

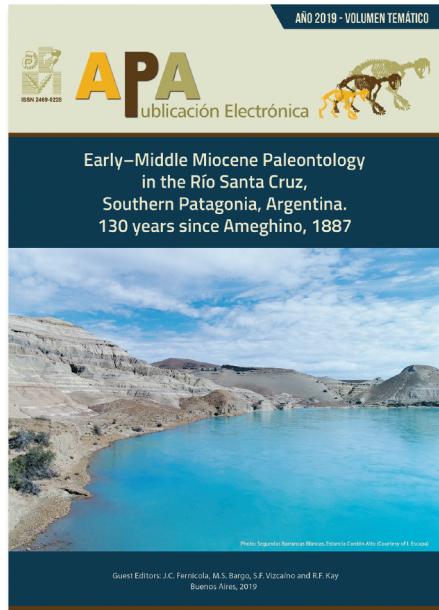


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NEW RECORDS OF BIRDS FROM THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIocene) AT THE RÍO SANTA CRUZ VALLEY, PATAGONIA, ARGENTINA

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Key words. Avifauna. Phorusrhacidae. Tinamidae. Rheidae. Neogene.

Palabras clave. Avifauna. Phorusrhacidae. Tinamidae. Rheidae. Neógeno.

THE SANTA CRUZ FORMATION (SCF) constitutes one of the most representative units of the Early–Middle Miocene (Burdigalian–early Langhian) of South America for its abundant fossil record and the richness of its bird species. This record was collected during paleontological expeditions from the mid-nineteenth century along extensive outcrops exposed throughout a large area of the homonymous province. Seventeen species grouped in 15 genera and at least 10 families (Rheidae, Tinamidae, Phorusrhacidae, Cariamidae, Aramidae, Threskiornithidae, Falconidae, Brontornithidae, Anhimidae?, Anatidae and Anhingidae) constitute the diversity of extinct birds known so far (Degrange *et al.*, 2012).

The SCF crops out in much of the territory of the Province of Santa Cruz (Argentina), in the northwest, in the surroundings of Lago Posadas, the central region along Río Santa Cruz (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016) and Río Chalía (= Sehuén; Vizcaíno *et al.*, 2018) and, in the southeast, along the Atlantic coast (Vizcaíno *et al.*, 2012). It is a continental unit composed of mudstones, tuffaceous sandstones and tuffs deposited in fluvial environments under the influence of intense explosive pyroclastic input. For extensive geological descriptions, see Cuitiño *et al.* (2016, 2019a). The radiometric ages for the entire SCF span the interval ~18 to 15.60 Ma, being ~18–16 Ma for the Atlantic coastal

localities (Fleagle *et al.*, 2012; Perkins *et al.*, 2012); ~18.20–15.60 Ma for the Río Bote and the Río Santa Cruz localities (Cuitiño *et al.*, 2016), and ~18–14 Ma for the Lago Posadas region (Perkins *et al.*, 2012; Cuitiño *et al.*, 2019b).

The SCF along Río Santa Cruz was recently studied and described in three locations by Fernicola *et al.* (2014) and Cuitiño *et al.* (2016, 2019a); that is, from east to west: Barrancas Blancas (BB; Estancias Santa Lucía and Aguada Grande), Segundas Barrancas Blancas (SBB; Estancias Cordón Alto, El Tordillo and Rincón Grande) and Yaten Huageno (YH; Estancia El Refugio) (Fig. 1). In the present contribution, we present and describe the first records of birds from these localities, with accurate geographic and stratigraphic provenances, along Río Santa Cruz.

MATERIAL AND METHODS

Recent fieldwork carried out throughout 2013 and 2014 by joint expeditions of Museo de La Plata (MLP), La Plata, Argentina, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina, and Duke University, North Carolina, USA, recovered nine remains of fossil birds. This collection belongs to Museo Regional Provincial "Padre Manuel Jesús Molina" (MPM-PV), Río Gallegos, Argentina. The specimens collected exclusively include postcranial elements (e.g., fragmentary long bones,

several pes and manus elements). These were recovered from three fossiliferous localities: Barrancas Blancas (BB; seven specimens), Segundas Barrancas Blancas (SBB; one specimen) and Yaten Huageno (YH; one specimen). The osteological nomenclature follows Howard (1929) and Baumel and Witmer (1993).

SYSTEMATIC PALEONTOLOGY

Order CARIAMIFORMES Verheyen, 1957

Family PHORUSRACIDAE (Ameghino, 1889)

Genus *Psilopterus* Moreno and Mercerat, 1891

Type species. *Psilopterus comunis* Moreno and Mercerat, 1891. Santa Cruz Formation, Province of Santa Cruz, Argentina.

Psilopterus lemoinei (Moreno and Mercerat, 1891)

Figure 2.1–14

Referred material. MPM-PV 18897, associated fragments of a single specimen consisting of right scapula, two proximal ends of humeri (one right and one left), distal end of left radius, left proximal phalanx of *digitus majoris*, synsacrum plus pelvis, two distal ends of femora (one right and one left), distal end of left tibiotarsus, right proximal and right distal ends of tarsometatarsi, and proximal end of an indetermi-

nate phalanx of the foot; MPM-PV 18898, synsacrum plus articulated pelvis and partial vertebral column.

Geographic occurrence. Both specimens come from the BB locality in the Estancia Santa Lucía, Province of Santa Cruz.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. The specimen MPM-PV 18897 is referred to *Psilopterus lemoinei* based on the following diagnostic characters described by Degrange and Tambussi (2011): humerus with *crista deltopectoralis* weakly developed and lacking pneumatic foramen; femur with *crista lateralis* of *sulcus patellaris* interrupted proximally before the contact with shaft; tibiotarsus with *sulcus extensorius* deep and medially positioned; tarsometatarsus with *hypotarsus* possessing two reduced *cristae hypotarsi* on the plantar surface: *crista medialis hypotarsi* lightly furrowed, with short posterior development, and *crista lateralis hypotarsi* slightly convex; margin of *hypotarsus* not protruded proximally; *foramina vascularia proximalia* visible in plantar view and placed at the same level; ridge of *cotyla medialis* high and oval; *eminentia intercotylaris* well developed.

The synsacrum MPM-PV 18898 is also referred to *Psilopterus* based on the presence of a well-developed process of the ilium, which constitutes a cranially directed spine, caudally located with respect to the *foramen ilioischadicum* (Degrange *et al.*, 2015b). Additionally, the size of this specimen is similar to that of MPM-PV 18897, precluding its

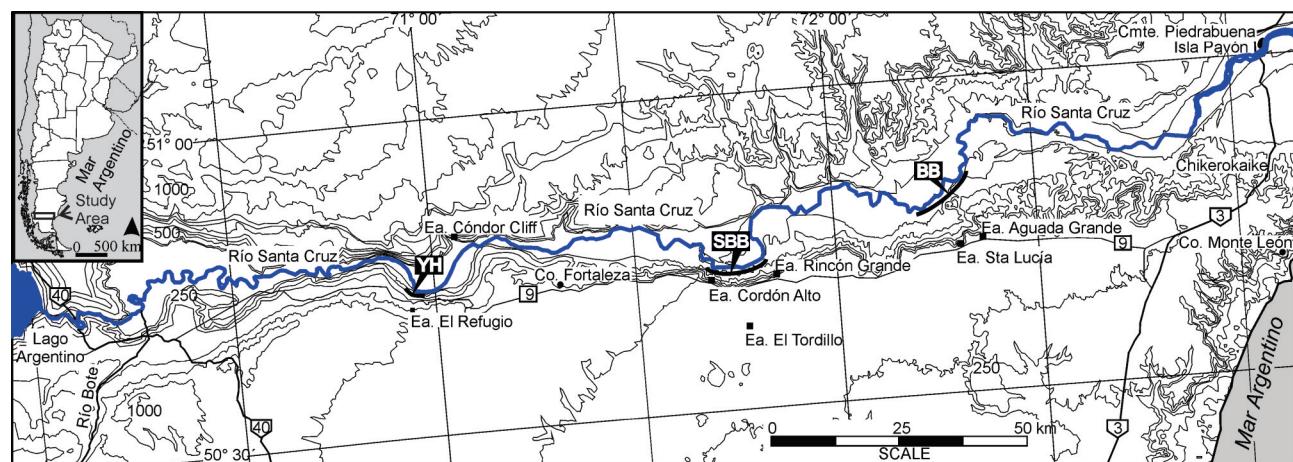


Figure 1. Geographical location of the fossiliferous localities studied at Río Santa Cruz. SBB, Segundas Barrancas Blancas; BB, Barrancas Blancas; YH, Yaten Huageno; Ea., Estancia. Modified from Fernicola *et al.* (2014).

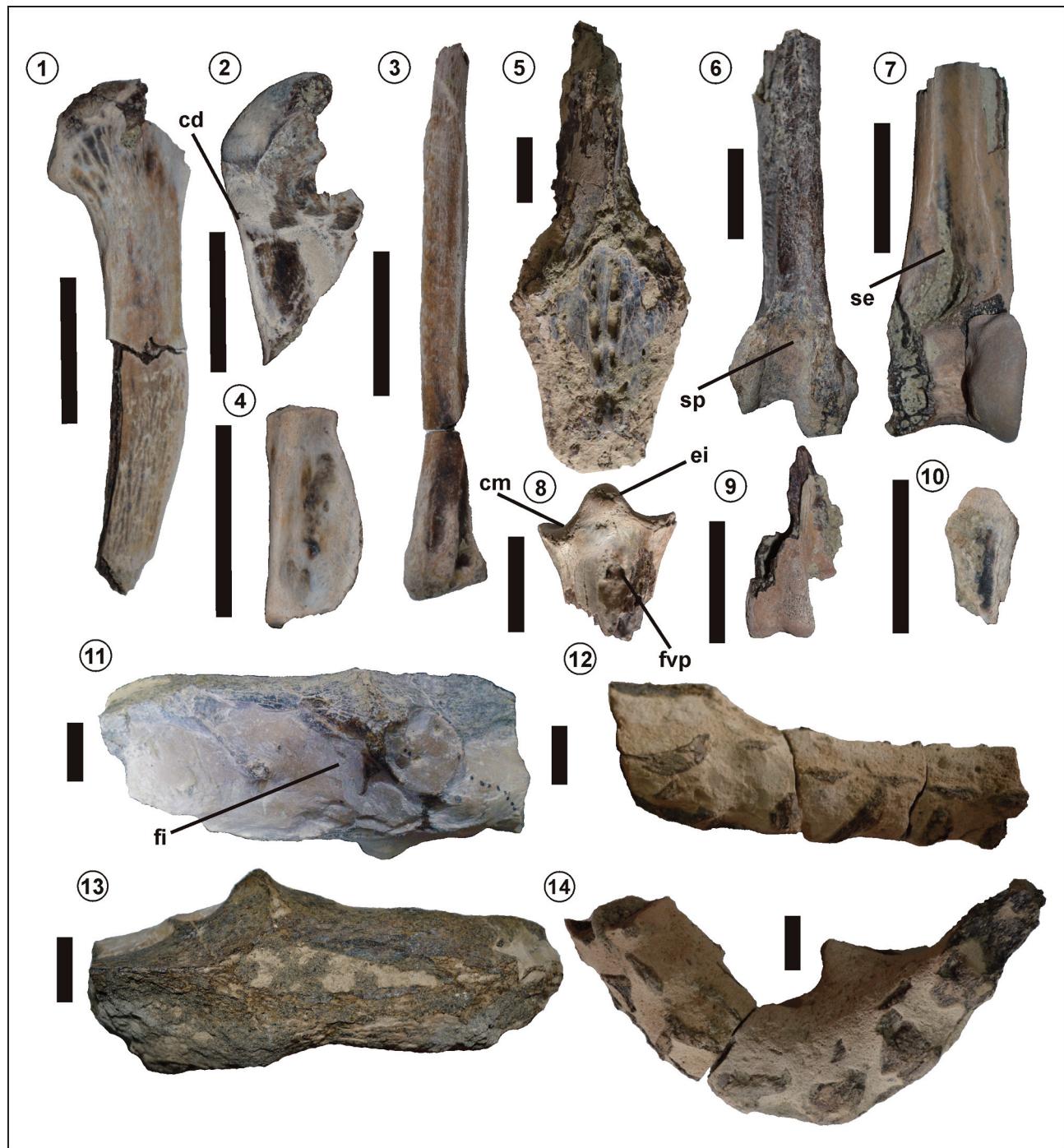


Figure 2. *Psilopterus lemoinei*. MPM-PV 18897, 1–10; 1, fragments of right scapula, in dorsal view; 2, proximal end of right humerus in cranial view; 3, distal end of left radius in cranial view; 4, left phalanx proximal *digitus majoris* of the wing in dorsal view; 5, fragments of synsacrum in dorsal view; 6, distal end of left femur in cranial view; 7, distal end of left tibiotarsus, in cranial view; 8, proximal end of right tarsometatarsus in dorsal view; 9, distal end of left tarsometatarsus in dorsal view; 10, proximal end of indeterminate phalanx of the foot, in dorsal view. MPM-PV 18898, 11–14; 11, fragments of synsacrum, in lateral view; 12, fragments of posterior ends of column in lateral view; 13, fragments of synsacrum in dorsal view; 14, fragments of anterior ends of column in lateral view. Abbreviations: cd, crista deltopectoralis; cm, cotyla medialis; ei, eminentia intercotylaris; fi, foramen ilioschiadicum; fvp, foramina vascularia proximale; se, sulcus extensorius; sp, sulcus patellaris. Scale bars=2 cm.

assignment to *Psilopterus bachmanni* (Moreno and Mercerat, 1891) and *Procarriama simplex* Rovereto, 1914 (see Alvarenga and Höfling, 2003, table 8).

Psilopterus sp.

Figure 3.1–2

Referred material. MPM-PV 18901, distal fragment of left tibiotarsus; MPM-PV 18902, distal fragment of left tibiotarsus; MPM-PV 18905, distal end of left tarsometatarsus.

Geographic occurrence. MPM-PV 18901 and MPM-PV 18905 come from BB (Estancia Aguada Grande), while MPM-PV 18902, from SBB (Estancia Cordón Alto), Province of Santa Cruz.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. The distal end of tarsometatarsus (MPM-PV 18905) resembles that of *Psilopterus lemoinei* because its *trochlea metatarsi III* have flanges more proximally convergent than that of *P. affinis* (Ameghino, 1899) (see Degrange and Tambussi, 2011). The distal fragments of tibiotarsi (MPM-PV 18901, MPM-PV 18902) resemble those of *P. lemoinei* and differ from those *P. bachmanni* by having a wide *pons supratendineus* with a well-developed distal lip and lateral tubercle (Degrange and Tambussi, 2011). In addition, both remains can be distinguished from *P. bachmanni* by their greater size (see Alvarenga and Höfling, 2003, tab. 8). However, both the tibiotarsus and the tarsometatarsus do not present other characters that allow their complete

distinction among the species of *Psilopterus* and, hence, their tentative assignment to *Psilopterus* sp.

Order RHEIFORMES (Forbes, 1884)

Family RHEIDAE Bonaparte, 1849

Genus *Opisthodactylus* Ameghino, 1891

Type species. *Opisthodactylus patagonicus* Ameghino, 1891. Santa Cruz Formation, Monte Observación, Province of Santa Cruz.

Opisthodactylus patagonicus Ameghino, 1891

Figure 4.1

Referred material. MPM-PV 18903 and MPM-PV 18904, distal ends of left tibiotarsi.

Geographic occurrence. MPM-PV 18903 comes from BB (Estancia Santa Lucía) and MPM-PV 18904, from YH (Estancia El Refugio), Province of Santa Cruz.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. These specimens are assigned to *Opisthodactylus patagonicus*. They can be distinguished from other extant and extinct Rheidae by the following character combination (Noriega *et al.*, 2017): prominence for attachment of medial ligament continuous with insertion for transverse ligament (not separated by the distal end of the *sulcus extensorius*); *sulcus extensorius* markedly excavated, well delimited and ending proximally; cross-section of distal shaft more markedly compressed anteroposteriorly. Several of the characters observed in both specimens are shared between *O. patagonicus* and *O. kirchneri* Noriega, Jordan, Vezzosi and Areta, 2017 but differ from those of *O. horacioperezi* Agnolín and Chafrat, 2015 (see Noriega *et al.*, 2017): greater size; *trochlea cartilaginea tibialis* larger and more proximodistally developed in anterior view at the point where it joins the medial margin of the *condylus lateralis*; ridge that delimits *trochlea cartilaginea tibialis* proximally higher or more proximally extended; in medial view, medial ligamentary ridge sharper, ending distally in a more robust medial ligamental prominence; in lateral view, *epicondylus medialis* more marked and more proximally placed. The portion of the *sulcus m. fibularis* located medially to the *tuberculum retinaculi m. fibularis* is developed as in *O. patagonicus* but deeper than in *O. kirchneri*.

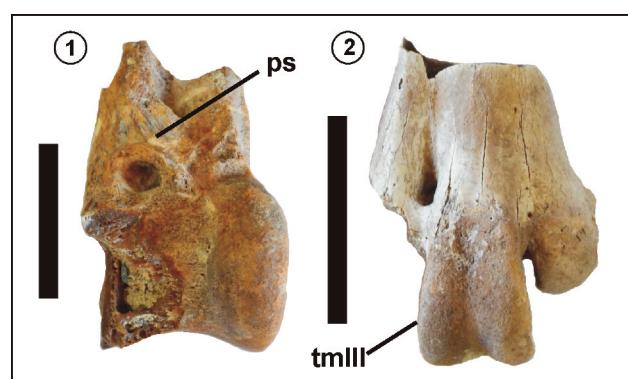


Figure 3. *Psilopterus* sp. 1, MPM-PV 18902, distal ends of left tibiotarsus in cranial view; 2, MPM-PV 18905, distal ends of left tarsometatarsus in dorsal view. Abbreviations: ps, *pons supratendineus*; tmIII, *trochlea metatarsi III*. Scale bars= 2 cm.

Order TINAMIFORMES Huxley, 1872

Family TINAMIDAE Gray, 1840

TINAMIDAE gen. et sp. indet.

Figure 4.2

Referred material. MPM-PV 18900, proximal end of left carpometacarpus.

Geographic occurrence. BB (Estancia Santa Lucía), Province of Santa Cruz.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. A deep pit for an aponeurotic insertion –tentatively identified as the attachment for the *ligamentum ulno-carpometacarpale ventralis* (Bertelli *et al.*, 2014)– located on the ventral surface of the proximal end, caudal to the *processus pisiformis*, which is observed in MPM-PV 18900, is an automorphic character for Tinamidae (Bertelli, 2002). *Nothocercus* Gray, 1867 is the only exception because this pit varies from virtually absent to deep (Bertelli *et al.*, 2014). Additionally, this specimen has the *processus extensorius* well developed, condition shared with all the tinamids and the European *Palaotis* Lambrecht, 1928 among the palaeognathous genera (Mayr, 2015). Other diagnostic character present in MPM-PV 18900 is the “caudal rim” of the *trochlea carpalis*, which is clearly notched like in some tinamous (e.g., *Nothocercus*, *Tinamus* Hermann, 1783, *Crypturellus* Brabourne and Chubb 1914, *Eudromia* Geoffroy Saint-Hilaire, 1832) (Bertelli *et al.*, 2014).

CONCLUDING REMARKS

The state of knowledge of the Santacrucian avian diversity was recently summarized by Degrange *et al.* (2012). The fossil record includes at least 17 formally described species grouped in 15 genera and at least 10 families: rheas (*Opisthodactylus patagonicus*), tinamous (*Crypturellus reai* Chandler, 2012), terror birds (*Phorusrhacos longissimus* Ameghino, 1887; *Patagornis marshi* Moreno and Mercerat, 1891; *Psilopterus bachmanni* (Moreno and Mercerat, 1891), *Psilopterus lemoinei* (Moreno and Mercerat, 1891)), seriemas (*Miocariama patagonica* Noriega and Mayr, 2017), limpkins (*Anisognathus excavatus* (Ameghino, 1891)), spoonbills (*Protibis clemialis* Ameghino, 1891), falcons (*Badiostes patagoniscus*

Ameghino, 1895, *Thegornis musculosus* Ameghino, 1895, *T. debilis* Ameghino, 1895), waterfowls (*Brontornis burmeisteri* Moreno and Mercerat, 1891; *Eoneornis australis* Ameghino, 1895, *Eutelornis patagonicus* Ameghino, 1895, *Ankonetta larriestrai* Cenizo and Agnolín, 2010) and darters (*Anhinga hesterna* (Ameghino, 1895)).

Most of these taxa were originally erected at the end of the 19th century (Ameghino, 1887, 1891, 1895; Moreno and Mercerat, 1891) or restudied at the beginning of the 20th century (Dolgopol de Sáez, 1927; Kraglievich, 1931; Sinclair and Farr, 1932) on the basis of material without precise stratigraphic position or even of dubious geographic provenance.

The most prospected levels of the SCF that have provided the largest amount of avian fossil remains are exposed close to or along the Atlantic Ocean coast (see Fernicola *et al.*, 2019: fig. 5), e.g., Monte León, Monte Observación, La Cueva, Yegua Quemada, Jack Harvey, Puesto Estancia La Costa (Corriguen- Kaik) and Monte Tigre (Ameghino, 1891, 1895; Brodkorb, 1964; Tonni, 1980; Degrange *et al.*, 2012;

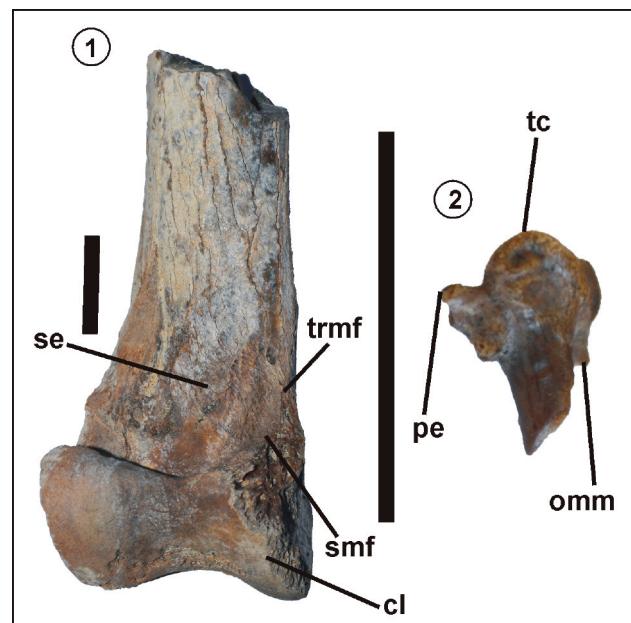


Figure 4. Palaeognathae. 1, *Opisthodactylus patagonicus* MPM-PV 18903, distal end of left tibiotarsus in cranial view; 2, Tinamidae indeterminated MPM-PV 18900, proximal end of left carpometacarpus in dorsal view. Abbreviations: *cl*, *condylus lateralis*; *omm*, *os metacarpale minus*; *pe*, *processus extensorius*; *se*, *sulcus extensorius*; *smf*, *sulcus m. fibularis*; *tc*, *trochlea carpalis*; *trmf*, *tuberculum retinaculi m. fibularis*. Scale bars= 2 cm.

Vizcaíno *et al.*, 2012). Other exposures, such as those in the Río Santa Cruz and Río Chalía (= Sehuén) valleys, have provided limited published information about the fossil record of birds. For example, Carlos Ameghino collected the type specimen of *Phorusracos longissimus* Ameghino, 1887 from the Río Santa Cruz outcrops but failed to specify a location. Both the distal end of the tarsometatarsus assigned to the purported limpkin *Anisognathus excavatus*, as well as the material referred to *Psilopterus lemoinei* come from Karaiken, north to the rising of Río Santa Cruz, near Lago Argentino; while fragmentary specimens referred to *Opisthodactylus patagonicus* and *Phorusracos longissimus* are reported from localities in Río Chalía (Brodkorb, 1964; Tonni, 1980). Recently, new remains assigned to *Phorusracos longissimus* were found near Lago Belgrano (Degrange *et al.*, 2019).

Renewed intensive collecting field trips developed by researchers of MLP, MACN and Duke University, together with paleontological and geologic studies performed since 2003 in the SCF (Vizcaíno *et al.*, 2012; Fornicola *et al.*, 2014), are bringing out the possibility to overcome the historical difficulties concerning the provenances of fossil materials. Thus, the knowledge about some old known Santacrucian bird taxa like the falconid *Thegornis musculosus* (Noriega *et al.*, 2009, 2011; Noriega and Mayr, 2017) or the phorusrhacid *Psilopterus bachmanni* (Degrange *et al.*, 2015a) has been substantially improved with new complete or better-preserved available specimens with accurate provenances.

As a result of the paleontological discoveries within the framework of these projects, we present the first fossil birds collected with precise geological provenance from different localities in the Río Santa Cruz valley. They include fragmentary specimens referred to *Opisthodactylus patagonicus* (Rheidae) and an indeterminate genus and species of tinamous (Tinamidae), as well as other more complete specimens assigned to *Psilopterus lemoinei* (Phorusrhacidae). No new remains of *Phorusracos longissimus* were recorded.

Santacrucian paleoenvironments were characterized by the presence of alternating areas of herbaceous vegetation with shrubby or wooded areas based on the extrapolation of habitat preferences of living birds for their extinct analogs (Degrange *et al.*, 2012). Habitat preferences of extant rheas, tinamids and seriemas (analog to phorusrhacids) are con-

sistent with open areas because of their cursorial capabilities. Additionally, waterfowls, limpkins, spoonbills and darters would indicate the existence of temporarily flooded savannas or permanent water bodies in forested areas (Degrange *et al.*, 2012).

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