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A NEW SPECIES OF THE FALCON GENUS *Thegornis* (AVES) FROM THE MIOCENE OF NORTHWESTERN ARGENTINA

Una nueva especie de halcón del género Thegornis *(Aves) del Mioceno del Noroeste de Argentina*

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Abstract. The aim of the present contribution is to describe a new species of the extinct falcon genus *Thegornis*. The species is based on the distal end of a tarsometatarsus coming from late Miocene beds of Catamarca province, Argentina. The new taxon is distinguished from closely related forms by details in tarsometatarsus trochleae. It constitutes the second bird genus from Miocene Catamarca province that is shared with fossil bird assemblages of early-middle Miocene of Santa Cruz province, Argentina.

Keywords. Herpetotherinae, *Thegornis*, Andalhualá Formation, Miocene, northwestern Argentina.

Resumen. La finalidad de la presente contribución es la de describir una nueva especie del género de halcón extinto *Thegornis*. La especie está basada en el extremo distal de un tarsometatarso procedentes de capas del Mioceno tardío de la provincia de Catamarca, Argentina. El nuevo taxón es distinguible de formas cercanamente relacionadas por detalles de las trócleas del tarsometatarso. Constituye el segundo registro de un género aviano del Noroeste de Argentina que es compartido con las asociaciones de aves del Mioceno temprano-medio de la provincia de Santa Cruz, Argentina.

Palabras clave. Herpetotherinae, *Thegornis*, Formación Andalhualá, Mioceno, noroeste de Argentina.

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, resulting in the best known avian assemblage from the early Neogene of South America (see references in Tonni, 1980; Tambussi and Noriega, 1996; Tambussi and Degrange, 2013; Agnolín, 2016, 2022; Degrange *et al*., 2012, Tambussi *et al*., 2023).

Otherwise, information of birds from the Miocene of northern Argentina is almost restricted to those coming from the Paraná River, at the eastern side of the country (Noriega and Agnolín, 2008; Diederle and Noriega, 2013). Few findings of fossil birds are also known from late Miocene beds of northwestern Argentina, particularly Tucumán, Catamarca and La Rioja provinces (Tambussi and Degrange, 2013; Tambussi *et al*., 2021).

The aim of present contribution is to describe a new species of falcon belonging to the subfamily Herpetotherinae, coming from Late Miocene beds of Catamarca province, northwestern Argentina.

MATERIALS AND METHODS

Geological and geographical settings

The specimen here described comes from an unknown exact locality of the Puerta de Corral Quemado area, at Santa María Department, Catamarca province, Argentina. There is no indication of collector or date of collection of the material.

The label accompanying the specimen indicates that it was collected at the "Formación Araucana", an old term that is nearly equivalent to the lower levels of the Andalhualá Formation (Late Miocene) of the Santa María group (northwestern Argentina). This unit is the thickest formation of the group (Marshall and Patterson 1981) and it is constituted by a succession of sandstones, with abundant conglomerates and some pelitic beds (Anzótegui *et al*. 2007; Bossi and Muruaga 2009). Its lower levels are considered as being late Miocene in age (Huayquerian SALMA or Tortonian Global Stage/ Age; Bossi and Muruaga, 2009; Reguero and Candela, 2011; Esteban *et al*., 2014), and Herrera and Ortiz (2005) and Prevosti *et al*. (2021) stated that the temporary boundaries for the Formation are between 7.14 and 3.54 Ma.

Andalhualá Formation has yielded a great amount of fossil vertebrate remains, including fossils of birds, reptiles, and especially mammals (Rovereto, 1914; Reguero and Candela, 2011; Esteban *et al*., 2014). In contrast with the rich mammalian assemblage, fossil birds from Andalhualá Formation are much scarcer, and previous reports include phorusrhacids (i.e., *Procariama, Hermosiornis, Andalgalornis*; Patterson and Kraglievich, 1960; Vezzosi and Noriega, 2017), teratornithids (Campbell, 1995), palaelodids (Agnolín, 2009), rheids (Noriega *et al*., 2017) and a bird of prey referred to the accipitrid genus *Geranoaetus* (Agnolín, 2006). The latter was identified by Agnolín based on specimen MACN PV 5431, which was at then, still embedded within sedimentary matrix. Additional preparation of the specimen indicates that the generic identification by Agnolín (2006) was wrong and that the specimen in fact belongs to the extinct genus *Thegornis*, and the specimen

is redescribed here as a new species of this genus.

Nomenclature

We follow the taxonomic nomenclature employed by Griffiths *et al*. (2004) and Fuchs *et al*. (2011, 2015). Based on these authors the subfamily Herpetotherinae includes the extant genera *Herpetotheres* Vieillot, 1817 and *Micrastur* Gray, 1841.

Extinct herpetotherines include the early-middle Miocene Santacrucian *Badiostes patagonicus* Ameghino, 1895 and the genus *Thegornis*. 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, 2006). However more recently, Noriega *et al.* (2011) based on newly collected specimens, including a nearly complete 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 that is followed here. More recently, Agnolín (2022) described the species *T. spivacowi*, coming from roughly coeval or slightly younger beds than those that yielded *T. musculosus* at Santa Cruz province, Argentina.

The osteological nomenclature employed by Baumel and Witmer (1993) is used here, but with terms in Latin translated to the English language. The Romerian terminology of "anterior" instead of dorsal or cranial and "posterior" instead of plantar or caudal is employed.

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

SYSTEMATIC PALEONTOLOGY

Falconiformes Sharpe, 1874
Falconidae Leach, 1820
Herpetotherinae Lesson, 1842
Genus *Thegornis* Ameghino, 1895

Thegornis sosae nov. sp.
Holotype. MACN PV 5431, distal end of left tarsometatarsus (Figure 1).
Diagnosis. Large species of the genus *Thegornis*, the size of *T. musculosus*, which difers from other species of the genus by the following combination of characters trochlea III with its lateral surface strongly concave, which results in a more obliquely oriented trochlear body (straight to slightly convex lateral margin in *S. spivacowi* and *S. musculosus*), trochlea III closely appressed to trochlea IV (widely spaced by a wide intertrochlear incisure in *T. spivacowi* and *T. musculosus*), and trochlea IV subquadrangular in contour (subrectangular in contour in *T. spivacowi* and *T. musculosus*, being proximodistally longer than transversely wide), proximodistally narrow posteromedial wing of trochlea II, which results in a subtriangular contour in side view (similar to *T. musculosus,* but much stouter and subtriangular in contour in side view in *T. spivacowi*) (Figure 2).
Etymology. The species is named in honor of the singer and performer Haydeé Mer-

cedes Sosa (1935-2009) who represented the northwestern Argentinean roots in the folk music.

DESCRIPTION

The distal end of the tarsometatarsus belongs to a relatively large *Thegornis* species (its maximum transverse width is 2.3 cm; Figure 1). In anterior view the distal end of the bone is subtriangular in contour, with a prominent lateral anterior ridge, and obliquely oriented medial margin of the shaft and a slightly concave lateral margin. The surface for the m. abductor digiti II is very wide and well-defined, and subtriangular shaped in contour. 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

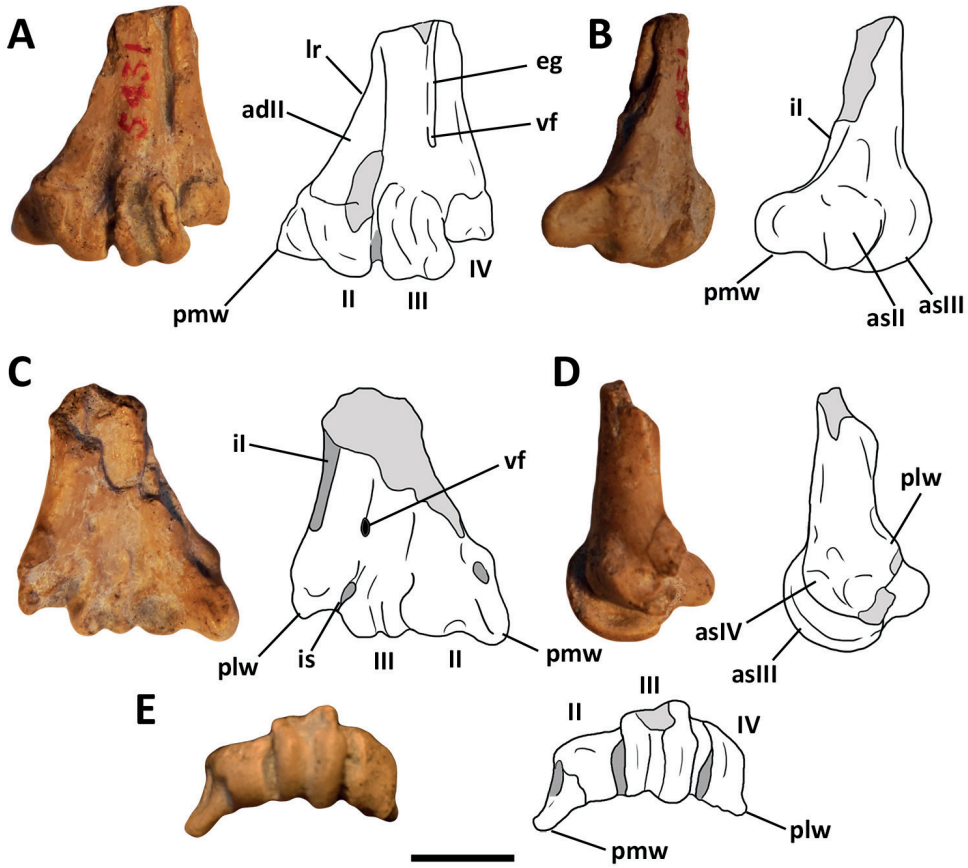

Figure 1 - *Thegornis sosae* nov. sp. (MACN PV 5431, holotype), distal end of left tarsometatarsus in **A**, anterior; **B**, medial; **C**, posterior; and **D**, lateral views. Abbreviations. asII, anterior articular surface of trochlea II; asIII, anterior articular surface of trochlea III; adII, impression of the *m. adductor digiti II*; eg, extensor groove of digit IV; il, metatarsal I fossa; plw, posterolateral wing; pmw, posteromedial wing; lr, lateral ridge; vf, distal vascular foramen. II-IV, metatarsal trochleae. Scale bar. 1 cm.

longitudinal plantar ridges. Metatarsal I impression is deep and crescent-shaped.

The second metatarsal trochlea has a distinctively-formed and rounded articular body, which is ovoidal in contour. The posteromedial wing is well-defined, medially tilted and separated from the main body of the trochlea by a groove and a smooth depression. In side view, this wing is relatively narrow and roughly subrectangular in contour, with subparallel proximal and distal margins.

Metatarsal III trochlea is separated from the II trochlea by a well-defined but narrow intertrochlear incisure. The outer rim of trochlea III is more prominent than the inner rim. Its lateral margin is notably concave, which results in an obliquely oriented metatarsal body. The articular groove is notably deep and well-defined. The trochlea III is separated from the trochlea IV by a narrow intertrochlear incisure.

The articular surface of trochlea IV is relatively transversely wide and is quadrangular in contour. The posterolateral wing is lateroposteriorly oriented, and lacks the sigmoidal contour diagnostic of *T. spivacowi* (Agnolín, 2022).

Figure 2 - Comparison between different *Thegornis* species. *Tarsometatarsus* in **A-C**, anterior; **D-F**, posterior; **G-I**, medial; **J-L**, lateral; and **M-N**, distal views. A,D,G,J,M, *Thegornis sosae* nov. sp. (MACN PV 5431, holotype), distal end of left tarsometatarsus; B,E,H,K,N, *Thegornis spivacowi* (MACN-SC 1407, holotype), distal end of right tarsometatarsus (reversed); C,F,I,L, *Thegornis musculosus* (BMNH A-600, holotype), distal end of right tarsometatarsus with incomplete III trochlea (reversed). Photographs C,F,I,L,N, courtesy of Sandra Chapman (BMNH) and Jorge Noriega. Scale bar. A,C,D,F,G,I,J,L-N, 1 cm; B,E,H,K,M, 5 mm.

DISCUSSION

The material belonging to *T. sosae* nov. sp. was previously identified as a member of the genus *Geranoaetus* by Agnolín (2006). This wrong identification was due to the unprepared condition of the specimen, which was partially embedded in the sedimentary matrix. The new preparation of the specimen clearly indicates that it should be nested among herpetotherine falconids based on the following combination of traits: 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,

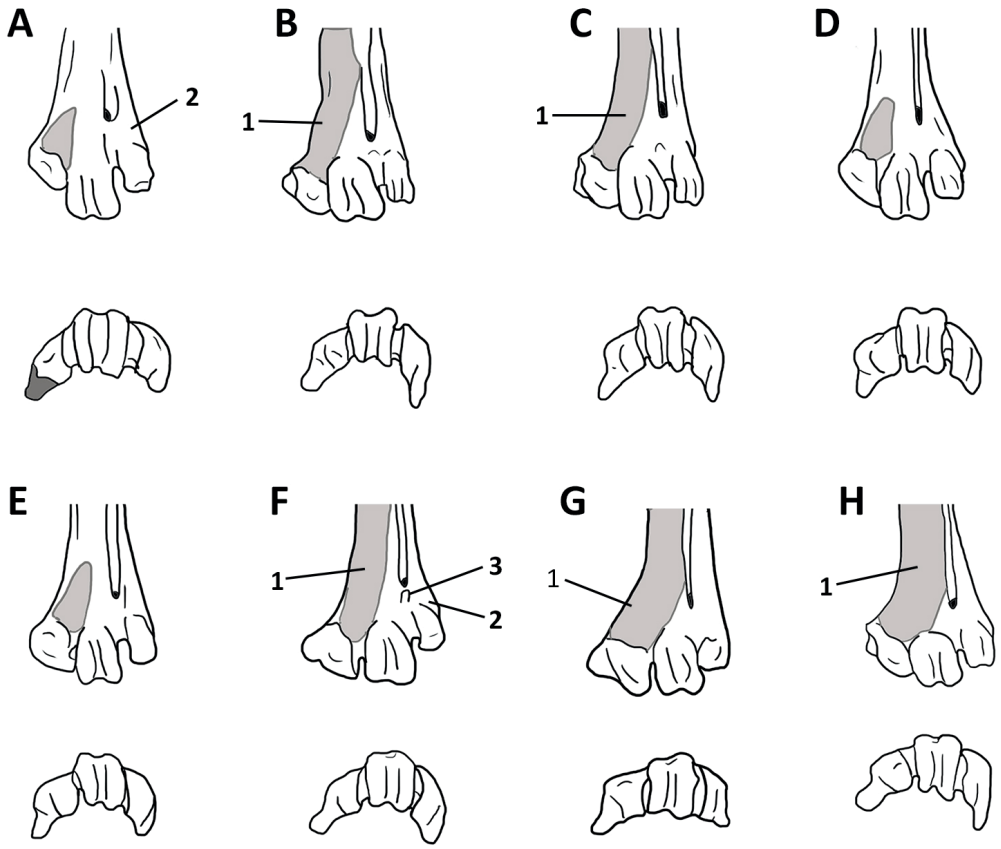

Figure 3 – Left tarsometatarsus of selected falconids in anterior view, **A,** *Antarctoboenus carlini*; **B,** *Herpetotheres cachinans* (Herpetotheriinae); **C,** *Micrastur semitorquatus* (Micrasturinae); **D,** *Polyborus plancus* (Polyborini); **E,** *Spiziapteryx circumcincta* (Polyborini); **F,** *Falco femoralis* (Falconini); **G,** *Thegornis sosae* nov. sp. (Herpetotheriinae); **H,** *Thegornis musculosus* (Herpetotheriinae). Abbreviations. 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. In F-M, the surface shaded light grey represents the surface for the m. abductor digiti II. Not to scale. A-F,H, modified from Agnolín (2023).

the lateral trochlear rim of metatarsal III trochlea more posteriorly extended than the medial one, and extensive posterior wing of metatarsal IV trochlea (Noriega *et al.*, 2011; Cenizo *et al.*, 2016; Agnolín, 2022; Figure 3). *Thegornis sosae* nov. sp. comfortably fits within the genus *Thegornis,* with which it shares a tarsometatarsus with the 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, trochlea II slightly grooved, and posteromedial wing of trochlea II relatively thin, well-defined and strongly medially tilted (Noriega *et al.*, 2011; Agnolín, 2022). These features as a whole separate *T. sosae* nov. sp. from the extant genera *Micrastur* and *Herpetotheres* (Figure 3).

As indicated above, the genus *Thegornis* is represented by two species, based

on distal end of tarsometatarsus, coming from early-middle Miocene beds of Santa Cruz province, Argentina. *T. musculosus* Ameghino, 1895 is known by several specimens, including a partial skeleton including the skull (Noriega *et al*., 2011), and it is known in several localities of Santa Cruz and Chubut provinces (Tambussi and Degrange, 2013). A second, recently described species, *T. spivacowi* is known from several distal end of tarsometatarsi, coming from a couple of localities at Santa Cruz (Agnolín, 2022). Both species are distinguished from details of distal metatarsal trochleae. The holotype specimen of *T. sosae* nov. sp. is a tarsometatarsus that can be comfortably compared with those of other species of the genus. However, because of the paucity of the available material, it is not possible to propose to which previously described *Thegornis* species it was more closely related.

Fossil birds from Andalhualá Formation are almost represented by phorusrhacids, teratornithids, rheids and palaelodids (Patterson and Kraglievich, 1960; Campbell, 1995; Agnolín, 2009; Vezzosi and Noriega, 2017; Noriega *et al*., 2017). Phorusrhacids from Andalhualá Formation belong to genera also reported from Paraná, La Pampa, and Buenos Aires latest Miocene-lower Pliocene beds (Alvarenga and Hofling, 2003; Vezzosi, 2012). More recently, Noriega *et al*. (2017) reported the presence of a new species of the rheid genus *Opisthodactylus*, previously known from early-middle Miocene beds of Patagonian Río Negro and Santa Cruz provinces (Tambussi and Degrange, 2013; Agnolín and Chafrat, 2015). This indicates that *Opisthodactylus* could have occupied a very large area along the southern tip or South America (Noriega *et al*., 2017). Similarly, present record of *Thegornis* is separated from more than 2000 kilometers from previous reports, being similar to the distribution inferred for *Opisthodactylus*. As in the latter, it is possible that *Thegornis* species may be inhabitants of a mixture of open temperate semiarid forests alternating with shrubby-herbaceous elements typical of Chacoan floras (Noriega *et al*., 2017). This is also in agreement with the ecological requirements of extant herpetotherine falcons (Noriega *et al*., 2011).

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