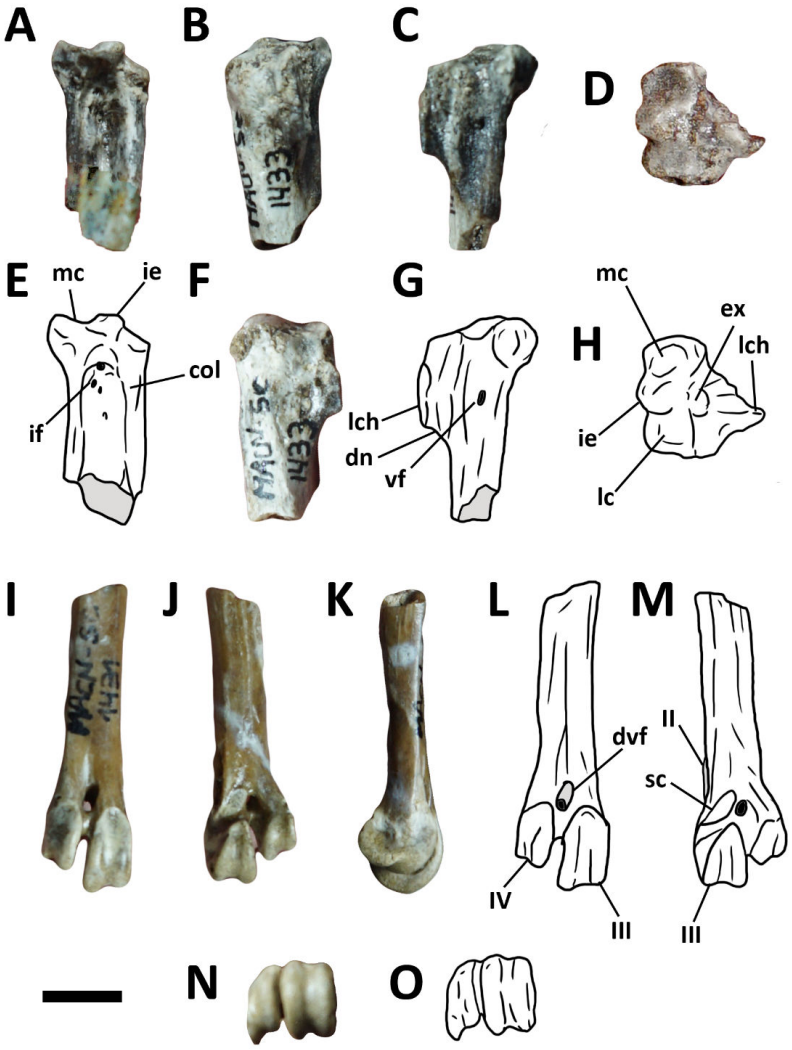

FIGURE 9. Indeterminate Rallidae. A-H, proximal end of left tarsometatarsus (MACN SC 1433) in A,E, anterior; B, posterior; C,G, medial; D,H, proximal; and F, lateral views. I-O, incomplete distal end of right tarsometatarsus (MACN SC 1431) in I,L, anterior; J,M, posterior; K, lateral; and N-O, distal views. Abbreviations. col, surface for the colateral lateral ligament; dn, distal notch; dvf, distal vascular foramen; ex, proximal excavation; ie, intercotylar eminence; if, infracotylar fossa; lc, lateral cotye; lch, lateral crest of hypotarsus; mc, medial cotyle; sc, muscular scar; vf, proximal vascular foramen; II, base of metatarsal trochlea II; III-IV, distal metatarsal trochleae. Eroded areas shaded in grey. Scale bar 5 mm.

FIGURA 9. Rallidae indeterminados. A-H, extremo proximal de tarsometatarso izquierdo (MACN SC 1433) en vistas A,E, anterior; B, posterior; C,G, medial; D,H, proximal; y F, lateral. I-O, extremo distal incompleto de tarsometatarso derecho (MACN SC 1431) em vistas I,L, anterior; J,M, posterior; K, lateral; y N-O, distal. Abreviaturas. col, superficie para el ligamento colateral lateral; dn, muesca distal; dvf, foramen vascular distal; ex, excavación proximal; ie, eminencia intercotilar; if, fosa infracotilar; lc, cótilo lateral; lch, crestalateral del hipotarso; mc, cótilo medial; sc, cicatriz muscular; vf, foramen vascular proximal; II, base de la tróclea metatarsal II; III-IV, trócleas metatarsales distales. Áreas deterioradas sombreadas en gris. Barra de escala: 5 mm.

end of the bone with proximally extended articular surfaces of trochleae, trochlea II proximally positioned and tilted, and a large and prominent scar proximal to metatarsal III in posterior view (Mayr, 2006, 2016a, 2019; Mayr and Smith, 2001).

Among rallids, the position of the specimens reported here is uncertain. The size and proportions are very similar to members of the genus *Rallus* (Olson, 1974). They lack the flattened tarsometatarsus with an acute medial edge diagnostic of *Porphyrio* and kin (Mayr, 2019; Olson, 1973). The metatarsal II trochlea is proximally positioned, in contrast with the more distal location observed in *Himantornis* (Olson, 1973).

Regrettably, the incomplete nature of the specimens reported here precludes a more accurate phylogenetic position among rallids.

Gruoidea sensu Wetmore, 1960
Gruidae Vigors, 1825
?Gruinae Vigors, 1825
Genus *Patagogrus* **nov. gen.**

Diagnosis. Medium-sized gruid diagnosed on the basis of the following combination of characters: 1- distal end of the bone with its anteroposterior length subequal to transverse width (shared with *Palaeogrus*; much transversely wider than anteroposteriorly long in *Grus*); 2- intercondylar groove in distal view narrow and with subparallel lateral and medial margins (relatively wide and forming an opened "V" or "U" in *Grus* and *Palaeogrus*); 3- distal end of lateral condyle with a well-developed notch (shared with *Grus*, nearly absent in *Palaeogrus*); 4- medial condyle strongly anteriorly projected and with its anterior end acute and transversely narrow (shared with *Palaeogrus*; narrower in *Grus*); 5- medial epicondyle poorly developed (well-developed and exposed when viewed distally in *Grus* and *Palaeogrus*); 6- tubercle lateral to supratendinal bridge poorly developed (shared with *Palaeogrus*, in *Grus* the tubercle is very strong); and 7- proximodistally extended supratendinal bridge (shared with *Grus*).

Etymology. Patago, from Patagonia, and *Grus*, the type genus of Gruidae.

Type and only included species. *Patagogrus olsoni* **nov. sp.**

Patagogrus olsoni **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 1423, distal end of right tibiotarsus (Figure 10).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Etymology. The specific epithet honours Storrs L. Olson (1944-2020), one of the most important paleornithologists from the XX and XXI centuries.

Description. Cross-section of the shaft roughly crescent-shaped, with a flattened anterior surface. Distal end with lateral condyle much larger than the medial one, with a thicker base and anteroposteriorly shorter (21 milimeters of maximum transverse width through the distal condyles). Distal margin of lateral condyle with a poorly-developed notch. Medial epicondyle present but not strongly developed and not surpassing the medial condyle medially. In distal view the distal trochlea do not strongly taper posteriorly. Intercondylar groove transverselly narrow and subrectangular in contour, with nearly straight medial and lateral margins and with a distinct sub-horizontal scar anteriorly. Presence of a well-developed tubercle located at the lateral edge of the supratendinal bridge and not in contact with lateral condyle. Distal opening of extensor groove proximodistally narrow and transversely wide, located at the medial half of the bone. Supratendinal bridge proximodistally extensive and with a concave anterior surface. Lateral retinacular tubercle ridge-like, strongly developed and subvertically oriented. It is placed medially to the fibularis muscle groove and is separated from the tubercle located at the lateral surface of the supratendinal bridge by a shallow subvertical groove. The medial retinacular tubercle is obliquely oriented with respect to the main axis of the extensor groove; it is poorly developed and ridge-like. This tubercle is located medially with respect to the medial margin of the extensor groove.

In posterior view the distal trochlea is relatively proximodistally low and shows shallow rings and a poorly developed transverse ridge.

Remarks. *Patagogrus* **nov.gen.** shows a unique combination of characteristics shared with Gruidae, including flat anterior face of the tibiotarsus, proximodistally low distal trochlea in posterior view, anteriorly divergent condyles, lateral condyle anteroposteriorly long, with a shallow notch on its distal margin, medial condyle more anteriorly projected than the lateral one, anterior end of medial condyle transversely narrow, the presence of a tubercle lateral to the base of the supratendinal bridge, well developed ridge delimiting the lateral margin of the extensor groove, and supratendinal bridge proximodistally tall (Clarke *et al.*, 2005; Cracraft, 1973a; Livezey, 1998; Mayr, 2013a). *Patagogrus* differs from psilopterine phorusrhacids by having a slimmer configuration, more dorsoventrally lower and transversely wider distal condyles, by having a subelliptical external rim on the lateral condyle, a medial condyle much more deflected medially, not alligned with the medial margin of the shaft, an anterior intercondylar fossa, and a poorly excavated extensor groove, among other anatomical details (see Noriega *et al.* 2009).

Patagogrus clearly differs from cariamids in having the lateral condyle not anteriorly projected and with a reduced epicondyle, a proximodistally high supratendinal bridge, a transversely wide and proximodistally low distal opening of the supratendinal bridge, the presence of a tubercle lateral to the supratendinal bridge, and absence of a ridge connecting the lateral edge of the supratendinal bridge with the medial margin of the lateral condyle, among other features (Cracraft, 1968; Noriega *et al.*, 2009).

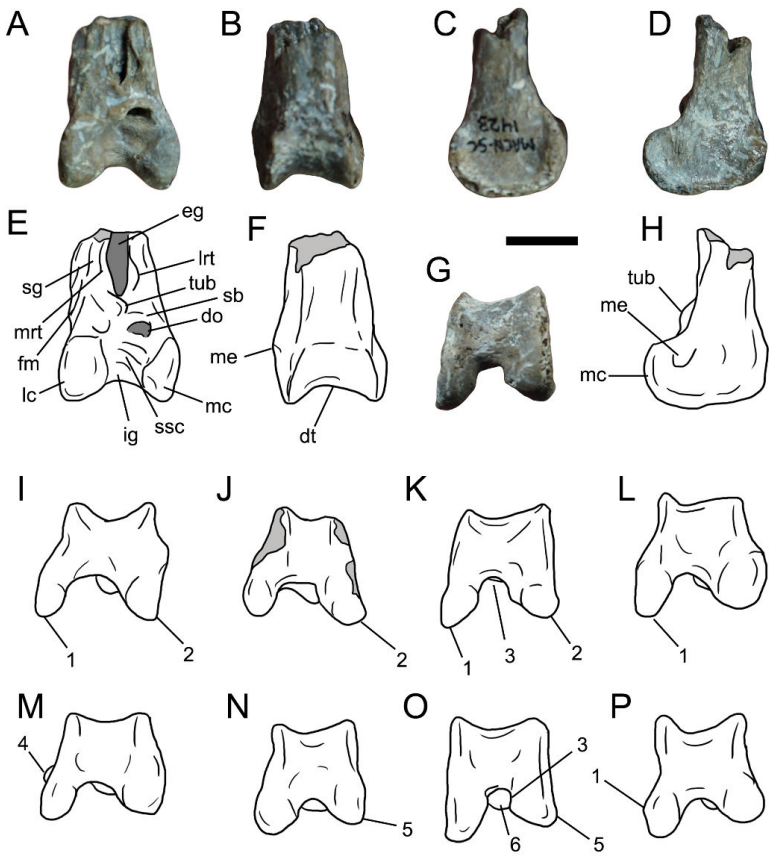

FIGURE 10. *Patagogrus olsoni* A-H, K, distal end of right tibiotarsus (MACN SC 1423) in A,E, anterior; B,F, posterior; C, lateral; D,H, medial; and G,K, distal views. I-P, distal end of right tibiotarsus of selected Gruiformes: I, *Grus*; J, *Palaeogrus*; K, *Patagogrus*; L, *Camusia*; M, *Aramus*; N, *Balearica*; O, *Psilopterus*; P, *Psophia*. J, modified from Gohlich (2003); I,L,M,O,P, modified from Cracraft (1973a). Abbreviations. do, distal opening of the extensor groove; dt, distal trochlea; eg, extensor groove; fm, fibularis muscle groove; ig, intercondylar groove; lc, lateral condyle; lrt, lateral retinacular tubercle; mc, medial condyle; me, medial epicondyle; mrt, medial retinacular tubercle; sb, supratendinal bridge; sg, subvertical groove; ssc, subhorizontal muscle scar; tub, tubercle located at the lateral edge of the supratendinal bridge. 1, medial condyle medially deflected and transversely narrow; 2, laterally oriented lateral condyle; 3, narrow, subpralallel-sided intercondylar groove; 4, prominent medial epicondyle; 5, robust and subparallel-sided distal condyles; 6, prominent and very large tubercle located at the lateral edge of the supratendinal bridge. Scale bar: 1 cm.

FIGURA 10. *Patagogrus olsoni* A-H, K, extremo distal de tibiotarso derecho (MACN SC 1423) en vistas A,E, anterior; B,F, posterior; C, lateral; D,H, medial; y G,K, distal. I-P, extremo distal de tibiotarso derecho de algunos Gruiformes: I, *Grus*; J, *Palaeogrus*; K, *Patagogrus*; L, *Camusia*; M, *Aramus*; N, *Balearica*; O, *Psilopterus*; P, *Psophia*. J, modificado de Gohlich (2003); I,L,M,O,P, modificado de Cracraft (1973a). Abreviaturas. do, apertura distal del surco extensor; dt, tróclea distal; eg, surco extensor; fm, surco para el músculo fibular; ig, surco intercondilar; lc, cóndilo lateral; lrt, tubérculo retinacular lateral; mc, cóndilo medial; me, epicóndilo medial; mrt, tubérculo retinacular medial; sb, puente supratendinoso; sg, surco subvertical; ssc, cicatriz muscular subhorizontal; tub, tubérculo localizado al margen lateral del puente supratendinoso. 1, cóndilo medial orientado medialmente y transversalmente estrecho; 2, cóndilo lateral orientado lateralmente; 3, surco intercondilar estrecho y de lados subparalelos; 4, epicóndilo medial prominente; 5, cóndilos distales robustos y de lados subparalelos; 6, tubérculo prominente y de gran tamaño ubicado en el margen lateral del puente supratendinoso. Barra de escala: 1 cm.

Among gruids, *Patagogrus* clearly differs from *Balearica* and extinct Balearicinae, previously referred to as *Probalearica* (Mourer Chauviré, 2001), in that balearicines exhibit a robust distal end of the tibiotarsus with a strongly anteroposteriorly flattened shaft, a strongly medially deflected medial condyle, and a transversely expanded extensor groove (Feduccia and Voorhies, 1992; Mourer Chauviré, 2001). On the other side, *Patagogrus* resembles gruines in having a progressive (not abrupt) widening of the distal end of the bone, in the presence of a strong tubercle lateral to the supratendinal bridge, a relatively long lateral condyle, a transversely narrow extensor groove occupying only the medial part of the cranial face of the bone, and a notch at the distal edge of lateral

condyle forming an indentation that is much less pronounced in the Balearicinae (Göhlich, 2003; Mourer Chauviré, 2001).

Tertiary gruines are still poorly known. Several previously published records rest on weak evidence and they are considered to be of uncertain phylogenetic affinities (Cracraft, 1973a; Göhlich, 2003), which makes comparisons of *Patagogrus* with other fossil gruines difficult. The only Tertiary extinct gruine genera that rest on relatively robust evidence are *Palaeogrus* and *Camusia* (e.g., Göhlich, 2003; Mayr *et al.*, 2020b; Mourer-Chauviré, 2001; Seguí, 2002; Zelenkov, 2015). Comparisons between *Patagogrus, Palaeogrus* and the extant genus *Grus* were made in the diagnosis of *Patagogrus* following characteristics noted by previous authors (Cracraft, 1973a; Göhlich, 2003; Northcote and Mourer-Chauviré, 1988). *Camusia* is very different from *Patagogrus* and any other gruid genus (Seguí, 2002). It differs from *Patagogrus* in several anatomical details, including a tibiotarsus with a much transversely wider and anteroposteriorly flattened distal end, by having narrower and a more medially projected medial condyle and a prominent and elongate medial epicondyle.

The combination of characteristics enumerated above indicates that *Patagogrus* is a valid gruid genus. Among other anatomical details, it is distinctive in having a transversely narrow distal end of the tibiotarsus, as is shown by the shape of the intercondylar groove in distal view.

Psophiidae Bonaparte 1831

Genus *Archaeopsophia* **nov. gen.**

Diagnosis. A medium-sized gruoid closely related to psophiids and parvigruids from which it differs in the following combination of characteristics: 1- proximally extended and well-defined intercotylar eminence (condition similar to Psophiidae; much lower in Parvigruidae); 2- hypotarsus distally located (very proximally located in Parvigruidae, close to the level of the proximal cotyles; similar condition to *Archaeopsophia* is present in Psophiidae); 3- medial crest for the flexor digitorum longus anteroposteriorly short (long in Psophiidae; condition similar to Parvigruidae); 4- hypotarsus lateral to the flexor digitorum longus groove forming a nearly subparallel surface with respect to the main transverse axis of the bone (disposed on an oblique angle in Psophiidae; condition similar to Parvigruidae); 5- groove for the fibularis longus shallower than in Psophiidae; and 6- groove for the flexor hallucis longus notably transversely wide (very narrow in Parvigruidae).

Etymology. Archaeo, from the Greek, meaining ancient; *Psophia*, the type genus of Psophiidae.

Type and only included species. *Archaeopsophia aoni* nov. sp.

Archaeopsophia aoni **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 3422, proximal end of right tarsometatarsus (Figure 11).

Locality and horizon. The specimen comes from the Santa Cruz Formation (Early-Middle Miocene), at the well-known fossiliferous locality of Monte Observación, Monte León National Park, Santa Cruz province, Argentina. Collected in 1991.

Etymology. Aoni, from the Aonikenk, meaning south.

Description. Proximal end of tarsometatarsus poorly transversely expanded (21 milimeters of maximum transverse width). The intercotylar eminence is distinctly proximally extended and anteroposteriorly narrow. Proximal cotyles strongly concave and delimited by rising outside margins. The medial cotyle is situated farther proximally than the lateral one. The infracotylar fossa is deep and well-defined, and shows three very small proximal vascular foramina.

In proximal view the medial cotyle is much larger than the lateral one, and exhibits a subrectangular contour. Intercotylar area relatively wide, subrectangular in contour and deeply excavated.

In posterior view the hypotarsus is distally displaced and is separated from the proximal cotyles by a very deep and well-defined subhorizontally oriented excavation. The hypotarsus is relatively complex and is not strongly posteriorly projected. It does not enclose bony canals. Its most prominent crest is the medial crest for the flexor digitorum longus, which is not strongly posteriorly extended and is close in size to the lateral crest for the flexor digitorum longus. The medial crest for the flexor digitorum longus is proximodistally long. The grooves for the flexor digitorum longus and flexor hallucis longus are well-defined, especially when viewed posteriorly. The lateral crest for the flexor hallucis longus is thick and blunt, but not prominent.

The fossa parahypotarsalis lateralis appears to have been poorly developed. There is a low crista plantaris lateralis along the midsection of the shaft.

Remarks. *Archaeopsophia aoni* **nov. sp.** shows a hypotarsal morphology exclusive to Gruoidea: there is a lateral sulcus for the tendon of musculus fibularis longus, the hypotarsus forms a laterally slanted embossment, there is a groove for the flexor digitorum longus tendon, and a proximodistally long crista medialis partially or entirely enclosing such a groove (Cracraft, 1973a; Mayr, 2016a). Among gruoids, *Archaeopsophia* exhibits a hypotarsal morphology that only fits with that of the Psophiidae and Parvigruidae. In most ralloids, and in

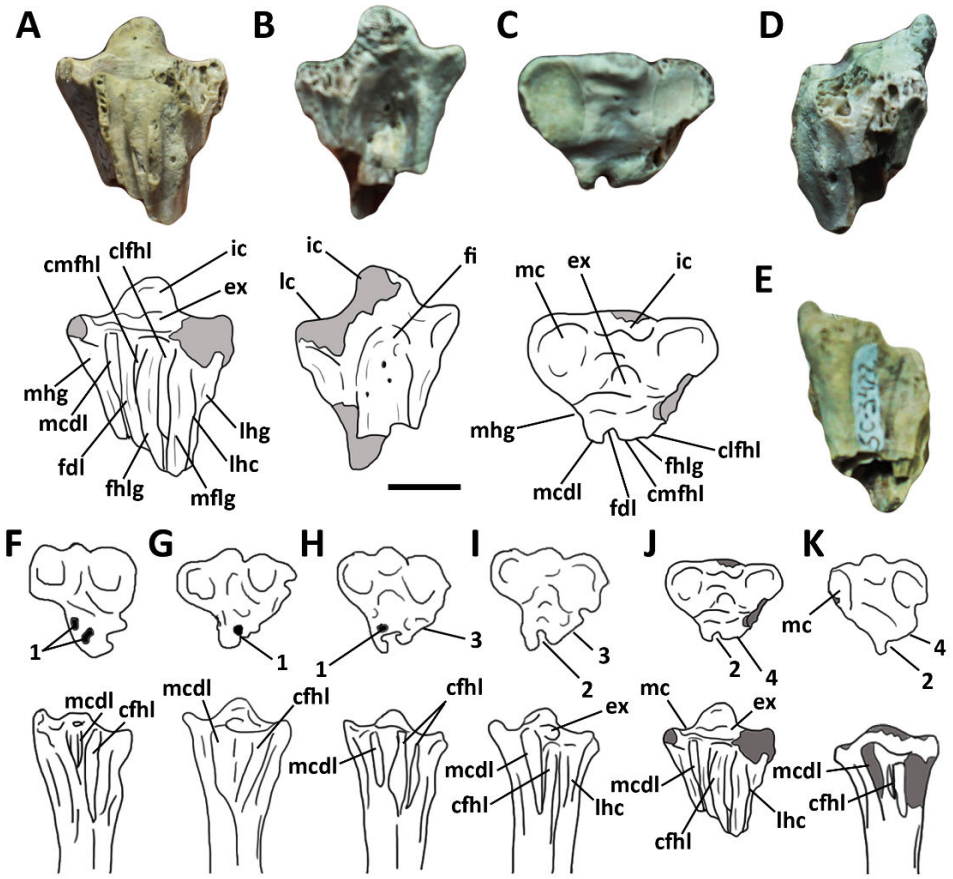

FIGURE 11. *Archaeopsophia aoni* (MACN SC 3422, holotype) proximal end of right tarsometatarsus in A, posterior; B, anterior; C, proximal; D, lateral, and E, medial views. F-K, proximal end of right tarsometatarsus of selected gruiforms in proximal (top) and posterior (bottom) views; F, *Rallus sanguinolentus*; G, *Grus canadensis*; H, *Aramus guarauna*; I, *Psophia crepitans*; J, *Archaeopsophia aoni*; K, *Parvigrus* sp. (redrawn and modified from Mayr, 2012 and personal inspection of specimens). Abbreviations. cfhl, crest for the flexor hallucis longus; cmfhl, medial crest of the flexor hallucis longus; clfhl, lateral crest of the flexor hallucis longus; ex, excavation; fdl, groove for the flexor digitorum longus; fi, infracotylar fossa; ic, intercotylar eminence; lc, lateral c0tyle; lhc, lateral hypotarsal crest; lhg, lateral hypotarsal groove; mc, medial cotyle; mcdl, medial crest of the digitorum longus; mflg, groove for the musculus fibularis longus; mhg; medial hypotarsal groove; 1, enclosed canals (flexor digitorum longus); 2, opened canal (groove) for the flexor digitorum longus; 3, hypotarsus lateral to the flexor digitorum longus groove forming an oblique surface with respect to the main transverse axis of the bone; 4, hypotarsus lateral to the flexor digitorum longus groove forming a nearly subparallel surface with respect to the main transverse axis of the bone. Scale bar: A-E, 1 cm; F-K, not to scale.

FIGURA 11. *Archaeopsophia aoni* (MACN SC 3422, holotipo) extremo proximal de tarsometatarso derecho en vistas A, posterior; B, anterior; C, proximal; D, lateral, y E, medial. F-K, extremo proximal de tarsometatarso derecho de algunos gruiformes en vistas proximal (arriba) y posterior (debajo); F, *Rallus sanguinolentus*; G, *Grus canadensis*; H, *Aramus guarauna*; I, *Psophia crepitans*; J, *Archaeopsophia aoni*; K, *Parvigrus* sp. (redibujado y modificado de Mayr, 2012 e inspección personal de material). Abreviaturas. cfhl, cresta para el flexor hallucis longus; cmfhl, cresta medial del flexor hallucis longus; clfhl, cresta lateral del flexor hallucis longus; ex, excavación; fdl, surco para el flexor digitorum longus; fi, fosa infracotilar; ic, eminencia intercotilar; lc, cótilo lateral; lhc, cresta hipotarsal lateral; lhg, surco hipotarsal lateral; mc, cótilo medial; mcdl, cresta medial del digitorum longus; mflg, surco para el músculo fibularis longus; mhg; surco hipotarsal medial; 1, canales cerrados (flexor digitorum longus); 2, canal abierto (surco) para el flexor digitorum longus; 3, hipotarso lateral al surco del flexor digitorum longus formando una superficie oblícua con respecto al eje mayor transverso del hueso; 4, hipotarso lateral al surco del flexor digitorum longus formando una superficie subparalela con respecto al eje transverso mayor del hueso. Barra de escala: A-E, 1 cm; F-K, no a escala.

all gruids and aramids, the canal for the flexor digitorum longus is entirely closed, whereas in *Archaeopsophia*, Psophiidae, and Parvigruidae it is represented by an opened groove (Mayr, 2013a, 2016a). Furthermore, in *Archaeopsophia*, *Psophia,* and gruoids more derived than parvigruids the medial crest for the flexoris digitorum longus is proximodistally extensive, whereas in *Parvigrus* it is notably shorter (Mayr, 2013a). In addition, *Archaeopsophia* resembles psophiids and differs from parvigruids in having a proximally extended and well-defined intercotylar eminence, a distally displaced hypotarsus, and a groove for the flexor hallucis longus that is notably transversely wide. Furthermore, as in Psophiidae and Aramidae, there exits a well-defined groove for the flexor hallucis longus lateral to the medial hypotarsal crest. The hypotarsus of *Archaeopsophia* is very different from the condition exhibited by cariamiforms, which share a block-like hypotarsus lacking deep grooves and crests (Alvarenga and Hofling, 2003; De Pietri and Mayr, 2014). On the basis of this combination of characters, *Archaeopsophia* is referred here to the Psophiidae.

Anisolornis excavatus is an enigmatic bird coming from early Miocene Santacrucian beds at the Karaiken fossil site in Santa Cruz province. The specimen was originally considered by Ameghino as being a phororhacoid bird (1891) and later as a galliform bird (1895). More recently, Cracraft (1973a) included it among aramids and Olson (1985) noted resemblances to Psophiidae. However, the affinities of *Anisolornis* with psophiids, and even gruiformes, are far from being well-settled (Tambussi and Degrange, 2013). *Anisolornis* is based on a distal tarsometatarsus, and thus, direct comparisons with *Archaeopsophia* are not possible. In any case, *Anisolornis* belongs to a relatively large bird, much bigger than *Archaeopsophia* (see Cracraft, 1973a).

Parvigruidae Mayr, 2005

Genus *Alhuenia* **nov. gen.**

Diagnosis. Small-sized gruoid closely related to psophiids and parvigruids from which it differs in the following combination of characteristics: 1- distal end of the humerus anteroposteriorly flattened (similar to *Psophia* and gruids, thicker in *Parvigrus*); 2- robust dorsal condyle with a bulbous distal end (narrower in *Parvigrus* and narrow and ventrally excavated in *Psophia*); 3- attachment of the tendon of the *m. carpi radialis* represented by low and elongate scar (more prominent in *Parvigrus*); 4- proximal margin of the brachial fossa poorly delimited (similar to *Parvigrus*, more excavated and delimited by a ridge in *Psophia*); 5- flexor tubercle not distally extended (similar to *Parvigrus*, strongly distally projected in *Psophia*); 6- distal end of the humerus not ventrally slanted (slanted in *Parvigrus* and ralloids); and 7- humerotricipital groove not delimited by subvertical ridges (ridges present in *Parvigrus*).

Etymology. Alhue, from the Mapundugún, meaning phantom.

Type and only included species. *Alhuenia eduardotonnii* **nov. sp.**

Alhuenia eduardotonnii **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 1439, distal end of right humerus (Figure 12).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Description. The distal end of the humerus of *Alhuenia* is not strongly transversely expanded (13 milimeters of maximum transverse width). In spite of being not entirely preserved, the flexor process was not strongly ventrally projected, a condition shared with gruoids and different from ralloids (Mayr, 2013a). This results in the ventral edge of the bone being straight and not ventrally slanted.

The entepicondylar process is strongly anteriorly projected and is proximally continuous with a ridge that delimits the medial margin of the bone, a condition shared with gruoids excluding parvigruids (Mayr, 2013a). The attachment scar for the tendon of the anterior articular ligament, distal to the entepicondylar process, is prominent. The brachial fossa is not well-excavated and roughly ellipsoidal in contour. It is centrally positioned, as occurs in most gruoids (Mayr, 2013a), and is not distally displaced. Both dorsal and ventral condyles are prominent and rounded, and are separated by a deep and wide intercondylar groove. The ventral condyle is roughly subcircular in contour. Proximal to the dorsal condyle, there is a thick attachment area for the tendon of *m. carpi radialis*. This area is elongate and is not prominent.

In posterior view, both scapulotricipitalis and humerotricipitalis grooves are wide and shallow. The olecranal fossa is relatively deep and well-defined.

Remarks. The distal end of the humerus of *Alhuenia* **nov. gen.** clearly differs from other gruiforms and cariamiforms, and resembles parvigruids in the following unique combination of characteristics: distal end of the bone not ventrally slanted (a condition shared with gruoids and contrasting with rallids, messelornithids and other gruiforms and cariamiforms; Mourer-Chauviré, 1983; 1995) and not strongly transversely expanded (notably expanded in *Psophia*), the proximal end of the ectepicondylar process is markedly projected

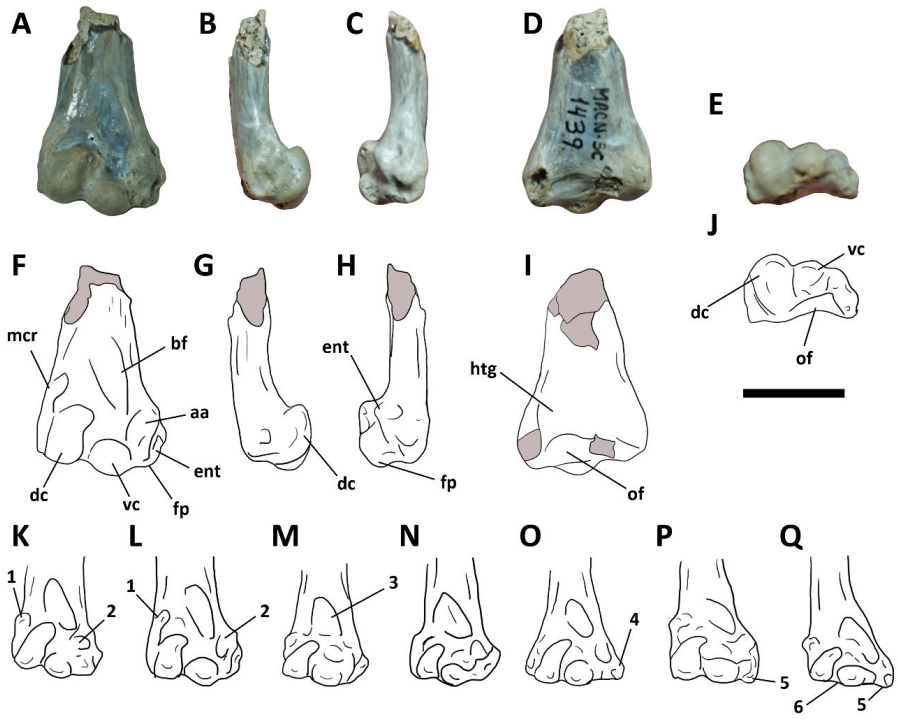

FIGURE 12. *Alhuenia eduardotonnii* (MACN SC 1439, holotype), distal end of right humerus in A,F, anterior; B,G, lateral; C,H, medial; D,I, posterior; and E,J, distal views. K-Q, anterior view of right humerus of selected gruiforms and cariamiforms, K, *Parvigrus* sp. (redrawn from Mayr, 2013a); L, *Alhuenia eduardotonnii* nov. sp.; M, *Aramus guarauna*; N, *Balearica* sp.; O, *Psophia crepitans*; P, *Rallus sanguinolentus*; Q, *Cariama cristata*. Abbreviations. aa, anterior articular ligament; bf, brachial fossa; dc, dorsal condyle; ent, entepicondylar process; fp, flexor process; htg, humerotricipital groove; mcr, scar for the *m. carpi radialis*; of, olecranal fossa; vc, ventral condyle. 1, attachment of the tendon of the *m. carpi radialis* represented by low and elongate scar; 2, prominent attachment for anterior articular ligament; 3, centrally located brachial fossa; 4, transversely expanded distal end of humerus; 5, ventrally extended flexor process; 6, ventrally slanted distal end of humerus. Scale bar: A-J, 1 cm.; K-Q, not to scale.

FIGURA 12. *Alhuenia eduardotonnii* (MACN SC 1439, holotipo), extremo distal de húmero derecho em vistas A,F, anterior; B,G, lateral; C,H, medial; D,I, posterior; y E,J, distal. K-Q, vista anterior del extremo distal de húmero derecho de algunos gruiformes y cariamiformes, K, *Parvigrus* sp. (redibujado de Mayr, 2013a); L, *Alhuenia eduardotonnii* nov. sp.; M, *Aramus guarauna*; N, *Balearica* sp.; O, *Psophia crepitans*; P, *Rallus sanguinolentus*; Q, *Cariama cristata*. Abreviaturas. aa, superficie para el ligamento articular anterior; bf, fosa braquial; dc, cóndilo dorsal; ent, proceso entepicondilar; fp, proceso flexor; htg, surco húmerotricipital; mcr, cicatriz del *m. carpi radialis*; of, fosa olecraneana; vc, cóndilo ventral. 1, superficie de anclaje del *m. carpi radialis* representado por una cicatriz elongada; 2, superficie de anclaje del ligamento articular anterior prominente; 3, fosa braquial centralizada; 4, extremo distal del húmero transversalmente expandido; 5, proceso flexor extendido ventralmente; 6, extremo distal del húmero inclinado distalmente. Barra de escala: A-J, 1 cm.; K-Q, no a escala.

anteriorly (weakly elevated in gruoids, including psophiids; Mayr, 2013a), attachment for anterior articular ligament prominent (Mayr, 2013a), brachial fossa shallow and not proximally delimited by a ridge (more excavated in psophiids and gruids; Mayr, 2013a); brachial fossa intermediate in position between the centrally located position of gruoids and the ventrally situated position of ralloids (Mayr, 2013a), dorsal condyle robust and not strongly compressed (shared also with gruids; strongly compressed in *Psophia*; Mayr, 2002, 2013a), ventral condyle globular and distally extended beyond the level of the flexor process and dorsal condyle (Mayr and Smith, 2001), and ventral condyle separated from the dorsal one by a deep groove (groove shallower and ventral condyle elongate in cariamiforms; Mayr, 2002). Furthermore, *Alhuenia* shows important differences with *Psophia* which include a very different shape of the dorsal condyle and much narrower and not strongly distally divergent humeral margins (see Mayr, 2013a).

As indicated in the diagnosis, *Alhuenia* shows several features that distinguish it from the parvigruids *Parvigrus* and *Rupelrallus*, particularly

the less distally extensive flexor tubercle and the more robust and globose dorsal condyle, among other anatomical details (see Mayr, 2005; 2013). In spite of not being directly compared to the psophiid *Archaeopsophia* and the enigmatic *Anisolornis*, the distal humerus of *Alhuenia* belongs to a much smaller bird than expected for *Archaeopsophia* and *Anisolornis*, as inferred by their tarsometatarsi.

Falconiformes Sharpe, 1874

Falconidae Leach, 1820

Genus *Caroohierax* **nov. gen.**

Diagnosis. Very small falconid diagnosed on the basis of the following unique combination of characters: 1- subtriangular cross-section of metatarsal shaft; 2- well-delimited and deep extensor groove forming a canal; 3- poorly defined surface of the impression for the *m. abductor digiti II*; 4- posterior surface of the shaft lacking prominent plantar crests; 5- metatarsal II trochlea strongly distally extended and transversely narrow, well-separated from the posteromedial wing; 6- posteromedial wing strongly medially oriented and proximally extended; and 7- metatarsal trochlea IV laterally delimited by a wide, flattened and obliquely oriented lateral surface.

Etymology. Caroo, from the Aonikenk language, meaning carancho (in spanish) or caracara; hierax, from the Greek, meaning falcon.

Type and only included species. *Caroohierax rapoporti* **nov. sp.**

Caroohierax rapoporti **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 1400, distal end of left tarsometatarsus with somewhat eroded distal trochleae (Figure 13).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Etymology. In honour of Eduardo Rapoport (1927-2017) one of the most prominent Argentine biologists who greatly contributed to the knowledge of the biogeography and ecology of the southern cone.

Description. Very small falconid (maximum preserved distal width of tarsometatarsus is 4 mm).

The distal end of the tarsometatarsus shows a roughly subtriangular cross-section of the shaft with a nearly flattened anterior surface and a poorly excavated posterior one. The preserved proximal portion is relatively narrow, which suggests a gracile and elongate shaft. Plantar crests are not well-defined.

The distal end of the extensor groove is very deep and delimited by prominent margins. It lacks any sign of a double opening. The opening of the distal vascular foramen is relatively small and is distally positioned. In posterior view the impression of the *adductor digiti II* is transversely narrow and well-defined.

In anterior view the surface for the *m. abductor digiti II* is poorly developed, barely defined, and not medially extended. Proximal to the IV metatarsal trochlea there is a wide, anterolaterally facing flattened surface that is obliquely oriented.

The metatarsal fossa I is shallow and distally positioned. The opening of the distal interosseus canal is situated at the lateral intertrochlear incisure. A well defined posterior supratrochlear fossa is present.

In anterior view the distal trochleae are subequally distally extended, with the trochlea II more slightly distally extended than trochlea III. The preserved part of trochlea metatarsal IV indicates a prominent posterior wing. Metatarsal II trochlea with a prominent posteromedial wing is strongly medially oriented. In spite of being poorly preserved, its base indicates that it was strongly proximodistally extended. In lateral view a well-defined lateral fossa for the collateral ligament is present. The articular surface of metatarsal II trochlea is nearly flat, transversely narrow, and subrectangular in shape in anterior view.

The III metatarsal trochlea in anterior view appears to be relatively elongate, with deep and well-defined rims separated by a deep and well-defined longitudinal groove. In distal view the trochlear rims are relatively prominent and acute.

Remarks. In spite of the poor preservation of the only known *Caroohierax* specimen, it strongly departs from the morphology of other Miocene falconids. In fact, it shows a unique combination of features that make it difficult to assign it to any falconid subclade (see Becker, 1987; Cenizo *et al.*, 2013; Noriega *et al.*, 2011). It shows several features similar to that of Herpetotheriinae, including a subtriangular cross-section of the shaft, and a prominent and posteriorly oriented wing on metatarsal trochlea IV. Furthermore, *Caroohierax* differs from Falconini and Polyborini in that the extensor groove of digit IV lacks any sign of a double opening (Cenizo *et al.*, 2013), the opening of the distal interosseus canal is located within the lateral intertrochlear incisure and lacks a proximally extended posterior notch. Additionally, *Caroohierax* differs from polyborines in the different shape and proportions of the distal trochleae, as well as in the absence of rugosities and pits delimiting the distal end of the surface for the *m. abductor digiti II*.

However, in spite of the similarities noted above, *Caroohierax* differs from herpetotheriines in having a small and poorly defined surface for the *m.*

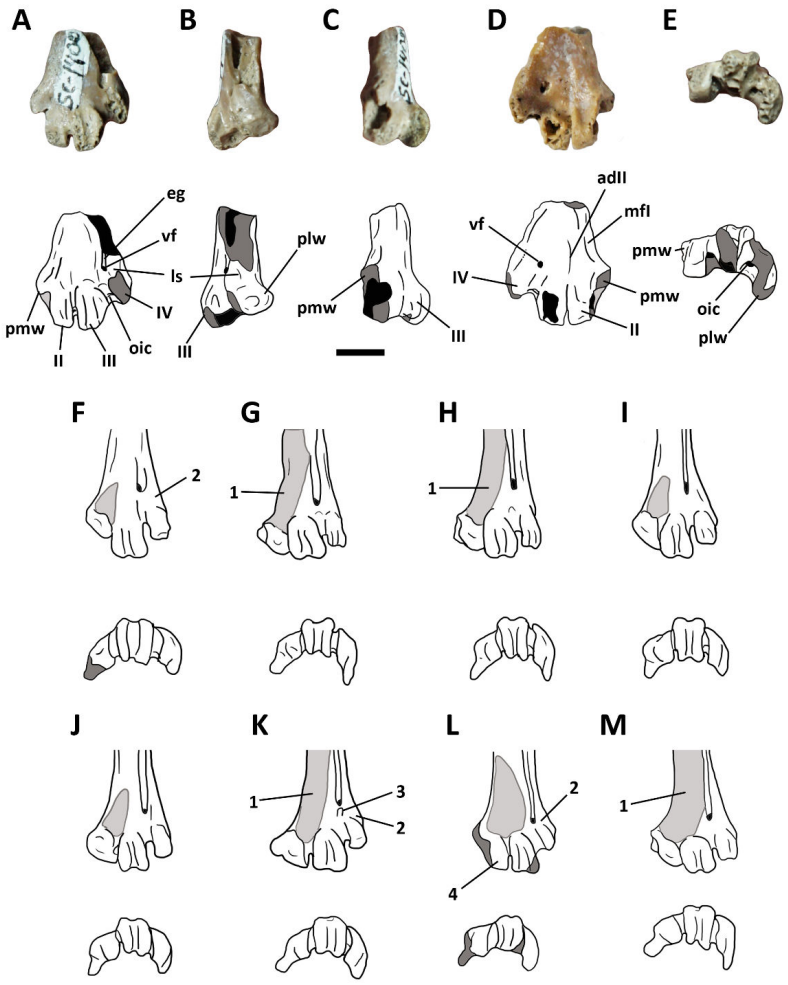

FIGURE 13. *Caroohierax rapoporti* (MACN SC 1400, holotype) distal end of left tarsometatarsus in A, anterior; B, lateral; C, medial; D, posterior; and E, distal views. F-M, left tarsometatarsus of selected falconids in anterior view, F, *Antarctoboenus carlini*; G, *Herpetotheres cachinans* (Herpetotheriinae); H, *Micrastur semitorquatus* (Micrasturinae); I, *Polyborus plancus* (Polyborini); J, *Spiziapteryx circumcincta* (Polyborini); K, *Falco femoralis* (Falconini); L, *Caroohierax rapoporti*; M, *Thegornis musculosus* (Herpetotheriinae). Abbreviations. adII, impression of the *m. adductor digiti II*; eg, extensor groove of digit IV; ls, lateral surface delimiting the trochlea IV; mfI, metatarsal I fossa; oic, distal opening of interosseous canal; plw, posterolateral wing; pmw, posteromedial wing of trochlea II; vf, distal vascular foramen. 1, expanded, deep and well-defined surface for the *m. abductor digiti II*; 2, wide lateral surface proximally delimiting trochlea IV; 3, double opening of distal vascular foramen; 4, subrectangular-shaped and transversely narrow body of trochlea II. In F-M, the surface shaded light grey represents the surface for the *m. abductor digiti II*. Scale bar: A-E, 2 mm.; F-M, not to scale. F-K, redrawn from Cenizo *et al.* (2013) and personal inspection of specimens; M, redrawn from Noriega *et al.* (2011).

FIGURA 13. *Caroohierax rapoporti* (MACN SC 1400, holotipo) extremo distal de tarsometatarso izquierdo en vistas A, anterior; B, lateral; C, medial; D, posterior; y E, distal. F-M, tarsometatarso izquierdo de algunos falcónidos en vista anterior, F, *Antarctoboenus carlini*; G, *Herpetotheres cachinans* (Herpetotheriinae); H, *Micrastur semitorquatus* (Micrasturinae); I, *Polyborus plancus* (Polyborini); J, *Spiziapteryx circumcincta* (Polyborini); K, *Falco femoralis* (Falconini); L, *Caroohierax rapoporti*; M, *Thegornis musculosus* (Herpetotheriinae). Abreviaturas. adII, impresión del *m. adductor digiti II*; eg, surco extensor del dedo IV; ls, superficie lateral delimitando la tróclea IV; mfI, fosa metatarsal I; oic, apertra distal del canal interósseo; plw, ala posterolateral; pmw, ala posteromedial de la tróclea II; vf, foramen vascular distal. 1, superficie del *m. abductor digiti II* amplia, y bien definida; 2, tróclea IV proximalmente delimitada por una amplia superficie lateral; 3, doble apertura del foramen vascular distal; 4, tróclea II de contorno subrectangular y con el cuerpo transversalmente comprimido. En F-M, la superficie sombreada en gris representa la superficie para el *m. abductor digiti II*. Barra de escala: A-E, 2 mm.; F-M, no a escala. F-K, redibujada de Cenizo *et al.* (2013) e inspección personal de los especímenes; M, redibujado de Noriega*et al.* (2011).

abductor digiti II (such a wide surface is also widespread in falconines), in lacking well-defined plantar ridges and strongly excavated anterior and posterior metatarsal surfaces, and in lacking a wide and deep impression for the *m. adductor digiti II*. The shape of trochlea II in *Caroohierax* differs from that of herpetotheriines such as *Thegornis, Herpetotheres* and *Micrastur* in having a narrow and distally extended articular body (see Noriega *et al.*, 2011).

Caroohierax differs from the basal falconid *Antarctoboenus* in having a deep and well-defined impression for the *m. adductor digiti II*, in the distal extension of trochlea II, in having narrow intertrochlear spaces, a narrow and deep extensor groove, and in stouter distal trochleae, among other features (Cenizo *et al.*, 2013).

Herpetotheriinae Lesson, 1842

Genus *Thegornis* Ameghino, 1895

Thegornis spivacowi **nov. sp.**

Diagnosis. Very small *Thegornis* species distinguishable by the following combination of characters: 1- tarsometatarsus in distal view with metatarsal IV trochlea having the posterior wing well-separated from the main body of the trochlea, resulting in a sigmoidal outer margin of the trochlea IV; 2- trochlea II robust and rounded, with a distal notch separating the anterior articular surface from the posterior wing; and 3- proximal ridge resulting in a medial prominence dorsal to the articular surface of trochlea II.

Holotype. MACN-SC 1407, distal end of right tarsometatarsus (Figure 14).

Paratypes. MACN-SC 1390, distal end of left tarsometatarsus lacking II trochlea (Figure 15 A-F); MACN-SC 1393, distal end of left tarsometatarsus lacking IV trochlea (Figure 15 J-M); MACN-SC 1396, distal end of left tarsometatarsus lacking IV trochlea (Figure 15 Q-S); MACN-SC 4510, distal end of right tarsometatarsus lacking IV trochlea (Figure 15 G-I); MACN-SC 4511, distal end of left tarsometatarsus with partially eroded distal trochleae (Figure 15 N-P).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation. The specimen MACN-SC 4511 comes from the Portezuelo Sumich locality (see Bown and Larriestra, 1990).

Etymology. Honouring José Boris Spivacow (1915-1994), editor of EUDEBA and Centro Editor de América Latina. Due to his efforts, more than 5000 titles were published, and without any doubt his projects have been of capital importance for Argentine cultural heritage.

Description. Small-sized *Thegornis* species (the largest tarsometatarsus, MACN-SC 1407, having 1.7 cm. of maximum distal transverse width). The metatarsal shaft is roughly "H"-shaped in cross-section. It shows a well defined, but shallow anterior metatarsal groove that is delimited by longitudinal ridges, the lateral one much more prominent than the medial one, resulting in the lateral half being more anteroposteriorly extended than the medial half of the bone. The extensor groove ends on a large and proximodistally extended distal vascular foramen. This groove forms a well-defined and deep canal.

In posterior view the metatarsal shaft is deeply excavated and delimited by two longitudinal plantar ridges. Metatarsal I impression is deep and crescent-shaped, with a proximal margin delimited by a prominent ridge.

The second metatarsal trochlea has a distinctively-formed articular body, which is rounded and ovoidal in contour. The posteromedial wing is well-defined and separated from the main body of the trochlea by a groove and a smooth depression. Metatarsal III trochlea is separated from the II trochlea by a well-defined and narrow intertrochlear incisure. The outer rim of trochlea III is more prominent than the inner rim.

The articular surface of trochlea IV is relatively transversely narrow and subrectangular in contour. In distal view it is laterally inclined. The posterior wing is slightly medially oriented and is separated from the main body of the trochlea by a transverse constriction. This also grades into a concave lateral margin of the main body of the trochlea, which results in a sigmoidal outline.

Remarks. The material belonging to *T. spivacowi* **nov. sp.** was previously identified as a caracarine falconid by Chiappe (1991). On the contrary, *Thegornis spivacowi* nov. can be nested among herpetotheriine falconids based on having the following combination of features, including the roughly "H" shaped metatarsal shaft with a prominent lateral anterior ridge, resulting in a nearly subtriangular general contour and in a very wide and extended impression of the *m abductor digiti II*, metatarsal II trochlea with posteromedial wing slightly medially oriented, rounded and prominent articular surface of trochlea II, the lateral trochlear rim of metatarsal III trochlea more posteriorly extended than the medial one, relatively thin trochlea IV and extensive posterior wing of metatarsal IV trochlea (Noriega *et al.*, 2011; Cenizo *et al.*, 2013). *Thegornis spivacowi* comfortably fits within the genus *Thegornis,* with which it shares a tarsometatarsus with the anterior surface excavated and delimited by sharp ridges intermediate in size between *Micrastur* and *Herpetotheres*, an

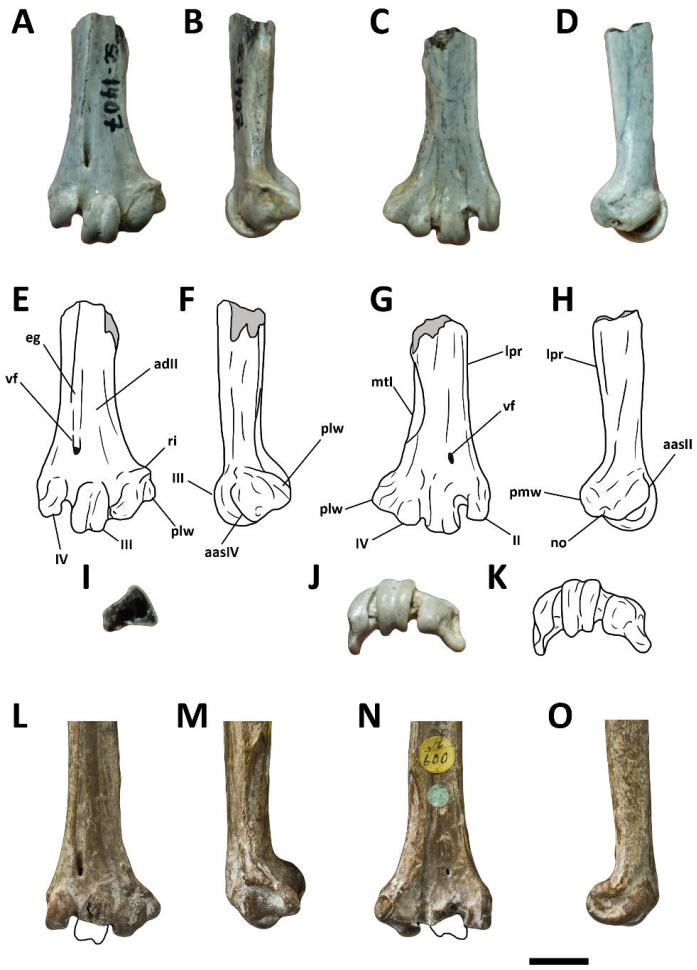

FIGURE 14. *Thegornis spivacowi* (MACN-SC 1407, holotype), A-K, distal end of right tarsometatarsus in A,E, anterior; B,F, lateral; C,G, posterior; D,H, medial; I, cross section of shaft and J-K, distal views. *Thegornis musculosus* (BMNH A-600, holotype), L-O, distal end of right tarsometatarsus with incomplete III trochlea in L, anterior; M, lateral; N, posterior; and O, medial views. Abbreviations. aasII, anterior articular surface of trochlea II; adII, impression of the *m. adductor digiti II*; eg, extensor groove of digit IV; lpr, lateral plantar ridge; mfI, metatarsal I fossa; no, distal notch; plw, posterolateral wing; pmw, posteromedial wing; ri, ridge; vf, distal vascular foramen. II-IV, metatarsal trochleae. Photographs L-O, courtesy of Sandra Chapman (BMNH) and Jorge Noriega. Scale bar A-K, 5 mm; L-O, 1 cm.

FIGURA 14. *Thegornis spivacowi* (MACN-SC 1407, holotipo), A-K, extremo distal de tarsometatarso derecho en vistas A,E, anterior; B,F, lateral; C,G, posterior; D,H, medial; I, sección de las diáfisis y J-K, vista distal. *Thegornis musculosus* (BMNH A-600, holotipo), L-O, extremo distal de tarsometatarso derecho con la tróclea III incompleta en vistas L, anterior; M, lateral; N, posterior; y O, medial. Abreviaturas. aasII, superficie articular anterior de la tróclea II; adII, impresión del *m. adductor digiti II*; eg, surco extensor del dedo IV; lpr, cresta plantar lateral; mfI, fosa metatarsal I; no, muesca distal; plw, ala posterolateral; pmw, ala posteromedial; ri, cresta; vf, foramen vascular distal. II-IV, trócleas metatarsales. Fotografías L-O, cortesía de Sandra Chapman (BMNH) y Jorge Noriega. Barra de escala: A-K, 5 mm; L-O, 1 cm.

anterolateral margin of shaft elevated as a prominent border, resulting in a roughly subtriangular contour of the shaft, a relatively low posterior lateral metatarsal ridge, large and deep metatarsal I fossa that it is proximally delimited by a prominent ridge, trochlea II slightly grooved, and posteromedial wing of trochlea II relatively thin, well-defined and strongly medially tilted.

Ameghino (1895) coined the falconid genus *Thegornis* with the aim of including the Santacrucian species *Thegornis musculosus* and *T. debilis*, which were distinguished mostly by their disparate size. Later, *Thegornis* was assigned to Accipitridae (Brodkorb, 1964; Agnolín, 2006b). However more recently, Noriega *et al.* (2011) based on newly collected specimens, including a nearly complete

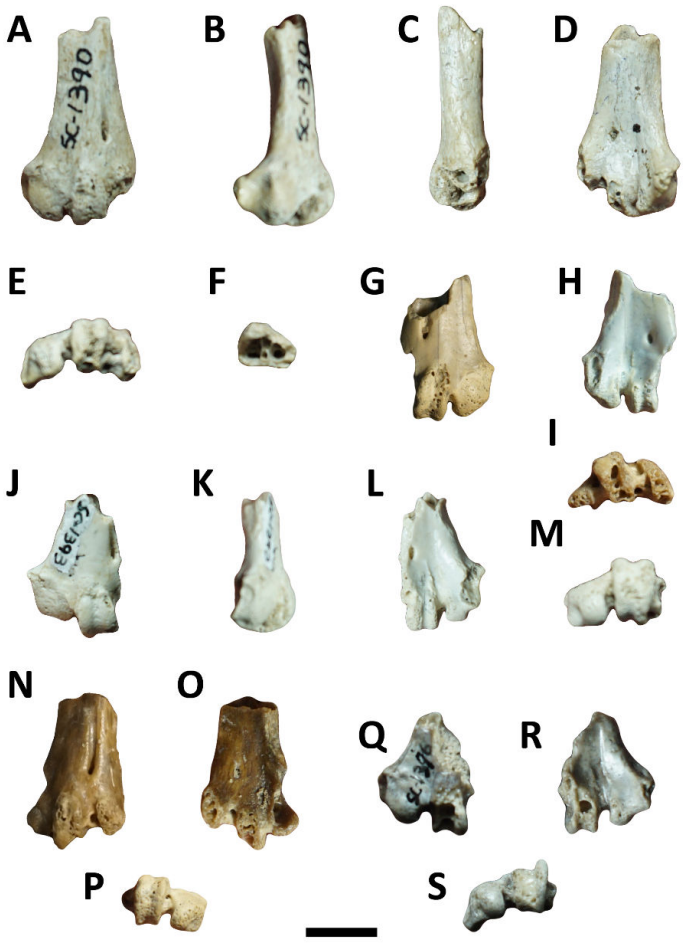

Figure 15. *Thegornis spivacowi*. A-F, distal end of left tarsometatarsus lacking II trochlea (MACN-SC 1390, paratype) in A, anterior; B, lateral; C, medial; D, posterior; and E, distal views; F, cross-section of the shaft. G-I, distal end of right tarsometatarsus lacking IV trochlea (MACN-SC 4510, paratype) in G, anterior, H, posterior, and I, distal views; J-M, distal end of left tarsometatarsus lacking IV trochlea (MACN-SC 1393, paratype) in J, anterior; K, medial; L, posterior; and M, distal views; N-P, distal end of left tarsometatarsus with partially eroded distal trochleae (MACN-SC 4511, paratype) in N, anterior; O, posterior; and P, distal views; Q-S, distal end of left tarsometatarsus lacking IV trochlea (MACN-SC 1396, paratype) in Q, anterior; R, posterior; and S, distal views. Scale bar 5 mm.

Figura 15. *Thegornis spivacowi*. A-F, extremo distal de tarsometatarso sin la tróclea II (MACN-SC 1390, paratipo) en vistas A, anterior; B, lateral; C, medial; D, posterior; y E, distal; F, sección de la diáfisis. G-I, extremo distal de tarsometatarso derecho sin la tróclea IV (MACN-SC 014, paratipo) en vistas G, anterior, H, posterior, y I, distal; J-M, extremo distal de tarsometatarso izquierdo sin la tróclea IV (MACN-SC 1393, paratipo) en vistas J, anterior; K, medial; L, posterior; y M, distal; N-P, extremo distal de tarsometatarso izquierdo con trócleas distales parcialmente erodadas (MACN-SC 015, paratipo) en vistas N, anterior; O, posterior; y P, distal; Q-S, extremo distal de tarsometatarso izquierdo sin la tróclea IV (MACN-SC 1396, paratipo) en vistas Q, anterior; R, posterior; y S, distal. Barra de escala: 5 mm.

skeleton, referred *Thegornis* to the family Falconidae, Subfamily Herpetotherinae. They also sustained that the size difference between *T. debilis* and *T. musculosus* may fit the sexual dimorphism present in extant falconids and considered that the only valid species is *T. musculosus*, a criterion with which I concur.

T. spivacowi comes from younger beds than those which yielded *T. musculosus*. In spite of their similarities, *T. spivacowi* is a smaller species that can be distinguished by details of the distal trochleae of tarsometatarsus. These include a different shape of metatarsal IV trochlea with a well-defined posterior wing and strongly sigmoidal lateral margin. The

prominent and rounded metatarsal II articular surface of *T. spivacowi* nov. resembles the condition of buteonine accipitrids (Noriega *et al.*, 2011). However, in contrast with *Thegornis musculosus* the ventral margin of the trochlea II is not complete, with the anterior articular surface being separated from the posteromedial wing by a distal notch.

STRIGIFORMES WAGLER, 1830

?Sophiornithidae Mourer-Chauviré, 1987

Genus *Enskenia* **nov. gen.**

Diagnosis. Medium-sized owl diagnosed on the basis of the following unique combination of features: 1- distal trochleae forming an opened "U" in distal view; 2- metatarsal trochlea IV small, poorly excavated, and laterally deflected; 3- metatarsal trochlea III proximodistally short (especially in posterior view), with a well-defined and proximally raised margin; 4- outer rim of metatarsal III trochlea obliquely oriented; 5- distal margin of metatarsal III trochlea distally concave; 6- medial metatarsal plantar ridge prominent and acute; and 7- distal vascular foramen wide and distally positioned, distally surrounded by a concave pit.

Etymology. Ensken, meaning "night" in Aonikenk language.

Type and only known species. *Enskenia galeanoi* **nov. sp.**

Enskenia galeanoi **nov. sp.**

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 1609, distal end of right tarsometatarsus lacking trochlea II (Figure 16 A-I).

Paratypes. MACN SC 1421, distal end of right tarsometatarsus, lacking II and IV trochleae (Figure 16 J-N); MACN SC 1430, trochlea III of right tarsometatarsus (Figure 16 O-R).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas river, Santa Cruz province, Argentina. The specimen comes from beds belonging to the Early-Middle Miocene Pinturas Formation.

Etymology. Honouring Eduardo Galeano (1940-2015), born in Uruguay, one of the most preeminent Latin American writers.

Description. A medium-sized owl the size of *Asio flammeus* (maximum distal width of holotype is 12 milimeters). The preserved part of the tarsometatarsus suggests a relatively stout element with a transversely wide shaft. The lateral and medial margins of the shaft are gently concave.

The preserved portion of the shaft in anterior view is flattened and lacks any sign of excavation. The distal vascular foramen is slit-like and continues distally as a small fossa which distally ends on a deep pit. This fossa ends level to the proximal end of IV metatarsal trochlea. The IV metatarsal trochlea is strongly laterally deflected. The wing-like posterior flange of trochlea IV is deep. In distal view it forms an angle between 75° to 80° with the horizontal plane.

Metatarsal III trochlea is proximodistally short and stout, and it is well-raised with respect to the metatarsal shaft. The rims are relatively robust, well-defined, and are separated by a middle longitudinal groove. The trochlea III shows a subtle asymmetry in distal view, with the rims having subequal distal extent. The lateral rim of the trochlea is relatively thick and more posteriorly extended than the medial rim. In spite of having broken off, the II metatarsal trochlea shows a poorly-defined and low plantar ridge.

The distal end of the bone forms a wide arch, not strongly "U" shaped. Metatarsal I fossa is weakly indicated and located at the posterior margin of the shaft. Posterior metatarsal groove is very shallow.

Remarks. In spite of being poorly preserved, the tarsometatarsus of *Enskenia* **nov. gen.** shows a unique combination of characters that allows for recognizing its affinities among strigiforms. In contrast to crown-Strigiformes, Paleoglaucidae, Protostrigidae, and Ogygoptyngidae it shows poorly excavated anterior and posterior metatarsal grooves (despite being incompletely preserved, the anterior surface of the bone in most owls shows a concave surface that reaches the level of the distal vascular foramen), and a poorly arched distal end of the bone (Vickers Rich and Bohaska, 1981; Mourer-Chauviré, 1987, 1994; Mayr, 2016b), a combination of characteristics that distinguish the extinct clade Sophiornithidae. Furthermore, *Enskenia* differs from Protostrigidae, Paleoglaucidae, and Ogygoptyngidae in having a robust and transversely wide tarsometatarsus shaft (Martin and Black, 1972; Mayr, 2016b; Mourer-Chauviré, 1987, 1994; Peters, 1992; Vickers Rich and Bohaska, 1981). In spite of little overlapping material, *Enskenia* differs from the enigmatic *Primoptynx* in having a deeply grooved trochlea III with prominent condyles, and trochlea IV not strongly transversely compressed (Mayr *et al.*, 2021). Moreover, the tarsometatarsus of *Enskenia* appears to be much more robust than the elongate one of *Primoptynx* (Mayr *et al.*, 2020a).

Enskenia is very similar in shape and size to that of other sophiornithids, including the genera *Sophiornis* and *Berruornis* (Mourer-Chauviré, 1987, 1994). Comparisons with the genus *Sophiornis* are difficult because of few overlapping characteristics. However, *Enskenia* differs in having the distal end of the bone transversely narrower, and in having a more proximally positioned distal vascular foramen, which is far from the proximal margin of the trochlea III (a condition shared with *Berruornis*; Mourer-Chauviré, 1994). This contrasts with *Sophiornis,* where the foramen is located on level with the

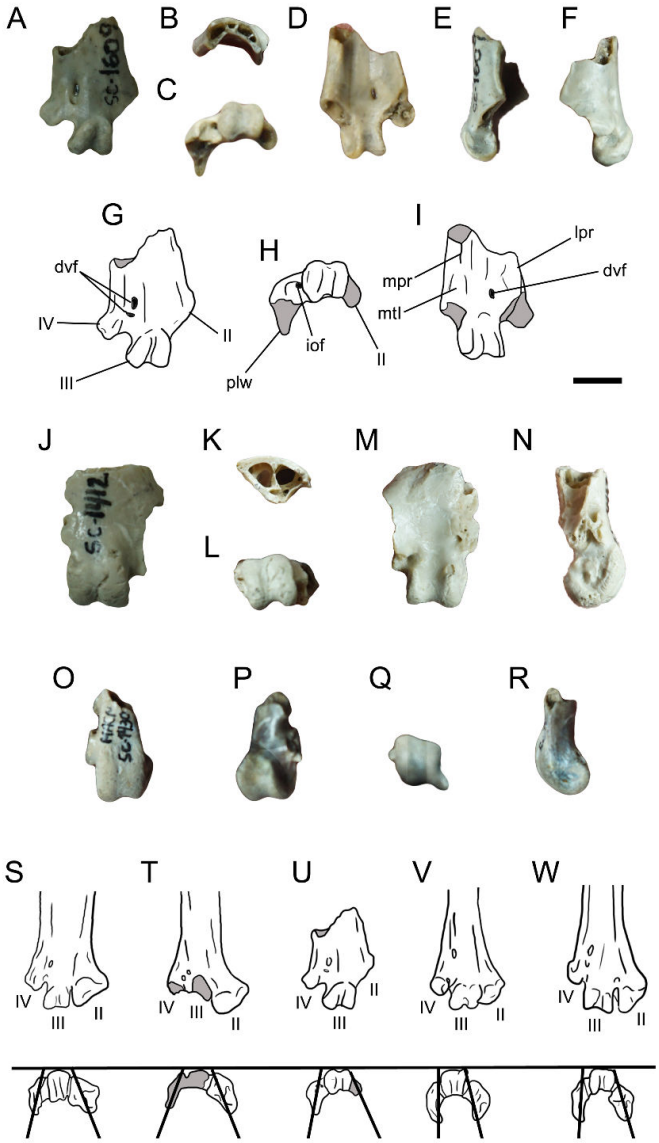

Figure 16. *Enskenia galeanoi*. A-I, distal end of right tarsometatarsus lacking trochlea II (MACN SC 1609, holotype) in A,G, anterior; B, proximal; C,H, distal; D,I, posterior; E, medial; and F, lateral views. J-N, distal end of right tarsometatarsus, lacking II and IV trochleae (MACN SC 1421, paratype) in J, anterior; K, proximal; L., distal; M, posterior; and N, medial views. O-R, trochlea III of right tarsometatarsus (MACN SC 1430, paratype) in O, anterior; P, posterior; Q, distal; and R, medial views. S-W, distal end of right tarsometatarsus of selected strigiforms in anterior (top) and distal (bottom) views: S, *Berruornis orbistanqui*; T, *Sophiornis quercynus*; U, *Enskenia galeanoi*; V, *Eostrix gulottai*; W, *Asio flammeus*. The lines at the bottom figures represent the main axis of the body of distal trochlea in distal view when compared with the horizontal plane. This evidences the much wider angle present in sophiornithids (S-U) when compared with other strigiforms. Abbreviations. dvf, distal vascular foramen; iof, interosseous opening; lpr, lateral plantar ridge; mpr, medial plantar ridge; mtI, metatarsal I fossa; plw, posterolateral wing of metatarsal IV trochlea. S-T, redrawn from Mourer-Chauviré (1994); V, redrawn from Mayr (2016). Scale bar: 5 mm.

Figura 16. *Enskenia galeanoi*. A-I, extremo distal de tarsometatarso derecho sin la tróclea II (MACN SC 1609, holotipo) en vistas A,G, anterior; B, proximal; C,H, distal; D,I, posterior; E, medial; y F, lateral. J-N, extremo distal de tarsometatarso derecho sin las trócleas II y IV (MACN SC 1421, paratipo) en vistas J, anterior; K, proximal; L., distal; M, posterior; y N, medial. O-R, tróclea III del tarsometatarso derecho (MACN SC 1430, paratipo) en vistas O, anterior; P, posterior; Q, distal; y R, medial. S-W, extremo distal de tarsometatarso derecho de algunos strigiformes en vistas anterior (arriba) y distal (debajo): S, *Berruornis orbistanqui*; T, *Sophiornis quercynus*; U, *Enskenia galeanoi*; V, *Eostrix gulottai*; W, *Asio flammeus*. Las líneas sólidas en las figuras inferiores representan el eje mayor del cuerpo de las trócleas distales en comparación con el plano horizontal. Este rasgo evidencia el mayor ángulo presente en los sophiornítidos (S-U) cuando es comparado con otros Strigiformes. Abreviaturas. dvf, foramen vascular distal; iof, apertura interósea; lpr, cresta plantar lateral; mpr, cresta plantar medial; mtI, fosa metatarsal I; plw, ala posterolateral de la tróclea IV. S-T, redibujado de Mourer-Chauviré (1994); V, redibujado de Mayr (2016). Barra de escala: 5 mm.

trochlea III and is very close to its proximal margin. Furthermore, in *Enskenia* the metatarsal I fossa is shallower and narrower than in *Sophiornis* (Mourer-Chauviré, 1987).

Enskenia differs from *Berruornis* in having metatarsal trochlea III strongly raised from the metatarsal shaft and with deep trochlear rims (Mourer-Chauviré, 1994). The trochlea IV in *Enskenia* is strongly laterally oriented, a condition that departs from that of *Berruornis*.

CORACIIFORMES *SENSU* MAYR, 1998

Coracii Wetmore and Miller, 1926
Coraciidae Batsch, 1788
Genus *Chehuenia* **nov. gen.**

Diagnosis. Coraciid diagnosed on the basis of the following unique combination of characteristics: 1- very large trochlea II with a proximally extended medial wing; 2- posteromedial wing of metatarsal trochlea II strongly posteriorly extended; 3- poorly excavated posterior surface of trochlea II; 4- IV metatarsal trochlea only slightly shorter than trochlea III and the latter longer than II metatarsal trochlea; 5- transversely narrow IV metatarsal trochlea; 6- proximally positioned distal vascular foramen; and 7- deep longitudinal groove separating metatarsals II and III in posterior view.

Etymology. Cheuen, from the Aonikenk language: little bird.

Type and only included species. *Chehuenia facongrandei* nov. sp.

Chehuenia facongrandei nov. sp.

Diagnosis. The same as for genus by monotypy.

Holotype. MACN SC 4512, distal end of left tarsometatarsus (Figure 17).

Locality and horizon. The specimen comes from the Santa Cruz Formation (Early-Middle Miocene), at the well-known fossiliferous locality of Monte León (the label indicates "Estaca 3"), Monte León National Park, Santa Cruz province, Argentina.

Etymology. facongrandei, honouring José Font "Facón Grande" (1883-1921), an Argentine worker and anarcho-syndicalist, killed during rural strikes in Patagonia by 1921.

Description and comparisons. The distal end of the tarsometatarsus is anteroposteriorly flat and transversely wide (4.5 milimeters of maximum distal width). On the anterior face, the distal vascular foramen is proximally positioned and is proximodistally elongate. As with other coraciids, the distal vascular foramen is obliquely oriented from its anterior opening, which is anterolaterally located to its posterior opening, which is posteromedially located. This foramen is located at the end of the very deep and well-defined outer extensor groove. Metatarsal trochlea IV is only slightly more distally extended with respect to trochlea III. II metatarsal trochlea is shorter than trochlea III, which shows well defined and prominent rims separated by a deep longitudinal groove. IV trochlea is transversely narrow and subrectangular in contour. II trochlea is robust and proximodistally extended, with a prominent medial wing that contrasts with the smaller one observed in other coraciids such as *Miocoracias* (Mourer-Chauviré *et al.*, 2013). The distal interosseous canal is deep and well defined.

In posterior view the shaft proximal to the trochleae is notably concave. The posterior opening of the distal vascular foramen is ovoidal in contour and is strongly proximomedially oriented. There is a proximal longitudinal groove separating metatarsals IV and III. The distal interosseous canal is shallow and poorly defined. II metatarsal trochlea is thick, with a very well-developed posteromedial wing. The proximal end of trochlea III is not raised. Posterior surface of trochlea II is poorly excavated. IV metatarsal trochlea has a well-developed posterior wing. Metatarsal fossa I is well-defined and proximally placed, as occurs in *Coracias*. In distal view the trochleae form a "U" shaped open arch.

Remarks. The tarsometatarsus of *Chehuenia* **nov. gen.** is referable to Coraciidae on the basis of the following unique combination of characteristics (Bourdon *et al.*, 2016; Degrange *et al.*, 2021; Mayr, 2022; Mayr and Mourer-Chauviré, 2000; Mourer-Chauviré, 1999; Mourer-Chauviré *et al.*, 2013): short, wide and flattened distal end of the tarsometatarsus, the anterior surface lacks a well-marked extensor groove, trochleae II and IV shorter than trochlea III, trochlea II reaches farther distally than trochlea IV (trochleae III and IV are subequally extended distally in Geranopteridae; Mayr and Mourer-Chauviré, 2000; Mourer-Chauviré, 1999), deep distal interosseous groove between trochleae III and IV, and enlarged distal vascular foramen.

In spite of being represented by several fossils in the past, the fossil record of Coraciidae is now restricted to the extinct genus *Miocoracias* and the still living genera *Coracias* and *Eurystomus* (Mourer-Chauviré *et al.*, 2013). Most other taxa previously referred as being fossil coraciids resulted as being part of other coraciiform lineages (Mayr, 2009; Mayr and Mourer-Chauviré, 2000; Mourer-Chauviré, 1999; Mourer-Chauviré *et al.*, 2013). Comparisons between *Chehuenia*, *Miocoracias, Coracias,* and *Eurystomus* indicate that the former is a distinctive taxon. In *Chehuenia* the distal vascular foramen is proximally positioned and is proximodistally elongate, being similar in both aspects to the extinct genus *Miocoracias*, and different from the condition of living genera *Coracias* and *Eurystomus* (Mourer-Chauviré *et al.*, 2013). Its metatarsal trochlea IV is only slightly distally extended than trochlea III, in

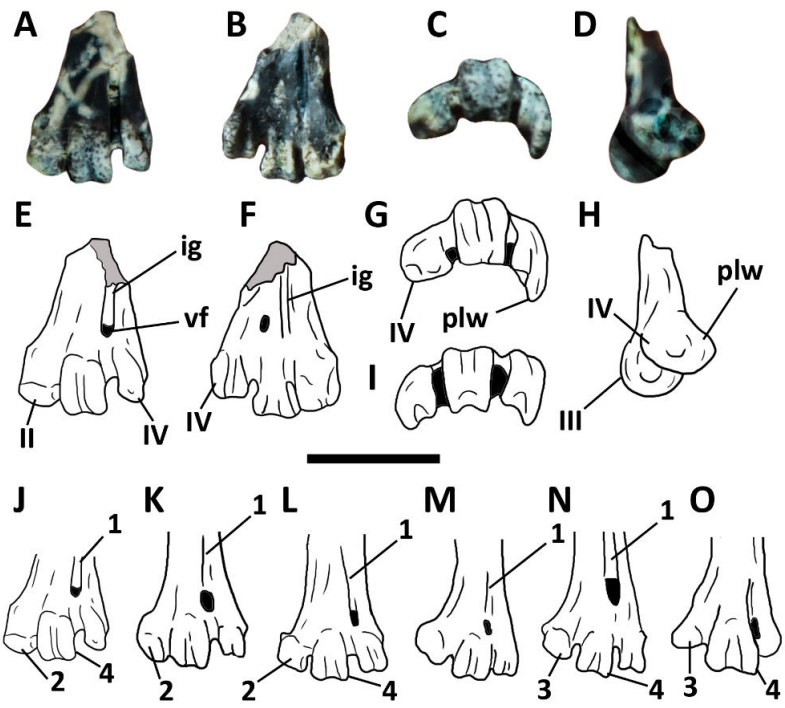

Figure 17. *Chehuenia facongrandei* (MACN SC 016, holotype) distal end of left tarsometatarsus in A,E, anterior; B,F, posterior; C,G, distal; and D,H, lateral views. I, *Miocoracias chenevali*, distal end of left tarsometatarsus in distal view. J-O, left tarsometatarsus in anterior view of selected coraciiforms: J, *Chehuenia facongrandei*; K, *Coracias garrulus* (Coraciidae); L, *Miocoracias chenevali*; M, *Eurystomus glaucurus* (Coraciidae); N, *Geranopterus alatus* (Geranopteridae); and O, *Ueekenkcoracias tambussiae*. Abbreviations. ig, interosseous groove; plw, posterolateral wing; vf, distal vascular foramen; II-IV, corresponding number of distal trochlea; 1, deep and well-defined anterior interosseous groove between metatarsals III and IV; 2, distal trochlea II more distally extended than trochlea IV, being close to the distal level of trochlea III; 3, proximally positioned trochlea IV; 4, distally splayed trochlea III. Scale bar: A-D, 5 mm; J-O, not to scale. I, L, redrawn from Mourer-Chauviré *et al.* (2013); K,M, redrawn from Mourer-Chauviré (1999); N, redrawn from Mayr and Mourer-Chauviré (2000); O, redrawn from Degrange *et al.* (2021).

Figura 17. *Chehuenia facongrandei* (MACN SC 016, holotipo) extremo distal de tarsometatarso izquierdo en vistas A,E, anterior; B,F, posterior; C,G, distal; y D,H, lateral. I, *Miocoracias chenevali*, extremo distal de tarsometatarso izquierdo en vista distal. J-O, tarsometatarso izquierdo en vista anterior de algunos Coraciiformes: J, *Chehuenia facongrandei*; K, *Coracias garrulus* (Coraciidae); L, *Miocoracias chenevali*; M, *Eurystomus glaucurus* (Coraciidae); N, *Geranopterus alatus* (Geranopteridae); y O, *Ueekenkcoracias tambussiae*. Abreviaturas. ig, surco interóseo; plw, ala posterolateral; vf, foramen vascular distal; II-IV, trócleas distales; 1, surco interóseo entre metatarsales III y IV profundo y bien definido; 2, tróclea distal II más extendida distalmente que la tróclea IV, cercana al nivel de la tróclea III; 3, tróclea IV ubicada proximalmente; 4, tróclea III distalmente expandida. Barra de escala: A-D, 5 mm; J-O, no a escala. I, L, redibujado de Mourer-Chauviré *et al.* (2013); K,M, redibujado de Mourer-Chauviré (1999); N, redibujado de Mayr y Mourer-Chauviré (2000); O, redibujado de Degrange *et al.* (2021).

contrast to the shorter condition shown by *Miocoracias* and *Coracias*. IV metatarsal trochlea in *Chehuenia* is transversely narrow and subrectangular in contour, contrasting with the subquadrangular condition present in *Miocoracias, Coracias,* and *Eurystomus.* Its metatarsal IV shows a well-developed posterior wing that is more developed than in *Miocoracias* and *Eurystomus*, whereas in *Coracias* this wing is nearly absent. Metatarsal III trochlea of *Chehuenia* shows well defined and prominent rims separated by a deep groove as in *Miocoracias*, and contrasting with *Coracias* and *Eurystomus*. II metatarsal trochlea is thicker than in *Miocoracias* and *Coracias*, and its posteromedial wing is very well-developed, and is as posteriorly extended as in *Coracias*. The posterior opening of the distal vascular foramen in *Chehuenia* is ovoidal in contour, as in *Coracias* and *Eurystomus*, but contrasting with the more elongate condition present in *Miocoracias*. In distal view the trochleae

form a "U" shaped opened arch, more marked than in *Eurystomus* and *Coracias*.

As remarked by the comparisons made above, the position of *Chehuenia* within Coraciidae is not clear. As indicated in the descriptive section, there are some differences with extant members of Coraciidae. In contrast to extant members of the clade, the trochlea metatarsi III is distally splayed (Mourer-Chauviré *et al.*, 2013). On the other side, some similarities are noted with *Miocoracias* from the Early Miocene of France, namely, the well developed posterior wing of metatarsal IV trochlea and arched trochleae in distal view (see Mourer-Chauviré *et al.*, 2013). The incomplete nature of the available specimen does not allow for refining the phylogenetic position of *Chehuenia* among coraciids.

The only previous fossil record of fossil coraciiforms in South America is *Ueekenkcoracias tambussiae*, from the Eocene of Chubut province, Patagonia (Degrange *et al.*, 2021; but see Mayr, 2022). *Chehuenia* differs from *Ueekenkcoracias* in having metatarsal trochlea IV more distally extended than trochlea II, and in that the II trochlea is not strongly medially deflected.

PASSERIFORMES LINNAEUS, 1758

Tyranni Wetmore and Miller, 1926

Indeterminate genus and species

Referred material. MACN SC 3300, incomplete distal end of right tarsometatarsus (Figure 18 F-H); MACN SC 3303, incomplete distal end of right tarsometatarsus (Figure 18 D-E); MACN SC 3304, incomplete distal end of left tarsometatarsus (Figure 18 A-C); MACN SC 3305, incomplete distal end of right tarsometatarsus (Figure 18 I-K).

Locality and horizon. Loma de la Lluvia fossil site, Pinturas River, Santa Cruz province, Argentina. The specimens come from beds belonging to the Early-Middle Miocene Pinturas Formation.

Description. Based on size and shape, three different morphotypes can be recognized.

The first morphotype is represented by specimen MACN SC 3303. It is the largest available specimen (2 milimeters of maximum transverse width). In spite of being incompletely preserved, it resembles in size and shape the furnariid genus *Pseudoseisura*. The distal end of the bone shaft is anteroposteriorly flattened. Medial and lateral margins of the shaft are strongly distally divergent. The IV trochlea slightly surpasses distally the proximal edge of the III trochlea. It is subrectangular in contour when viewed anteriorly and shows a well-developed excavation. Both trochlea IV and III are proximally delimited by subcircular and deep extensor pits. The preserved base of the trochlea III indicates that it was notably large. Intertrochlear grooves are well developed and are proximally extended along the shaft as shallow grooves that reach the level of the distal vascular foramen. The distal vascular foramen is relatively small and slit-like, and is proximally extended by a well defined and deep outer extensor groove. Scar for metatarsal I is crescent shaped, relatively well-excavated and well-delimited, but not strongly raised from the shaft.

Specimen MACN SC 3300 shows a combination of characteristics very similar to MACN SC 3303, but is much smaller (1.5 milimeters of maximum preserved width). The trochlea III is strongly excavated and is proximally continuous with the extensor pit. In posterior view the excavation of the trochlea is delimited by nearly symmetrical sharp medial and lateral rims.

Specimens MACN SC 3304 and MACN SC 3305 represent a third morphotype (1.7 milimeters of maximum preserved width between distal trochleae in MACN SC 3304). They are very similar in several features to the previously described morphotypes, but are much smaller. They show intermetatarsal grooves, proximally extending from the intertrochlear notches, much deeper and more well-defined than in other morphotypes. The trochlea III is well-excavated and distally flared, resulting in a subtriangular contour when viewed anteriorly. It is anteriorly raised from the rest of the metatarsal shaft. The preserved part of trochlea II indicates that it was relatively small and medially inflected.

Remarks. The specimens described here are referred to passeriforms because of the combined presence of distal trochlea in the same plane when viewed distally, with III trochlea notably larger than IV and IV, wide intertrochlear grooves, and the lateral plantar ridge not prominent (Hamon, 1964; Mayr and Manegold, 2004; see also Manegold, 2008). Furthermore, in spite of their incomplete nature, the specimens may be included among Tyranni suboscines by having the scar for metatarsal I not well-raised from the shaft, trochlea II relatively small, trochlea III slightly distally expanded, and trochlea IV somewhat laterally inflected and excavated (the later shared with Menurae; Ballmann, 1969; Boles, 1995a,b; Hamon, 1964; Manegold, 2008). Moreover, as in most Tyranni, the distal end of the bone proximal to the trochleae is strongly flattened (Pycraft, 1906).

Among Tyranni, the phylogenetic position of available specimens is not certain. They differ from Dendrocolaptidae because trochlea IV is much shorter and smaller than trochlea III and because the distal end of the bone does not suddenly broadens transversely (Feduccia, 1973; Manegold, 2008; Maurício *et al.*, 2012). In contrast to Thamnophilidae and "Furnariidae" trochlea IV is distinctly grooved (shared with Rhinocryptidae and Formicariidae;

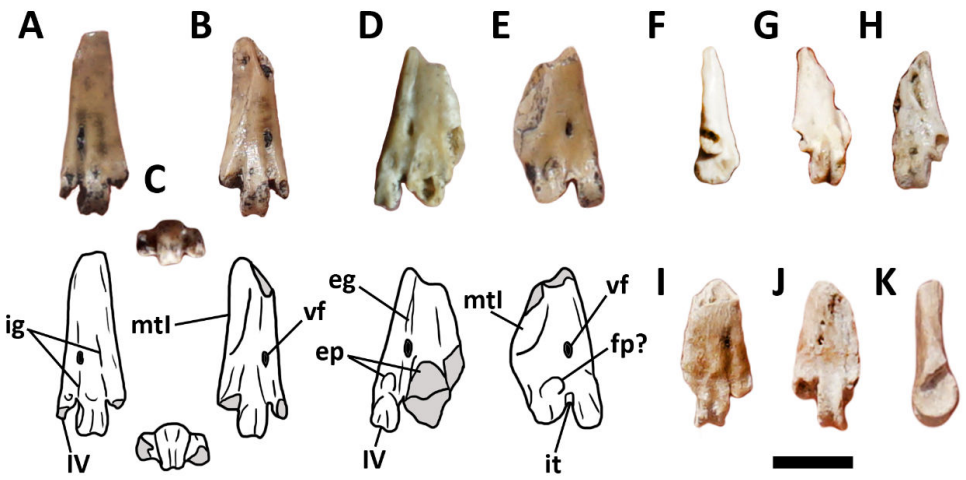

Figure 18. Tyranni indet. A-C, Morphotype 3 (MACN SC 3304), incomplete distal end of left tarsometatarsus in A, anterior; B, posterior; and C, distal views; D-E, Morphotype 1 (MACN SC 3303), incomplete distal end of right tarsometatarsus in D, anterior; and E, posterior views; F-H, Morphotype 2 (MACN SC 3300), incomplete distal end of right tarsometatarsus in F, lateral; G, anterior; and H, posterior views; I-K, Morphotype 3 (MACN SC 3305), incomplete distal end of right tarsometatarsus in I, anterior; J, posterior; and K, medial views. Abbreviations: eg, outer extensor groove; ep, extensor pit; fp?, possible flexor pit; ig, intermetatarsal grooves; it, intertrochlear groove; mtI, fossa for metatarsal I; vf, distal vascular foramen; IV, fourth metatarsal trochlea. Scale bar: 2 mm.

Figura 18. Tyranni indet. A-C, Morfotipo 3 (MACN SC 3304), extremo distal incompleto de tarsometatarso izquierdo en vistas A, anterior; B, posterior; y C, distal; D-E, Morfotipo 1 (MACN SC 3303), extremo distal incompleto de tarsometatarso derecho en vistas D, anterior; y E, posterior; F-H, Morfotipo 2 (MACN SC 3300), extremo distal incompleto de tarsometatarso derecho en vistas F, lateral; G, anterior; y H, posterior; I-K, Morfotipo 3 (MACN SC 3305), extremo distal incompleto de tarsometatarso derecho en vistas I, anterior; J, posterior; y K, medial. Abreviaturas: eg, surco extensor externo; ep, fosa extensora; fp?, posible fosa flexora; ig, surcos intermetatarsales; it, surco intertroclear; mtI, fosa para el metatarsal I; vf, foramen vascular distal; IV, tróclea metatarsal IV. Barra de escala: 2 mm.

Feduccia and Olson, 1982; Maurício *et al.*, 2012). Trochlea III shows a well-defined and deep groove, as occurs in Dendrocolaptidae, Rhinocryptidae and Formicariidae, contrasting with "Furnariidae" and Tyrannidae (see Feduccia and Olson, 1982; Manegold, 2008; Maurício *et al.*, 2012). In contrast to Dendrocolaptidae and "Furnariidae" trochlea II does not exceed the anterior surface of the tarsometatarsus (Manegold, 2008). In most of the above mentioned features, available specimens are similar to Formicariidae, but a taxonomic referral is far from certain. It is preferred here to leave the specimens as indeterminate Tyranni.

DISCUSSION

The new fossil bird remains described above belong to different avian clades and constitute important additions to the knowledge of Miocene birds from Patagonia.

Tinamidae. The description of the new genus and species of tinamid *Mininothura talenki* constitutes an important addition to the palaeognath clade. Despite being represented by distal humeri, the morphology of available elements indicates a very small species with distinctive anatomical features. *Mininothura*, together with previously described tinamid remains from the Santa Cruz and Pinturas Formations (Bertelli and Chiappe, 2005; Chiappe, 1991), show that the tinamid radiation was far more impressive than presumed. *Mininothura* and other tinamids from Santa Cruz and Pinturas beds do not comfortably fit any of the extant tinamid lineages and may have formed part of a stem-tinamid radiation that does not have direct relationships to extant members of the clade.

Anseriformes. The fossil record of anseriforms in the Paleogene and early Neogene in South America, particularly Patagonia, is still very patchy. However, it is enough to demonstrate that anseriforms were very diverse and included a large number of lineages and basal members of the group (see Cenizo and Agnolín, 2010).

Peioa is a basal anseriform of uncertain affinities. It lacks derived features characterizing most anseriform clades, but shows some features in common with the coeval *Eutelornis* and extant anseranatids. Regardless of its affinities, it reinforces

previous thoughts indicating that South America harbored a high diversity of basal anseriforms that are still very poorly known and waiting to be discovered (Cenizo and Agnolín, 2010).

Chainkanas koshon is a new member of the clade Anhimidae. Anhimids have a very poor fossil record. Its oldest members are *Chaunoides* and *Loxornis* from the Oligocene of Brazil and Patagonia, respectively (Alvarenga, 1999). Extant members of the Anhimidae have their southernmost records in Buenos Aires province, Argentina (De La Peña, 2013). *Chainkanas* is more than 1300 kilometers away from the southernmost records of the clade, which is congruent with other faunistic evidence (e.g., monkeys, porcupines, seriemas; Tonni and Carlini, 2008) indicative of a warmer and humid climate in southern Patagonia during early Miocene times.

Tadornine anatids described here include the new genera and species *Kaikenia mourerchauvirea* and *Tamtamia yzurietai*, both very different from each other in size and anatomical features. Both strongly differ from each other and also from the extant Patagonian tadornines of the genus *Chloephaga*. The differences between these anatids and other known members of the clade may indicate that they are not closely related to any extant tadornines and they may constitute extinct branches of the lineage.

It is worth mentioning that there are no fossil specimens belonging to the derived clade Anatini, which includes *Anas* and its kin (Livezey, 1991). This reinforces the idea that anatines arrived in South America during Pleistocene times, as indicated elsewhere (Agnolín and Tomassini, 2012). In addition, no remains of dendrocygnines were found, in contrast to the Miocene beds of Chubut province (Acosta Hospitaleche *et al.*, 2007) and early Pliocene of Buenos Aires province (Agnolín and Tomassini, 2012). However, it should be noted that the identification of the latter specimen is not certain. Important differences in the shape of the anterior articular ligament and strong compression of the distal end of the humerus reported by Agnolín and Tomassini (2012) are reminiscent of some waterbirds, such as phoenicopterids.

The finding of early Miocene basal Anseriformes, Anhimidae, and Tadorninae in Patagonia constitutes an important addition to extinct avifaunas from the Southern Cone and helps to fill important gaps in the anseriform fossil record.

Phoenicopteriformes. The fossil record of Tertiary phoenicopteriforms in South America is restricted to a few localities (Ubilla *et al.*, 1990; Alvarenga, 1990; Noriega and Agnolín, 2008; Agnolín, 2009). Ameghino (1899) described the new genus and species *Tiliornis senex* based on a coracoid coming from Oligocene beds in Santa Cruz province. However, his description is very brief and the specimen on which he based the description is now lost. This left *Tiliornis senex* as a *nomen dubium* (see Tonni, 1980).

Tiliornis aside, the oldest unambiguous record for Phoenicopteriformes in South America comes from the Oligocene Tremembé Formation in Brazil, where the presence of the genera *Agnopterus* and *Palaelodus* is reported (Alvarenga, 1990). The specimens described here constitute the second oldest records for the clade in South America, and indicate that *Juncitarsus*-like phoenicopteriforms were probably present in Patagonia during the early-middle Miocene. Despite the fact that *Juncitarsus* was traditionally included among phoenicopteriforms, recent authors have suggested that it may be the sister taxon to the clade formed by phoenicopteriforms and podicipediforms (Mayr, 2014).

Gruiformes. Fossil gruiforms from South America include ralloids, gruids (including the fossil species *"Aramus" paludigrus*; see Contreras *et al.*, 2019) from the late Miocene of Argentina and Colombia (Noriega and Agnolín, 2008; Contreras *et al.*, 2019), and cariamiforms of the clades Idiornithidae, Cariamidae and Phororhacoidea (Agnolín, 2009; Tambussi and Degrange, 2013).

Chiappe (1991) mentioned the presence of a cariamid within the Pinturas Formation, but I was not able to find the specimen. This record may be based on the specimen that is assigned in this work to the new genus and species of gruoid *Patagogrus olsoni*. As indicated previously by Chiappe (1991), phororhacoids are very scarce in the Pinturas Formation bird assemblage, being represented by incomplete remains of a possible Psilopterinae (pers. obs.).

Patagogrus constitutes the first gruid described from Patagonia. The fossil record of gruoids, and particularly gruids, is almost entirely restricted to North America and the Old World (Cracraft, 1973a; Olson, 1985). In South America, the fossil record of gruids is restricted to cf. *Grus* sp., from the late Miocene Ituzaingó Formation in northeastern Argentina (Noriega and Agnolín, 2008) and *"Aramus" paludigrus* from the middle Miocene of Colombia, which was originally considered to be a large species of the genus *Aramus* (Rasmussen, 1997) and more recently as a possible member of Gruidae (Contreras *et al.*, 2019). If the identification of *Patagogrus* is correct, it may constitute the oldest record for the clade in South America, and one of the few records on the entire continent. It also indicates that gruids were much more geographically widespread and diverse than previously assumed.

Gruids, together with coraciiforms, form two clades having fossil records in South America, but that had become regionally extinct by post-Miocene times (see Degrange *et al.*, 2021). Their geographical distribution during the Cenozoic is a pattern matched by several avian lineages that were much more widespread in the geologic past than today (see Mayr, 2011).

Parvigruids are an extinct clade of basal gruoids that has their fossil record restricted to the Oligocene of Europe (Mayr, 2005, 2009, 2013; Mayr and Smith, 2001). If correctly identified, the parvigruid *Alhuenia* may constitute the youngest record for the clade, but more importantly, the first record of parvigruids in South America. It represents an additional example of shared avifaunas between Europe and South America and also makes evident that the history of gruiforms in the continent is far from being satisfactorily known.

The Psophiidae is a small group of gruoids that are now represented by 8 species of the genus *Psophia,* geographically restricted to the tropics of South America (Oppenheimer and Silveira, 2009). *Archaeopsophia aoni* described here shares the unique combination of characteristics exhibited on the hypotarsus diagnostic of Psophiidae. Previously, Olson (1985) suggested that the early Miocene Patagonian *Anisolornis excavatus* was similar to psophiids, but this taxon is now regarded as an indeterminate gruiform (Tambussi and Degrange, 2013). A possible psophiid coracoid was described from the Oligocene of France (Mayr and Mourer-Chauviré, 2006), which is an additional example of shared bird taxa between South America and Europe (see Agnolín, 2016). Similar to the case of Anhimidae and other fossil birds, the record of Psophiidae in Santa Cruz is located far from the distribution of extant members of the clade, by more than 3000 kilometers, supporting the claim of more humid and warmer conditions for the area during the Miocene (Tonni and Carlini, 2008; Vizcaino *et al.*, 2012).

The fossil specimens reported here from the Pinturas Formation and belonging to Rallidae, constitute the oldest record for the family in South America. The previously undisputed oldest rallids were from the Pleistocene epoch (Cenizo *et al.*, 2015; Cuello, 1988). This implies that the regional paleontological record of rallids is very patchy, and indicates that the evolutionary history of the clade in the continent is nearly unknown.

Falconidae. Fossil falconids from the early Miocene of Patagonia were first noticed by Ameghino (1894, 1895, 1899) who described the genera *Badiostes* and *Thegornis* from Santacrucian beds. Noriega *et al.* (2011) indicated that *Thegornis* belongs to the falconid subfamily Herpetotherinae. Later, Agnolín (2016) referred to herpetetheriines the genus *Badiostes,* as well as an incomplete skull from the late Miocene of Chubut province, Patagonia, that was previously referred to Accipitridae (Picasso *et al.*, 2009). To this list of herpetotheriines we add here the new species *Thegornis spivacowi*, which is much smaller than the type species of the genus *Thegornis musculosus*. This reinforces the idea that herpetotheriines in the past were strongly diversified and widespread throughout Patagonia (Agnolín, 2016). Furthermore, the finding of *Thegornis* in both Santacrucian and Pinturan beds constitutes the first bird genus shared between both stratigraphical units. It is worth mentioning that no single bird species is shared by the aforementioned formations.

Adding here to the meager list of Patagonian fossil falconids, is the new genus and species *Caroohierax rapoporti*. Despite being known by an incomplete distal end of a tarsometatarsus, it is enough to conclude that it does not belong to any particular falconid clade. These records, together with the finding of a basal falconid from the Eocene of Antarctica (Cenizo *et al.*, 2013) support the view that falcons had an important chapter of their evolution on southern continents.

Strigiformes. *Enskenia galeanoi* constitutes the oldest record of Strigiformes from South America (as indicated by Chiappe, 1991), and is separated by more than 10 million years from the remaining records of the clade that are restricted to the Pleistocene (LoCoco *et al.*, 2020), indicating a very long gap in the fossil record for the entire continent.

Enskenia is known by incomplete tarsometatarsi that show plesiomorphic features when compared with recent Strigidae and Tytonidae. In several aspects it is similar to the Paleogene-early Neogene owls of the clade Sophiornithidae, geographically restricted to Europe (Mayr, 2009; Mourer-Chauviré, 1994). If this identification is correct, the Sophiornithidae may constitute an additional Tertiary bird clade shared between South America and Europe.

Coraciidae. Coraciiforms are represented in the fossil record of South America by the stem-Coracii *Ueekenkcoracias tambussiae* described from Eocene beds at Chubut province, Patagonia (Degrange *et al.*, 2021). Recently, Mayr (2022) questioned the affinities of this taxon and proposed that it belongs to a form closely related to the Eocene European genus *Palaeopsittacus*. In any case, the finding of the derived coraciid *Chehuenia facongrandei* in the early Miocene beds of Santa Cruz indicates that the coraciiforms were widespread both temporally and geographically in South America. Regrettably, its fossil record is still extremely biased. If correctly

identified, *Chehuenia* may constitute the first record for the family in the entire continent.

Although nowadays Coracii has a mainly paleotropical distribution, its fossil record includes several specimens from the Paleogene of Europe and North America (Mayr, 2009). *Chehuenia* (as well as *Ueekenkcoracias* if its coraciiform affinities are accepted), and a fossil coraciiform reported from the early Eocene of the Tingamarra fauna in Australia (Elzanowski and Boles, 2015) indicate that these arboreal birds were geographically widespread in the past. Together with gruids, coraciiforms constitute a bird clade that had a wide past geograhical distribution and are nowadays restricted to the Old World.

Passeriformes. Previous fossil records of Passeriformes in South America were restricted to Pliocene and Pleistocene beds (Noriega, 1998), with the exception of a distal end of humerus coming from the Pinturas Formation (Noriega and Chiappe, 1993) and an incomplete ulna from the Late Miocene (Cenizo *et al.*, 2012). Both the ulna and humerus were identified as belonging to Tyranni, a clade that is traditionally regarded as having a long history, and probably its own origin in South America (Cracraft, 1973b; Feduccia, 1977; Feduccia and Olson, 1982; Mayr, 1964), as well as probably former Gondwana landmasses (e.g., Claramunt and Cracraft, 2015; Cracraft, 2001; Edwards and Boles, 2002). However, recent findings of fossil Tyranni in Oligocene beds from Europe (e.g., Bochénski *et al.*, 2011, 2018, 2021; Manegold, 2008, 2009; Mayr, 2013b), indicate that the history of the clade is far more complex than perviously thought.

The fossils described here constitute the oldest member of passeriforms known in South America (Noriega and Chiappe, 1993). These indicate that a relatively high diversity of Tyranni was represented by early Miocene times in South America (at least three different morphotypes of tarsometatarsus in coeval beds were reported). Similarly, records from Oligocene-early Miocene in Australia (as reported earlier by Boles, 1995b), and Europe (having both members of Oscines and Tyranni; Manegold, 2008, 2009; Mayr, 2001 3b; Mayr and Manegold, 2004, 2006), together with the fact that Early Eocene passeriforms are known from Australia (Boles, 1997), suggest that the clade has a much deeper history than reflected by the meager fossil record (Ericson *et al.*, 2002), and that we are nearly unaware of its history in South America.

Members of Formicariidae are frequent in Pliocene beds from Buenos Aires province (Noriega, 1998). The tarsometatarsi described here share a combination of characteristics present in Formicariidae; if this tentative identification is correct, it may be indicative that members of that clade had a wide distribution and diversification throughout the Neogene in the Southern Cone.

In addition, the lack of bone remains having Oscine features in Miocene beds from Santa Cruz (Noriega and Chiappe, 1993; present contribution) and early Pliocene outcrops from the Argentine Pampas (Noriega, 1998) reinforces previous hypothesis sustaining the arrival of Oscines in South America during the GABI, during Pleistocene times (Feduccia, 1975; Noriega, 1998).

The newly described birds from Santacrucian and Pinturan beds include 12 new taxa belonging to disparate clades. Some of them lack previous records in South America (e.g., Psophiidae, Coraciidae, Parvigruidae, possibly Sophiornithidae), and some are the oldest (e.g., Gruidae, Strigiformes) or the youngest (e.g., Coraciiformes) occurrences of their respective lineages on the continent. This evidences that the knowledge of fossil birds in South America is far from satisfactory.

Adding here to the long list of shared avian taxa between Europe and South America during the Paleogene and Neogene are the Psophiidae, Parvigruidae, Gruidae, and Coraciidae. This reinforces previous biogeographical models that link Cenozoic European and South American avifaunas (Agnolín, 2016; Ezcurra and Agnolín, 2012).

The early Miocene birds described here do not belong to any extant genera, which, as noted by Tambussi *et al.* (1993; see also Tambussi, 2011), had their origins in post-early Miocene times. In this regard, the Late Miocene terrestrial avifaunas from Argentina, such as those of Paraná (Diederle and Noriega, 2013; Noriega, 1995; Noriega and Agnolín, 2008) and Cerro Azul (Cenizo *et al.*, 2012), lack some archaic lineages, such as coraciiforms, *Peioa,* and basal anseriforms (e.g., basal tadornines), and the bird composition is "modern" in aspect, or at least in some of its characteristics (Cenizo *et al.*, 2012); this contrasts with the bird assemblages described here. Such avifaunal differences may be the result not only of age differences, but also of important and high-scale landscape modifications that occurred during late Miocene times.

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REFERENCES

Agnolín, F.L. (2004). Revisión sistemática de algunas aves deseadenses (Oligoceno Medio) descriptas por Ameghino en 1899. *Revista del Museo Argentino de Ciencias Naturales Nueva Serie*, *6*(2), 239-244.

Agnolín, F.L. (2006a). Dos nuevos Anatidae (Aves, Anseriformes) del Pleistoceno inferior-medio de Argentina. *Studia Geologica Salmanticensia*, *42*, 81-95.

Agnolín, F.L. (2006b). Notas sobre el registro de Accipitridae (Aves, Accipitriformes) fósiles argentinos. *Studia Geologica Salmanticensia*, *42*, 67-80.

Agnolín, F.L. (2009). Una nueva especie del género Megapaloelodus (Aves: Phoenicopteridae: Palaelodinae) del Mioceno Superior del noroeste de Argentina. *Revista del Museo Argentino de Ciencias Naturales*, *11*(1), 23-32.

Agnolín, F.L. (2016). A brief history of South American birds. *Contribuciones del Museo Argentino de Ciencias Naturales "Bernaridino Rivadavia"*, *6*, 157-172.

Agnolín, F.L., and Tomassini, R.L. (2012). A fossil Dendrocygninae (Aves, Anatidae) from the early Pliocene of the Argentine Pampas and its paleobiogeographical implications. *Annales de Paléontologie*, 98, 191-201.

Alvarenga, H.M.F. (1990). Flamingos Fósseis da Bacia de Taubaté, estado de S o Paulo, Brasil: descrição de nova espécie. *Anais Academia Brasileira de Ciencias*, 62, 335-345.

Alvarenga, H.M. (1999). A Fossil Screamer (Anseriformes: Anhimidae) from the Middle Tertiary of Southeastern Brazil. *Smithsonian Contributions to Paleobiology*, 89, 223-230.

Alvarenga, H.M., and Höfling, E. (2003). Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papéis Avulsos de Zoologia*, *43*(4), 55-91.

Ameghino, F. (1891). Enumeración de las aves fósiles de la República Argentina. *Revista Argentina de Historia Natural*, 1, 441- 453.

Ameghino, F. (1894). Enumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias* (Córdoba), 13, 259- 452.

Ameghino, F. (1895). Sur les oiseaux fossiles de Patagonie. *Boletín del Instituto Geográfico Argentino*, 15, 501- 602.

Ameghino, F. (1898). Sinópsis Geológico-Paleontológica. Segundo Censo de la República Argentina. *Cap. I. Territorio, Tercera Parte*, *1*, 113-255.

Ameghino, F. (1899). *Sinopsis geologico-paleontologica... En segundo censo nacional de la República Argentina... 1898... Suplemento (adiciones y correcciones), Julio de 1899*. Imp. Encuadernacion "La Libertad", 19 pp.

Ballmann, P. (1969). Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana*, 1, 5-60.

Baumel, J.J., and Witmer, L.M. (1993). Osteologia. Handbook of Avian Anatomy: Nomina Anatomica Avium. *Nuttall Ornithological Club Publications*, 23, 45-132.

Becker, J.J. (1987). Revision of "*Falco*" *ramenta* Wetmore and the Neogene evolution of the Falconidae. *The Auk*, *104*(2), 270-276.

Bertelli, S. (2002). *Filogenia del orden Tinamiformes (Aves: Palaeognathae)* [Phylogeny of the order Tinamiformes (Aves: Palaeognathae)] [PhD thesis]. Tucumán: Universidad Nacional de Tucumán.

Bertelli, S. (2017). Advances on tinamou phylogeny: an assembled cladistic study of the volant palaeognathous birds. *Cladistics*, *33*(4), 351-374.

Bertelli, S., and Chiappe, L.M. (2005). Earliest tinamous (Aves: Palaeognathae) from the Miocene of Argentina and their phylogenetic position. Museum of Loas Angeles Contributions in Science, 502, 1-20.

Bertelli, S., Chiappe, L.M., and Mayr, G. (2014). Phylogenetic interrelationships of living and extinct Tinamidae, volant palaeognathous birds from the New World. *Zoological Journal of the Linnean Society*, *172*(1), 145-184.

Bocheński, Z.M., Tomek, T., Bujoczek, M., and Wertz, K. (2011). A new passerine bird from the early Oligocene of Poland. *Journal of Ornithology*, *152*(4), 1045-1053.

Bochenski, Z.M., Tomek, T., Wertz, K., Happ, J., Bujoczek, M., and Swidnicka, E. (2018). Articulated avian remains from the early Oligocene of Poland add to our understanding of passerine evolution. *Palaeontologia Electronica*, *21*, 32A.

Bochenski, Z.M., Tomek, T., Bujoczek, M., and Salwa, G. (2021). A new passeriform (Aves: Passeriformes) from the early Oligocene of Poland sheds light on the beginnings of Suboscines. *Journal of Ornithology*, *162*(2), 593-604.

Boles, W.E. (1995a). The world's oldest songbird. *Nature*, 374, 21-22.

Boles, W.E. (1995b). A preliminary analysis of the Passeriformes from Riversleigh, northwestern Queensland, Australia, with the description of a new species of lyrebird. Courier Forschungsinstitut Senckenberg, 181, 163-170.

Boles, W.E. (1997). Fossil songbirds (Passeriformes) from the early Eocene of Australia. *Emu*, 97, 43-50.

Bourdon, E., Kristoffersen, A.V., and Bonde, N. (2016). A roller-like bird (Coracii) from the Early Eocene of Denmark. *Scientific Reports*, 6(1), 1-9.

Bown, T.M., and Larriestra, C.N. (1990). Sedimentary paleoenvironments of fossil platyrrhine localities, Miocene Pinturas Formation, Santa Cruz Province, Argentina. In *The Platyrrhine Fossil Record* (pp. 87-119). Academic Press.

Bown, T.M., and Fleagle, J.G. (1993). Systematics, biostratigraphy, and dental evolution of the Palaeothentidae, later Oligocene to early-middle Miocene (Deseadan-Santacrucian) caenolestoid marsupials of South America. *Paleontological Society Memoir*, 29, 1-76.

Bown, T.M., Larriestra, C.N., and Powers, D.W. (1988). Analisis paleoambiental de la formación Pinturas (Mioceno inferior), Provincia de Santa Cruz. *Actas II Reunión Argentina de Sedimentología*, *1*, 31-35.

Brodkorb, P. (1964). Catalogue of Fossil Birds: Part 2: Anseriformes Through Galliformes. *Bulletin of the Florida State Museum*, 8, 1-150.

Cenizo, M.M., and Agnolín, F.L. (2010). The southernmost records of Anhingidae and a new basal species of Anatidae (Aves) from the lower-middle Miocene of Patagonia, Argentina. *Alcheringa*, *34*(4), 493-514.

Cenizo, M.M., Tambussi, C.P., and Montalvo, C.I. (2012). Late Miocene continental birds from the Cerro Azul Formation in the Pampean region (central-southern Argentina). *Alcheringa: An Australasian Journal of Palaeontology*, *36*(1), 47-68.

Cenizo, M.M., Agnolín, F.L. , and Pomi, L.H. (2015). A new Pleistocene bird assemblage from the southern Pampas (Buenos Aires, Argentina). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *420*, 65-81.

Cenizo, M.M., Noriega, J.I., and Reguero, M.A. (2016). A stem falconid bird from the Lower Eocene of Antarctica and the early southern radiation of the falcons. *Journal of Ornithology*, 157(3), 885-894.

Chandler, R.M. (2012). A new species of tinamou (Aves: Tinamiformes, Tinamidae) from the Early-Middle Miocene of Argentina. *PalArch's Journal of Vertebrate Palaeontology*, *9*(2), 01-08.

Chiappe, L.M. (1991). Fossil birds from the Miocene Pinturas Formation of southern Argentina. *Journal of Vertebrate Paleontology*, 11(Suppl), R21-22.

Claramunt, S., and Cracraft, J. (2015). A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science Advances*, *1*(11), e1501005.

Clarke, J.A., Norell, M.A., and Dashzeveg, D. (2005). New avian remains from the Eocene of Mongolia and the phylogenetic position of the Eogruidae (Aves, Gruoidea). *American Museum Novitates*, *2005*(3494), 1-17.

Contreras Roqué, J.R., Aguilar, H.A., Piloni, G., Agnolín, F., Delfino Aguayo, M.A., Giacchino, A., ... and Davies, Y.E. (2019). Historia natural del Carau: *Aramus guarauna*. Fundación de Historia Natural Félix de Azara, 166 pp.

Cracraft, J. (1968). A review of the Bathornithidae (Aves, Gruiformes), with remarks on the relationships of the suborder Cariamae. *American Museum Novitates*, 2326, 1-46.

Cracraft, J. (1973a). Systematics and evolution of the Gruiformes (class Aves). 3, Phylogeny of the suborder Grues. *Bulletin of the American Museum of Natural History*, 151, 1-127.

Cracraft, J. (1973b). Continental drift, paleoclimatology, and the evolution and biogeography of birds. *Journal of Zoology*, *169*(4), 455-543.

Cracraft, J. (2001). Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1466), 459-469.

Cuello, J.P. (1988). Lista de las aves fósiles de la región neotropical y de las islas antillanas. *Paula-Coutiana*, *2*, 3-79.

De la Peña, M.R. (2013). *Citas, observaciones y distribución de aves argentinas. Edición ampliada*. Serie: Naturaleza, Conservación, y Sociedad Nº 7, Buenos Aires: Ediciones Biológica. 786 pp.

De Pietri, V.L., and Mayr, G. (2014). The enigmatic Ibidopodia from the early Miocene of France-the first Neogene record of Cariamiformes (Aves) in Europe. *Journal of Vertebrate Paleontology*, 34(6), 1470-1475.

De Pietri, V.L., Scofield, R.P., Zelenkov, N., Boles, W.E., and Worthy, T.H. (2016). The unexpected survival of an ancient lineage of anseriform birds into the Neogene of Australia: the youngest record of Presbyornithidae. *Royal Society Open Science*, *3*(2), 150635.

Degrange, F.J. (2022). A new species of *Dryornis* (Aves, Cathartiformes) from the Santa Cruz Formation (Lower Miocene), Patagonia,

Argentina. *Journal of Vertebrate Paleontology*, *41*, e2008411.

Degrange, F.J., Noriega, J.I., and Areta, J.I. (2012). Diversity and paleobiology of the Santacrucian birds. *Early Miocene paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*, 138-155.

Degrange, F.J., Pol, D., Puerta, P., and Wilf, P. (2021). Unexpected larger distribution of paleogene stem-rollers (Aves, Coracii): new evidence from the Eocene of Patagonia, Argentina. *Scientific Reports*, *11*(1), 1-9.

Diederle, J.M., and Noriega, J.I. (2013). Aves del Mioceno de la provincia de Entre Ríos, Argentina. *Publicación Especial, Asociación Paleontológica Argentina*, 14, 97-108.

Diederle, J. M., & Noriega, J. I. (2019). New records of birds from the Santa Cruz Formation (Early-Middle Miocene) at the Río Santa Cruz Valley, Patagonia, Argentina. PEApa, 19, 55-61.

Edwards, S.V., and Boles, W.E. (2002). Out of Gondwana: the origin of passerine birds. *Trends in Ecology and Evolution*, *17*(8), 347-349.

Elzanowski, A., and Boles, W.E. (2015). A coraciiform-like bird quadrate from the Early Eocene Tingamarra local fauna of Queensland, Australia. *Emu-Austral Ornithology*, *115*(2), 110-116.

Ericson, P.G. (1999). New material of *Juncitarsus* (Phoenicopteriformes), with a guide for differentiating that genus from the Presbyornithidae (Anseriformes). *Smithsonian Contributions to Paleobiology*, 89, 245-251.

Ericson, P.G., Christidis, L., Cooper, A., Irestedt, M., Jackson, J., Johansson, U.S., and Norman, J.A. (2002). A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1488), 235-241.

Ezcurra, M.D., and Agnolín, F.L. (2012). A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. *Systematic Biology*, 61(4), 553-566.

Feduccia, A. (1973). Evolutionary trends in the Neotropical ovenbirds and woodhewers. *Ornithological Monographs*, (13), 1-69.

Feduccia, A. (1974). Morphology of the bony stapes in New and Old World suboscines: New evidence for common ancestry. *The Auk*, 91, 427-429.

Feduccia, A. (1976). Osteological evidence for shorebird affinities of the flamingos. *The Auk*, *93*(3), 587-601.

Feduccia, A. (1977). A model for the evolution of perching birds. *Systematic Biology*, *26*(1), 19-31.

Feduccia, A., and Olson, S. L. (1982). Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smithsonian Contributions to Zoology*, 366, 1-22.

Feduccia, A., and Voorhies, M.R. (1992). Crowned cranes (Gruidae: Balearica) in the Miocene of Nebraska. *Natural History Museum of Los Angeles County, Science Series*, 36, 239-248.

Fleagle, J.G., Bown, T.M., Swisher, C., and Buckley, G. (1995). Age of the Pinturas and Santa Cruz formations. *Actas Sexto Congreso Argentino de Paleontología y Bioestratigrafía*, 6, 129-135.

Fleagle, J.G., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor, F. (2012). Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation. Cambridge University Press, Cambridge, 41-58.

Göhlich, U.B. (2003). A new crane (Aves: Gruidae) from the Miocene of Germany. *Journal of Vertebrate Paleontology*, *23*(2), 387-393.

Hamon, J.H. (1964). Osteology and paleontology of the passerine birds of the Reddick, Florida, Pleistocene. *Florida Geological Survey Bulletin*, 44, 1-210.

Hiroshige, M., and Yoshikazu, H. (2007). Myology and osteology of the Whooper Swan (*Cygnus cygnus*) (Aves, Anatidae). Part I. Muscles attached to the sternum, coracoid, clavicle, scapula and humerus. *Bulletin of the Gunna Museum of Natural History*, 11, 7-14.

Houde, P. (1988). Palaeognathous birds from the early Tertiary of the Northern Hemisphere. *Publications of the Nuttall Ornithological Club*, 22, 1-148.

Howard, H. (1963). Fossil birds from the Anza-Borrego desert. Contributions in Science, Natural History Museum of los Angeles County, 73, 3-33

Howard, H. (1964). A new species of the "pygmy goose" *Anabernicula*, from the Oregon Pleistocene, with a discussion of the genus. *American Museum Novitates*, 2200, 1-14.

Lee, K., Feinstein, J. and Cracraft, J. (1997). The phylogeny of ratite birds: Resolving conflicts between molecular and morphological data sets. In *Avian Molecular Evolution and Systematics*, Edited by: Mindell, D. 193-208. New Haven: Yale University Press.

Livezey, B.C. (1991). A phylogenetic analysis and classification of recent dabbling ducks (Tribe Anatini) based on comparative morphology. *The Auk*, *108*(3), 471-507.

Livezey, B.C. (1998). A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Philosophical Transactions of the Royal*

Society of London. Series B: Biological Sciences, *353*(1378), 2077-2151.

LoCoco, G.E.L., Agnolín, F.L. , and Carrión, J.L.R. (2020). Late Pleistocene owls (Aves, Strigiformes) from Ecuador, with the description of a new species. *Journal of Ornithology*, *161*(3), 713-721.

Manegold, A. (2008). Earliest fossil record of the Certhioidea (treecreepers and allies) from the early Miocene of Germany. *Journal of Ornithology*, *149*(2), 223-228.

Manegold, A. (2009). The early fossil record of perching birds (Passeriformes). *Palaeontologia Africana*, *44*, 103-107.

Manegold, A., Mayr, G., and Mourer-Chauviré, C. (2004). Miocene songbirds and the composition of the European passeriform avifauna. *The Auk*, *121*(4), 1155-1160.

Mauricio, G.N., Areta, J.I., Bornschein, M.R., and Reis, R.E. (2012). Morphology-based phylogenetic analysis and classification of the family Rhinocryptidae (Aves: Passeriformes). *Zoological Journal of the Linnean Society*, 166(2), 377-432.

Mayr, E. (1964). Inferences concerning the Tertiary American bird faunas. *Proceedings of the National Academy of Sciences of the United States of America*, 51(2), 280.

Mayr, G. (2002). A new specimen of *Salmila robusta* (Aves: Gruiformes: Salmilidae n. fam.) from the Middle Eocene of Messel. *Paläontologische Zeitschrift*, *76*(2), 305-316.

Mayr, G. (2005). A chicken-sized crane precursor from the early Oligocene of France. *Naturwissenschaften*, 92(8), 389-393.

Mayr, G. (2006). A rail (Aves, Rallidae) from the early Oligocene of Germany. *Ardea-Wageningen*, *94*(1), 23-31.

Mayr, G. (2008). Phylogenetic affinities and morphology of the late Eocene anseriform bird *Romainvillia stehlini* Lebedinsky, 1927. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 248, 365-380.

Mayr, G. (2013a). Parvigruidae (Aves, core Gruiformes) from the early Oligocene of Belgium. *Palaeobiodiversity and Palaeoenvironments*, *93*(1), 77-89.

Mayr, G. (2013b). The age of the crown group of passerine birds and its evolutionary significance-molecular calibrations versus the fossil record. *Systematics and Biodiversity*, *11*(1), 7-13.

Mayr, G. (2014). The Eocene Juncitarsus-its phylogenetic position and significance for the evolution and higher-level affinities of flamingos and grebes. *Comptes Rendus Palevol*, *13*(1), 9-18.

Mayr, G. (2016a). Variations in the hypotarsus morphology of birds and their evolutionary significance. *Acta Zoologica*, *97*(2), 196-210.

Mayr, G. (2016b). The world's smallest owl, the earliest unambiguous charadriiform bird, and other avian remains from the early Eocene Nanjemoy Formation of Virginia (USA). *Palaeontologische Zeitschrift*, *90*(4), 747-763.

Mayr, G. (2019). Hypotarsus morphology of the Ralloidea supports a clade comprising Sarothrura and Mentocrex to the exclusion of Canirallus. *Acta Ornithologica*, *54*(1), 51-58.

Mayr, G. (2022). A partial skeleton of Septencoracias from the early Eocene London Clay reveals derived features of bee-eaters (Meropidae) in a putative stem group roller (Aves, Coracii). *Palaeobiodiversity and Palaeoenvironments*, 102, 449-463.

Mayr, G., and Manegold, A. (2004). The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften*, *91*(4), 173-177.

Mayr, G., and Manegold, A. (2006). New specimens of the earliest European passeriform bird. *Acta Palaeontologica Polonica*, *51*(2), 315-323.

Mayr, G., and Mourer-Chauviré, C. (2000). Rollers (Aves: Coraciiformes ss) from the middle Eocene of Messel (Germany) and the upper Eocene of the Quercy (France). *Journal of Vertebrate Paleontology*, *20*(3), 533-546.

Mayr, G., and Smith, R. (2001). Ducks, rails, and limicoline waders (Aves: Anseriformes, Gruiformes, Charadriiformes) from the lowermost Oligocene of Belgium. *Geobios*, *34*(5), 547-561.

Mayr, G., Alvarenga, H., and Clarke, J.A. (2011). An *Elaphrocnemus*-like landbird and other avian remains from the late Paleocene of Brazil. *Acta Palaeontologica Polonica*, *56*(4), 679-684.

Mayr, G., Gingerich, P.D., and Smith, T. (2020a). Skeleton of a new owl from the early Eocene of North America (Aves, Strigiformes) with an accipitrid-like foot morphology. *Journal of Vertebrate Paleontology*, *40*(2), e1769116.

Mayr, G., Lechner, T., and Böhme, M. (2020b). A skull of a very large crane from the late Miocene of Southern Germany, with notes on the phylogenetic interrelationships of extant Gruinae. *Journal of Ornithology, 161(4)*, 923-933.

Mourer-Chauviré, C. (1983). Les Gruiformes (Aves) Des Phosphorites Du Quercy (France): 1, Sous-ordre Cariamae (Cariamidae Et Phorusrhacidae): Systématique et Biostratigraphie. *Palæovertebrata*, 13, 83-143.

Mourer-Chauviré, C. (1987). Les Strigiformes (Aves) des Phosphorites du Quercy (France): systématique, biostratigraphie et paléobiogéographie. *Travaux et Documents des Laboratoires de Géologie de Lyon*, *99*(1), 89-135.

Mourer-Chauvire, C. (1994). A large owl from the Palaeocene of France. *Palaeontology*, *37*(2), 339-348.

Mourer-Chauviré, C. (1995): The Messelornithidae (Aves: Gruiformes) from the Paleogene of France. Courier Forschungsinstitut Senckenberg, 181, 95-105.

Mourer-Chauviré, C. (1999). Position systématique de *Nupharanassa bohemica* Mlíkovsky, 1999. *Comptes Rendus de l'Académie des Sciences, Series IIA, Earth and Planetary Science*, 329(2), 149-152.

Mourer-Chauvire, C. (2001). The systematic position of the genus Basityto Mlikovsky, 1998 (Aves: Gruiformes: Gruidae). *Proceedings of the Biological Society of Washington*, 114(4), 964-971.

Mourer-Chauviré, C., Peyrouse, J.B., and Hugueney, M. (2013). A new roller (Aves: Coraciiformes ss: Coraciidae) from the Early Miocene of the Saint-Gérand-le-Puy area, Allier, France. In *Paleontological Research 2013-Proceedings of the 8th International Meeting of the Society of Avian Palaeontology and Evolution* (pp. 81-92).

Noriega, J.I. (1995). The avifauna from the 'Mesopotamian' (Ituzaing6 Formation; Upper Miocene) of Entre Rios Province, Argentina. *Courier Forchungsinstitut Senckenberg*, 181, 141-148.

Noriega, J.I. (1998): Aspectos paleozoogeográficos del registro de los Passeriformes (Aves) del Plioceno y Pleistoceno en la Provincia de Buenos Aires. *Actas de las Quintas Jornadas Geológicas y Geofísicas Bonaerenses*, 1, 65-71.

Noriega, J.I., and Agnolín, F.L. (2008). El registro paleontológico de las Aves del "Mesopotamiense" (Formación Ituzaingó; Mioceno tardío-Plioceno) de la provincia de Entre Ríos, Argentina. *INSUGEO, Miscelánea*, 17, 271-290.

Noriega, J.I., and Chiappe, L.M. (1993). An early Miocene passeriform from Argentina. *The Auk*, 936-938.

Noriega, J.I., Vizcaíno, S.F., and Bargo, M.S. (2009). First record and a new species of seriema (Aves: Ralliformes: Cariamidae) from santacrucian (Early-Middle Miocene) beds of Patagonia. *Journal of Vertebrate Paleontology*, *29*(2), 620-626.

Noriega, J.I., Areta, J.I., Vizcaíno, S.F., and Bargo, M.S. (2011). Phylogeny and taxonomy of the patagonian Miocene falcon *Thegornis musculosus* Ameghino, 1895 (Aves: Falconidae). *Journal of Paleontology*, *85*(6), 1089-1104.

Northcote, E. M., and Mourer-Chauviré, C. (1988). The extinct crane Grus primigenia Milne-Edwards in Majorca (Spain). *Geobios*, *21*(2), 201-208.

Olson, S. L. (1973). A classification of the Rallidae. *Wilson Bulletin*, 85, 381-416

Olson, S. L. (1974). A new species of *Nesotrochis* from Hispaniola, with notes on other fossil rails from the West Indies (Aves: Rallidae). *Proceedings of the Biological Society of Washington*, 87, 439-450.

Olson, S. L. (1985). *The fossil record of birds*. In: Farner DS, King JR, Parkes KC (eds) Avian biology, vol 8. Academic Press, New York, pp 79-238

Oppenheimer, M., and Silveira, L.F. (2009). A taxonomic review of the Dark-winged Trumpeter *Psophia viridis* (Aves: Gruiformes: Psophiidae). *Papéis Avulsos de Zoologia*, 49, 547-555.

Peters, D.S. (1992). A new species of owl (Aves: Strigiformes) from the Middle Eocene Messel oil shale. *Natural History Museum of Los Angeles County Science Series*, 36, 161-169.

Picasso, M.B., Tambussi, C., and Dozo, M. T. (2009). Neurocranial and brain anatomy of a Late Miocene eagle (Aves, Accipitridae) from Patagonia. *Journal of Vertebrate Paleontology*, *29*(3), 831-836.

Rasmussen, T. 1997. Birds. In: Kay, R.F., R.H. Madden, R.L. Cifelli and J.J. Flynn (eds.). Vertebrate paleontology in the neotropics - the Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, 171-183.

Ré, G.H., Bellosi, E.S., Heizler, M., Vilas, J.F., Madden, R.H., Carlini, A.A., ... and Vucetich, M.G. (2010). A geochronology for the Sarmiento Formation at Gran Barranca. In *The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia* (pp. 46-60). Cambridge: Cambridge University Press.

Seguí, B. (2002). A new genus of crane (Aves: Gruiformes) from the Late Tertiary of the Balearic Islands, Western Mediterranean. *Ibis, 144*, 411–422.

Short, L.L. (1970). Mid-Pleistocene birds from western Nebraska, including a new species of sheldgoose. *The Condor*, 72(2), 147-152.

Tambussi, C.P. (2011). Palaeoenvironmental and faunal inferences based on the avian fossil record of Patagonia and Pampa: what works and what does not. *Biological Journal of the Linnean Society*, 103(2), 458-474.

Tambussi, C.P., and Degrange, F. (2012). *South American and Antarctic continental Cenozoic birds: Paleobiogeographic affinities and disparities*. Springer Science and Business Media. 113 pp.

Tambussi, C.P. and Noriega, J.I. (1996). Summary of the Avian Fossil Record from Southern South

America. *Müncher Geowissenschaftliche Abhandlungen*, 30, 245-264

Tambussi, C.P., Noriega, J.I., and Tonni, E.P. (1993). Late Cenozoic birds of Buenos Aires Province (Argentina): an attempt to document quantitative faunal changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 101(1-2), 117-129.

Tambussi, C.P., Degrange, F.J., De Mendoza, R.S., Sferco, E., and Santillana, S. (2019). A stem anseriform from the early Palaeocene of Antarctica provides new key evidence in the early evolution of waterfowl. Zoological Journal of the Linnean Society, 186 (3), 673-700.

Tauber, A.A. (1997a). Bioestratigrafía de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. *Ameghiniana*, 34(4), 413-426.

Tauber, A.A. (1997b). Paleoecología de la Formación Santa Cruz (Mioceno inferior) en el extremo sudeste de la Patagonia. *Ameghiniana*, 34(4), 517-529.

Tauber, A.A. (1999). Los vertebrados de la Formación Santa Cruz (Mioceno inferior-medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista española de Paleontología*, 14(2), 173-182.

Tonni, E.P. (1980). The present state of knowledge of the Cenozoic birds of Argentina. *Natural History Museum of Los Angeles County*, *Contributions in Science*, 330, 105-114.

Tonni, E.P. and Carlini A.A. (2008). Chapter 13: Neogene vertebrates from Argentine Patagonia: their relationship with the most significant climatic changes. In: "Late Cenozoic of Patagonia and Tierra del Fuego" J. Rabassa (Ed.). Elsevier.

Ubilla, M., Perea, D., Tambussi, C., and Tonni, E.P. (1990). Primer registro fósil de Phoenicopteridae (Aves: Charadriiformes) para el Uruguay (Mio-Plioceno). *Anais da Academia Brasileira de Ciências*, *62*, 61-68.

Vickers Rich, P., van Tets, G.F., Rich, T.H.V., and McEvey, A.R. (1987). The Pliocene and Quaternary flamingoes of Australia. *Memoirs of the Queensland Museum* 25, 207-225.

Vickers Rich, P., and Bohaska, D.J. (1981). The Ogygoptyngidae, a new family of owls from the Paleocene of North America. *Alcheringa*, *5*(2), 95-102.

Vizcaíno, S.F., Kay, R.F. , and Bargo, M.S. (Eds.). (2012). *Early Miocene paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 pp.

Woolfenden, G.E. (1961). Postcranial osteology of the waterfowl. *Bulletin of the Florida State Museum, Biological Sciences*, 6(1), 1-129.

Worthy, T.H. (2009). Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: Anatidae) from Australia. *Zoological Journal of the Linnean Society*, 156(2), 411-454.

Worthy, T.H., and Lee, M.S. (2008). Affinities of Miocene waterfowl (Anatidae: Manuherikia, Dunstanetta and Miotadorna) from the St Bathans Fauna, New Zealand. *Palaeontology*, 51(3), 677-708.

Worthy, T.H., Tennyson, A.J., Jones, C., McNamara, J.A., and Douglas, B.J. (2007). Miocene waterfowl and other birds from Central Otago, New Zealand. *Journal of Systematic Palaeontology*, 5(1), 1-39.

Worthy, T. H., Scofield, R. P., Hand, S. J., De Pietri, V. L., and Archer, M. (2022). A swan-sized fossil anatid (Aves: Anatidae) from the early Miocene St Bathans Fauna of New Zealand. *Zootaxa*, 5168(1), 39-50.

Zelenkov, N.V. (2015) The fossil record and evolutionary history of cranes. In: Ilyashenko EI, Winter SV (eds) Cranes of Eurasia (biology, distribution, captive breeding). 5. Proceedings of the International Scientific Conference "Cranes of Eurasia: biology, conservation, management", Daursky Nature Reserve, Transbaikalia, Russia, 1–4 September 2015. Crane Working Group of Eurasia, Moscow and Nizhny Tsasuchei, Russia, pp. 88-90

Zelenkov, N.V. (2021). A Revision of the Palaeocene-Eocene Mongolian Presbyornithidae (Aves: Anseriformes). *Paleontological Journal*, 55(3), 323-330.

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