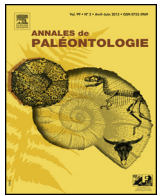




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Original article

# Oldest record of Thinocoridae (Aves, Charadriiformes) from South America



## *Le plus ancien thinocoridé (Aves, Charadriiformes) d'Amérique du Sud*

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### ABSTRACT

Here we describe an isolated distal end of tarsometatarsus coming from the late Miocene levels of the Loma de Las Tapias Formation (San Juan Province, Argentina). The specimen was identified as a Thinocoridae, and constitutes the oldest record for the clade. It also represents the only Tertiary finding for the family from South America and one of the scarce avian remains reported from central Argentina. This record provides new information on the palaeobiogeography of the clade.

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### RÉSUMÉ

Nous décrivons ici une extrémité distale isolée de tarsométatarses provenant du Miocène terminal de la Formation Loma de Las Tapias (Province de San Juan, Argentine). Le spécimen a été identifié comme un Thinocoridae, et constitue le plus ancien enregistrement de cette famille en Amérique du Sud. Il représente aussi la seule occurrence de thinocoridé dans le Tertiaire d'Amérique du Sud et l'un des rares restes d'oiseaux rapportés du centre de l'Argentine. Cette découverte fournit des informations sur la paléobiogéographie des représentants fossiles de ce clade.

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## 1. Introduction

The family Thinocoridae is a small clade of two genera and four living species, commonly known as seedsnipes (Sibley

et al., 1968; Remsen et al., 2014). The thinocorids are exclusively South American in distribution, especially in the Andean and Patagonian regions (Fjeldså, 1996). They inhabit a variety of harsh environments, including grasslands, steppes, deserts and alpine habitats (Olrog, 1963). Are unique among charadriiforms in being strictly vegetarian, having a strongly modified crop and entire digestive apparatus, adapted for vegetal consumption (Korzun et al., 2009).

These birds are particularly interesting because are usually considered as an example of isolated and endemic evolution of birds in the South American continent. In some aspects of their morphology and behaviour resemble different avian clades,

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including Galliformes, Charadriiformes, Columbiformes, and Gruiformes (Maclean, 1969; Sibley and Ahlquist, 1990; Fjeldså, 1996; Korzun et al., 2009).

Probably because of its low diversity and ecological requirements, thinocorids have a near non-existent fossil record. The oldest known remains come from the early–middle Pleistocene of the Pampean region of Argentina (De Mendoza et al., 2015), whereas sparse remains belonging to *Thinocorus* are known from the late Pleistocene of the Argentine Pampas (Tonni et al., 1998) and Perú (Campbell, 1979).

Because the fossil thinocorid records previously described are represented by only a couple of isolated bones, the finding and report of any thinocorid remain is worth to mention. On this basis, we here report the distal end of a tarsometatarsus of a Thinocoridae from the late Miocene levels (Chasicooan Stage/Age) of the Loma de Las Tapias Formation, outcropping at Loma de Las Tapias locality (San Juan Province, Argentina). This record represents an important addition to the knowledge of the Southern Cone extinct avifaunas.

Institutional abbreviations. INGEO-PV, Instituto de Geología Emiliano P. Aparicio, Universidad Nacional de San Juan (San Juan, San Juan Province, Argentina).

## 2. Geographical and stratigraphic context

The fossiliferous locality of Loma de Las Tapias (31° 28' S, 68° 40' W) is located approximately 20 km northwest of San Juan city (San Juan Province, Argentina) (Fig. 1). The specimen studied was recovered in the upper portion of the Limolita La Colmena Member of the Loma de Las Tapias Formation (Fig. 2). The bearing level mainly includes light-yellowish siltstones interbedded with reddish mudstones, though grayish fine to medium grained sandstones

are also present, and presents fine parallel lamination and desiccation cracks. Numerous vertebrate remains, principally mammals, were recovered from this member (Contreras and Baraldo, 2010). These deposits correspond to an alluvial plain environment associated with braided rivers (Bercowski et al., 1987; Rodríguez, 2004). On the basis of the faunal assemblage, radiometric datings and magnetostratigraphic studies, the bearing level was assigned to the late Miocene. From a biostratigraphic point of view, it corresponds to the Chasicooan Stage/Age (Bercowski et al., 1986; Contreras et al., 2001; Contreras and Baraldo, 2010).

## 3. Materials and methods

The specimen analyzed in this work (INGEO-PV 032) was previously included in a faunal list of the Loma de Las Tapias Formation by Contreras and Baraldo (2010). These authors identified the material as an indeterminate charadriiform.

Because of its peculiar morphology and uniqueness, the taxonomy and phylogenetic position of Thinocoridae was a matter of discussion by a large number of authors in the past (Lesson, 1831; Nitzsch and Burmeister, 1840; Gray, 1849; Lowe, 1922; Verheyen, 1958; Sibley et al., 1968). In spite of that, since the influential paper of Olson and Steadman (1981) recent authors agree in that Thinocoridae constitutes the sister group of the charadriiform Australian clade Pedionomidae (Sibley and Ahlquist, 1990; Paton et al., 2003; Thomas et al., 2004; Paton and Baker, 2006; Baker et al., 2007; Gibson and Baker, 2012; De Pietri et al., 2015), a criterion that is followed here. Both clades form part of the suborder Scolopaci, which is one of the three major clades of Charadriiformes (Ericson et al., 2003; Paton et al., 2003; Baker et al., 2007). The Scolopaci contains five family-level taxa, namely Rostratulidae, Jacanidae,

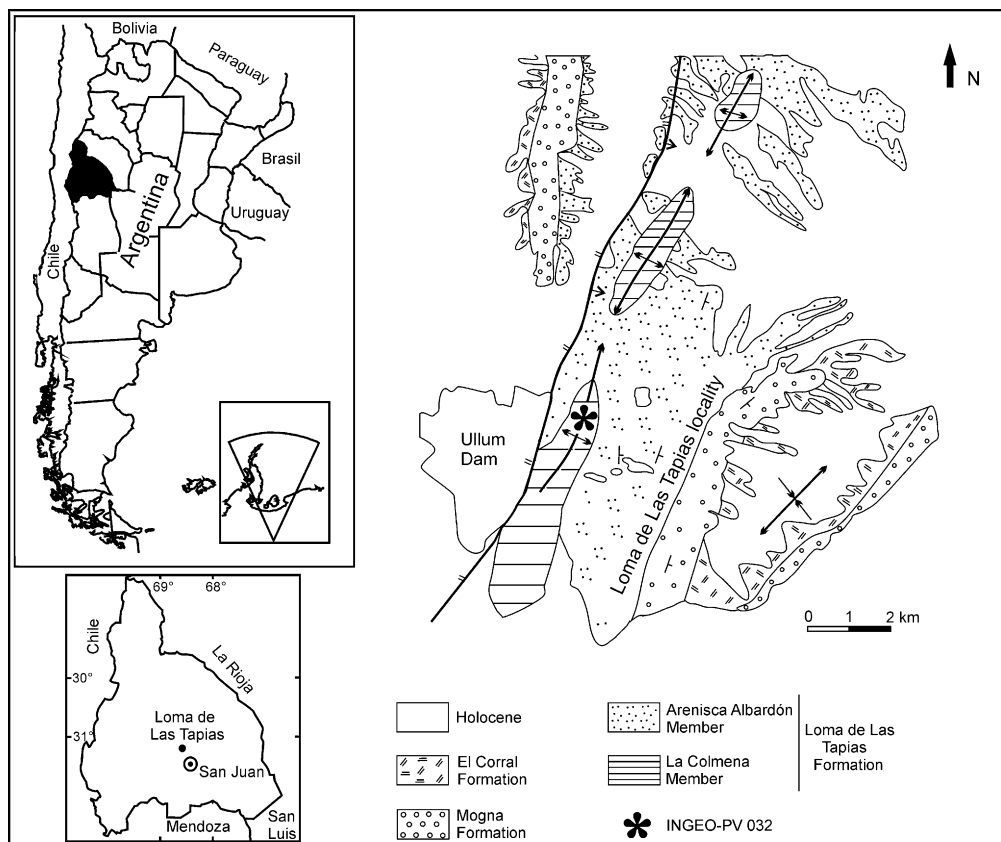


Fig. 1. Location map showing the Loma de Las Tapias locality (asterisk), San Juan Province, Argentina [planned for page width].  
Carte de localisation du site de Loma de Las Tapias (astérisque), Province de San Juan, Argentine.

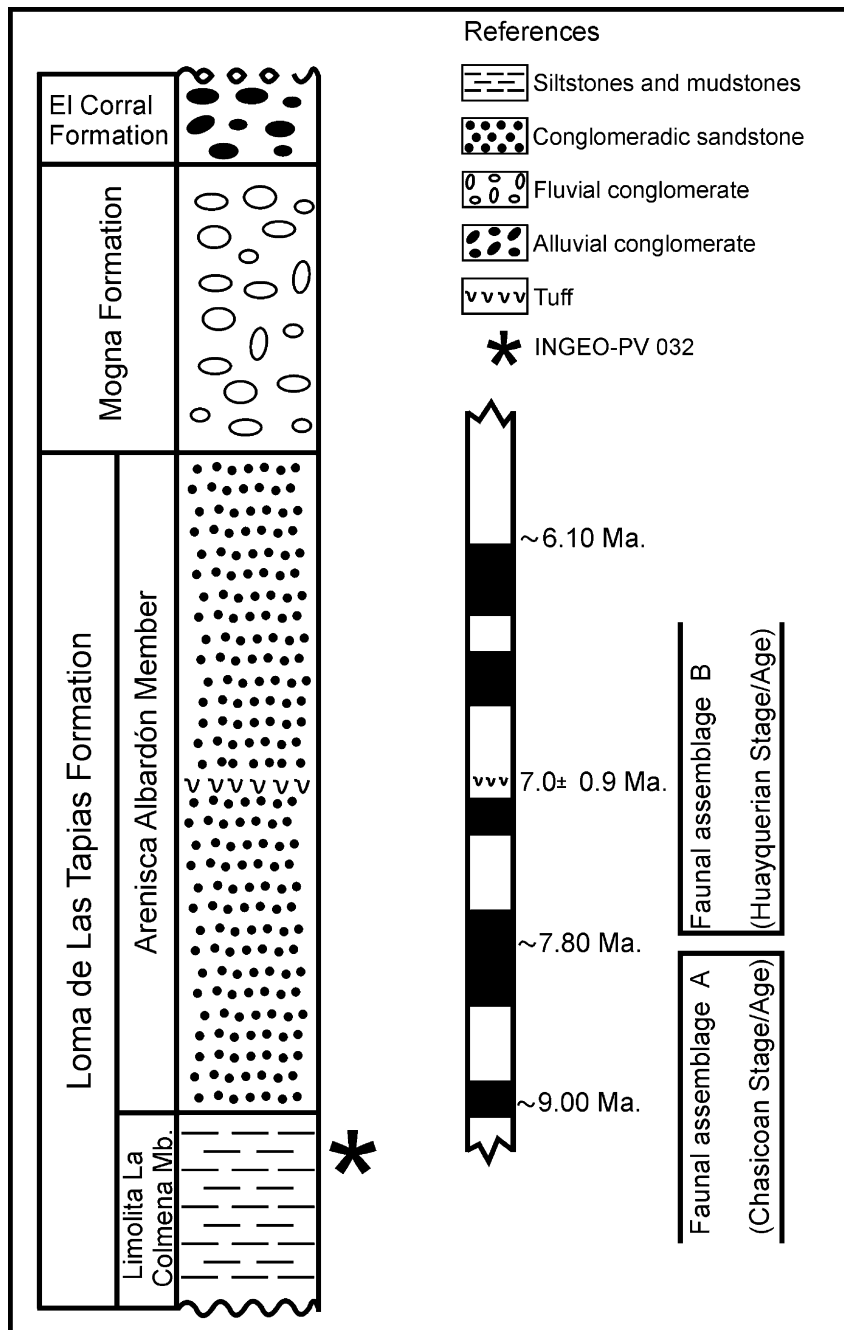


Fig. 2. Stratigraphic section at Loma de Las Tapias locality [planned for column width].  
*Coupe stratigraphique de la localité de Loma de Las Tapias.*

Thinocoridae, Pedionomidae, and the diverse radiation of Scolopacidae. This taxonomic arrangement is followed here.

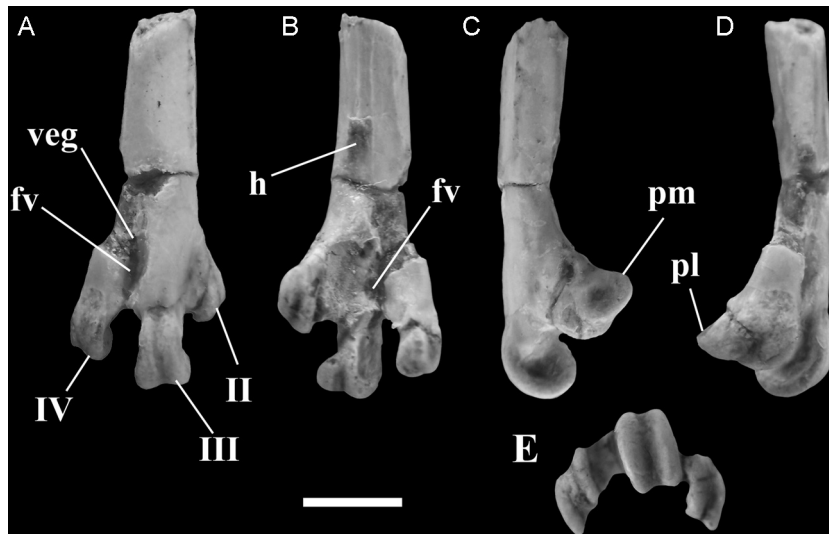
The anatomical terminology used in the descriptions follows Baumel and Witmer (1993) with modifications by Ballmann (2004). All measurements are in mm and were taken with a digital calliper and rounded to the near to 0.01 millimeter.

#### 4. Systematic paleontology

- Class Aves Linnaeus, 1758
- Order Charadriiformes Huxley, 1867
- Suborder Scolopaci Vigors, 1825
- Family Thinocoridae Gray, 1845
- Genus and species indeterminate

**Referred Specimen.** INGEO-PV 032, distal end of right tarsometatarsus with slightly displaced trochlea metatarsi IV (Fig. 3; Table 1).

**Description.** The shaft of the tarsometatarsus is transversely wide, and is not strongly transversely compressed above distal trochleae. The distal vascular foramen is relatively large (although much smaller than in charadriids) and a well-developed vascular extensor groove appears to be present. In plantar view, this foramen is subcircular in contour and much smaller than the osseous bridge that separates it from the intertrochlear incisure. The trochlea metatarsal III is robust and slightly distally divergent, being roughly subrectangular in contour. The articular surface is proximally delimited by a deep extensor pit. In plantar view the articular surface is strongly proximally convergent, being subtriangular in contour. The trochlea metatarsal IV is distally



**Fig. 3.** Distal end of right tarsometatarsus (INGEO-PV 032) of Thinocoridae indet. A, cranial view; B, caudal view; C, medial view; D, lateral view; E, distal view. Abbreviations: fv, distal vascular foramen; h, scar for the hallux; pl, lateroplantar process of trochlea metatarsi II; pm, medioplantar process of fourth distal trochlea; veg, vascular extensor groove; II, III, IV, distal trochleae II, III, and IV, respectively. Scale bar: 5 mm [planned for page width].

*Extrémité distale de tarsometatarsaire droit (INGEO-PV 032) de Thinocoridae indet. A, vue crânienne ; B, vue caudale ; C, vue interne ; D, vue latérale ; E, vue distale. Abréviations : fv, foramen vasculaire distal ; h, cicatrice pour l'hallux ; pl, processus postérolatéral de la deuxième trochlée distale ; pm, processus postéromédial de la quatrième trochlée distale ; veg, sillon extenseur vasculaire ; II, III, IV, trochlées distales II, III, et IV, respectivement. Barre d'échelle : 5 mm.*

extended, surpassing the level of the mid-length of the trochlea III. The articular surface is not strongly proximally extended and is delimited by a poorly defined transverse ridge of bone. The lateroplantar process is relatively acute, and separated from the rest of the trochlea by a poorly defined dorsal groove. The trochlea metatarsal II is proximally placed and plantarly oriented. The medioplantar process is slightly developed and is not separated from the main body of the trochlea. In distal view, as occurs in most charadriiforms, the trochleae are arranged in a “U” shaped arch, and the trochlea IV is medially deflected. The fossa metatarsi for the hallux is shallow and proximodistally extended. Its margins are not delimited by a strong ridge of bone.

## 5. Discussion

### 5.1. Taxonomic referral of INGEOPV 032

The general morphology and gracile proportions recognized in the tarsometatarsus INGEOPV 032 are very similar to the condition in the Charadriiformes. The new specimen further resembles this clade due the presence of a weak and poorly defined fossa metatarsi I (Olson and Steadman, 1981; Mayr, 2000), the distal trochlea metatarsi II retroverted and distinctly shorter than IV, and the trochlea metatarsi IV reaching distally to about the mid length of the trochlea metatarsi III (Mayr and Smith, 2001). This combination of traits may be present in some Rallidae, although the presence of a marked furrow in distal view on trochlea metatarsi IV is totally absent in rails.

Among charadriiforms, INGEOPV 032 is referred to Scolopaci by having relatively small distal vascular foramen (De Pietri and

Mayr, 2012), and the plesiomorphic retention of a fossa metatarsi I (absent in several charadriiforms, including all Charadriidae; Mayr and Smith, 2001).

Furthermore, the new specimen differs clearly from several charadriiform families in combinations of features. INGEOPV 032 differs from Charadriidae by having the middle trochlea much more robust, inner and outer trochleae more distally extended, and inner trochlea slightly inflected without a very well-defined and separated medioplantar process on the trochlea II (Olson and Steadman, 1979). Member of “Lari” differ from INGEOPV 032 in having cylindrical trochlea II, very large trochlea III and in having proximally extended and proximally rimmed articular surface of trochlea II (Mayr, 2000; De Pietri et al., 2013). INGEOPV 032 further differs from Phalaropodidae, which are characterized by having very elongate and transversally narrow distal end of tarsometatarsus, and a flat dorsal surface of metatarsal shaft (Campbell, 1979). Haematopodidae is very different from INGEOPV 032 in having a more robust and stout tarsometatarsus (Olson and Steadman, 1979, 1981; De Pietri et al., 2013), a condition also present in the peculiar genera *Chionis* and *Pluvianellus*. Further differentiates from Haematopodidae by lacking an enlarged distal vascular foramen, and lacking slightly plantarly oriented II and IV trochleae (Olson and Steadman, 1979). The Recurvirostridae can be distinguished on the basis of a greatly elevated trochlea II with very well-developed medioplantar process, reduced distal vascular foramen and very narrow tarsometatarsal shaft (Olson and Steadman, 1979). The Jacanidae and Glareolidae are distinct in several ways, especially the hypertrophied distal vascular foramen (Mayr and Smith, 2002; Mayr, 2011). In spite of the large amount of homoplasy in the tarsometatarsus (De Pietri et al., 2015), scolopacids differ from INGEOPV 032 in having a rather slender tarsometatarsus, specially on its stouter distal trochleae which form an angle of less than 35° (Shufeldt, 1903; Olson, 1976, 1984; Björklund, 1994). Further, in INGEOPV 032 the trochlea metatarsi II at the distal end is more proximally situated than that of most scolopacids, with exception of *Limnodromus* and *Gallinago* (De Pietri et al., 2015).

In addition to the above-mentioned characters, INGEOPV 032 exhibits some presumably derived features that are shared exclusively by Thinocoridae and Pedionomidae, as recognized in the

**Table 1**

Measurements (in mm) of the tarsometatarsus INGEOPV 032.  
Mesures (en mm) du métatarsaire INGEOPV 032.

INGEO-PV 032	Measurements
Preserved proximodistal length	10.7
Maximum transverse width of distal end	7.5
Shaft maximal transverse width	2.5

detailed analysis by De Pietri et al. (2015). INGENO-PV 032 shares with both families the following traits:

- a very proximally placed trochlea metatarsi II (convergently present in scolopacid genera *Gallinago* and *Limnodromus*);
- medial rim of trochlea metatarsi III shorter than lateral one, resulting in an asymmetrical trochlea when viewed plantarly;
- plantar projection on trochlea metatarsi II with notch separating it from the medial surface of the trochlea.

These features are totally absent as a whole in other charadriiforms, and character 2 appears to be unique to Thinocoridae and Pedionomidae (De Pietri et al., 2015).

Further, INGENO-PV 032 resembles Thinocoridae and differs from Pedionomidae (represented by *Pedionomus* and *Hakawai*) in the absence of a very deep and well-defined pit on proximal and dorsal surface of trochlea metatarsi III, and in retaining a relatively small distal vascular foramen (De Pietri et al., 2015). Further differs from Pedionomidae in having a more gracile tarsometatarsus with more widespread trochleae, specially that of digit IV. In sum, INGENO-PV 032 could be confidently identified as belonging to Thinocoridae.

Among thinocorids, INGENO-PV 032 resembles *Thinocorus* rather than *Attagis* in having a very plantarly inflected trochlea metatarsi II (Olson and Steadman, 1981). In spite of that, because of its fragmentary nature, INGENO-PV 032 is not identified beyond the family level.

Concluding, in spite of being a relatively high proportion of characters that exhibit homoplasy among Scolopaci families, especially in Scolopacidae, the unique combination of features shared by INGENO-PV 023 and living Thinocoridae is not replicated in any other charadriiform and represents strong evidence of thinocorid affinities for INGENO-PV 023.

## 5.2. Paleobiogeographic implications

Member of Charadriiformes are numerous and remarkably diverse in Miocene and Pliocene deposits of most continents (De Pietri et al., 2011, 2013; De Pietri and Mayr, 2012).

Regrettably, the remains of charadriiform birds from the South American Tertiary are very scarce, and mainly restricted to Argentina. The record includes cf. Charadriidae from the early Miocene of Patagonia (Agnolin and Chaftrat, 2015), and *Calidris* from the late Pliocene of Buenos Aires Province (Tambussi, 1995, 2011). Stucchi and Urbina (2005) mentioned, but not described, a Scolopacidae from the late Miocene of Perú.

Regarding the fossil record of Thinocoridae, it is restricted to the early and late Pleistocene of South American countries of Argentina and Perú, located within the distributional ranges of living taxa (Campbell, 1979; Tonni et al., 1998; De Mendoza et al., 2015). Living thinocorids typically occupy sandy semi-desert habitats with a sparse cover of creeping plants and shrubs, with many succulents (Fjeldsá, 1996; Laredo, 1996; Aramburú et al., 2007; Korzun et al., 2009), and show a large number of behavioral and morphological features that are advantageous in cold environments (Ibarguchi, 2011). Presence of fossil thinocorid in the Miocene of San Juan Province is in agreement with the current distribution of the clade (Navas and Bó, 1997) and with paleoenvironmental evidence indicating presence of opened grasslands with sparse flooded areas in the zone (see Contreras et al., 2001; Contreras and Baraldo, 2010).

## 6. Conclusions

Specimen INGENO-PV 032, recovered from the late Miocene levels of the Loma de Las Tapias Formation (San Juan Province, Argentina), was referred to Thinocoridae. This specimen constitutes the

oldest and first Tertiary record for the clade, which was previously restricted to the early–middle Pleistocene. This finding provides new and important information on the Southern Cone fossil avifaunas.

## Disclosure of interest

The authors declare that they have no competing interest.

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