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Source: Acta Palaeontologica Polonica, 53(4) : 593-600

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2008.0404>

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# First record of an extinct marabou stork in the Neogene of South America

JORGE IGNACIO NORIEGA and GERARDO CLADERA



Noriega, J.I. and Cladera, G. 2008. First record of an extinct marabou stork in the Neogene of South America. *Acta Palaeontologica Polonica* 53 (4): 593–600.

We describe a new large species of marabou stork, *Leptoptilus patagonicus* (Ciconiiformes, Ciconiidae, Leptoptilini), from the late Miocene Puerto Madryn Formation, Chubut Province, Argentina. The specimen consists mainly of wing and leg bones, pelvis, sternum, cervical vertebrae, and a few fragments of the skull. We provisionally adopt the traditional systematic scheme of ciconiid tribes. The specimen is referred to the Leptoptilini on the basis of similarities in morphology and intramembral proportions with the extant genera *Ephippiorhynchus*, *Jabiru*, and *Leptoptilos*. The fossil specimen resembles in overall morphology and size the species of *Leptoptilos*, but also exhibits several exclusive characters of the sternum, humerus, carpometacarpus, tibiotarsus, and pelvis. Additionally, its wing proportions differ from those of any living taxon, providing support to erect a new species. This is the first record of the tribe Leptoptilini in the Tertiary of South America.

**Key words:** Ciconiidae, *Leptoptilos*, Miocene, Argentina, South America.

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## Introduction

The stork family (Ciconiidae) is a well-defined group of waterbirds, traditionally divided into three tribes: the Mycteriini, the Ciconiini, and the Leptoptilini (Kahl 1971, 1972, 1979). They were already differentiated by the early Tertiary with the first record occurring in the early Oligocene of the Fayum series in Egypt (Olson 1985; Feduccia 1996). However, most fossil storks are known from the Tertiary of Europe, Asia, the Americas, and Africa, and are based on isolated and fragmentary remains that preclude our understanding on the phylogeny and relationships within the Ciconiidae (Feduccia 1996).

The oldest South American fossil stork, *Ciconiopsis antarctica* Ameghino, 1899, was described from the early Oligocene of Santa Cruz (Argentina), but its ordinal assignment has been questioned (Olson 1985; Agnolin 2004). More recently, isolated fragments of tarsometatarsi undoubtedly referable to the Mycteriini were reported from the late Miocene in Entre Ríos Province, Argentina (Noriega 1995; Noriega and Agnolin 2006). Recently, Louchart et al. (2005) described new Tertiary fossil Leptoptilini from Africa and revised previous records of other extinct Old World storks.

This contribution describes a new species of a large stork referable to the genus *Leptoptilos*, recovered from the late Miocene of Argentina. Fossils assignable to *Leptoptilos* have hitherto been unknown from Tertiary deposits of South America. Therefore, this finding constitutes the first record for both the genus and the tribe on this continent.

**Institutional abbreviations.**—BMNH, Natural History Museum, London, UK; CICYTTP, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; CNAR-KB3, collections of locality 3 of the Kossom Bougoudi area, Centre National d'Appui à la Recherche, N'Djamena, Chad; FMNH, Field Museum of Natural History, Chicago, USA; IRSN, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KNM-BN, collections of Baringo district and KNM-LT, collections of Lothagam, Kenya National Museums, Nairobi, Kenya; LAC-MNHN, Collections d'Anatomie Comparée, Muséum national d'Histoire naturelle, Paris, France; MEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MHNT, Muséum de História Natural de Taubaté, Brazil; MRAC, Musée Royal pour l'Afrique Centrale, Tervuren, Belgium; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; NME-SAG and NME-OMO, collections of the locality 1 of the Sagantole area and the Omo Shungura Formation, respectively, housed at the National Museum of Ethiopia, Addis Ababa, Ethiopia; UCBL, Université Claude Bernard-Lyon 1, Villeurbanne, France; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

## Methods

Comparisons were made with the extant species from the MHNT, LAC-MNHN, and CICYTTP collections: *Mycteria*

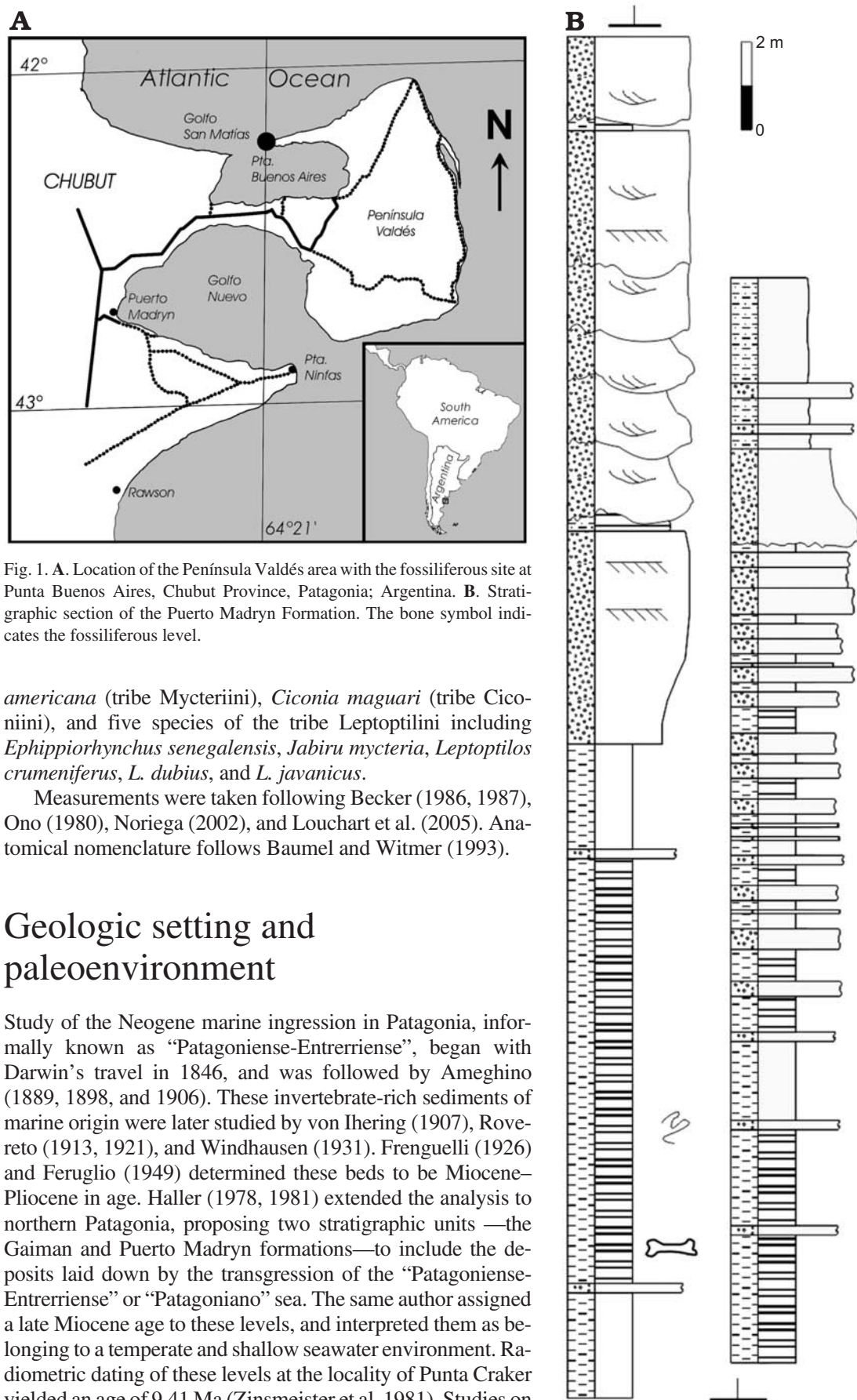


Fig. 1. **A.** Location of the Península Valdés area with the fossiliferous site at Punta Buenos Aires, Chubut Province, Patagonia; Argentina. **B.** Stratigraphic section of the Puerto Madryn Formation. The bone symbol indicates the fossiliferous level.

*americana* (tribe Mycterini), *Ciconia maguari* (tribe Ciconiini), and five species of the tribe Leptoptilini including *Ephippiorhynchus senegalensis*, *Jabiru mycteria*, *Leptoptilos crumeniferus*, *L. dubius*, and *L. javanicus*.

Measurements were taken following Becker (1986, 1987), Ono (1980), Noriega (2002), and Louchart et al. (2005). Anatomical nomenclature follows Baumel and Witmer (1993).

## Geologic setting and paleoenvironment

Study of the Neogene marine ingress in Patagonia, informally known as “Patagoniense-Entrerriense”, began with Darwin’s travel in 1846, and was followed by Ameghino (1889, 1898, and 1906). These invertebrate-rich sediments of marine origin were later studied by von Ihering (1907), Rovereto (1913, 1921), and Windhausen (1931). Frenguelli (1926) and Feruglio (1949) determined these beds to be Miocene–Pliocene in age. Haller (1978, 1981) extended the analysis to northern Patagonia, proposing two stratigraphic units—the Gaiman and Puerto Madryn formations—to include the deposits laid down by the transgression of the “Patagoniense-Entrerriense” or “Patagoniano” sea. The same author assigned a late Miocene age to these levels, and interpreted them as belonging to a temperate and shallow seawater environment. Radiometric dating of these levels at the locality of Punta Craker yielded an age of 9.41 Ma (Zinsmeister et al. 1981). Studies on

the distribution of facies and lateral correlations were made by Scasso and Del Río (1987), who proposed a unique sedimentary and regressive cycle for the “Patagoniense–Entrerriense” units. The sedimentation of the Puerto Madryn Formation, the fossil bearing unit, was characterized by a transition from off-shore to litoral environment (Scasso and Del Río 1987).

The fossil specimen described herein was recovered at the locality of Punta Buenos Aires at Península Valdés, Chubut Province, Argentina (Fig. 1A). The complete sequence of the Puerto Madryn Formation reaches a thickness of up to 50 m; however, the base of the formation does not emerge at the fossil locality (Fig. 1B). The base of the profile has green and gray mudstone and limestone units, corresponding to Facies 4a of Scasso and Del Río’s profile (1987). The fossil stork comes from this mudstone deposit.

## Systematic paleontology

Order Ciconiiformes Bonaparte, 1854

Suborder Ciconiae Bonaparte, 1854

Family Ciconiidae Gray, 1831

Tribe Leptoptilini Mayr and Cottrell, 1979

Genus *Leptoptilos* Lesson, 1831

*Leptoptilos patagonicus* sp. nov.

Figs. 2, 3.

*Etymology*: After its geographic provenance from the Patagonian region of Argentina, South America.

*Holotype*: MEF 1363. Associated partial skeleton of one individual with wing and leg bones, and a few fragments of the skull, collected by Pablo Puerta in 2000.

*Type locality*: Punta Buenos Aires, Península Valdés, Chubut Province, Patagonia, Argentina (Fig. 1A).

*Type horizon*: Puerto Madryn Formation (Fig. 1B), informally known as “Entrerriense” unit; late Miocene (Haller 1978, 1981).

*Material*.—The specimen includes tip of the mandible, fragments of the ramus mandibulae and of the articular bone, right humerus missing proximal end, right distal ulna, left ulna missing proximal end, right radius with incomplete distal end, left radius with incomplete proximal end, complete left and right carpometacarpi, complete left cuneiform, right ilium, ischium and pubis, complete right tibiotarsus with proximal end lightly damaged, complete carina and incomplete corpus of sternum (Figs. 2, 3).

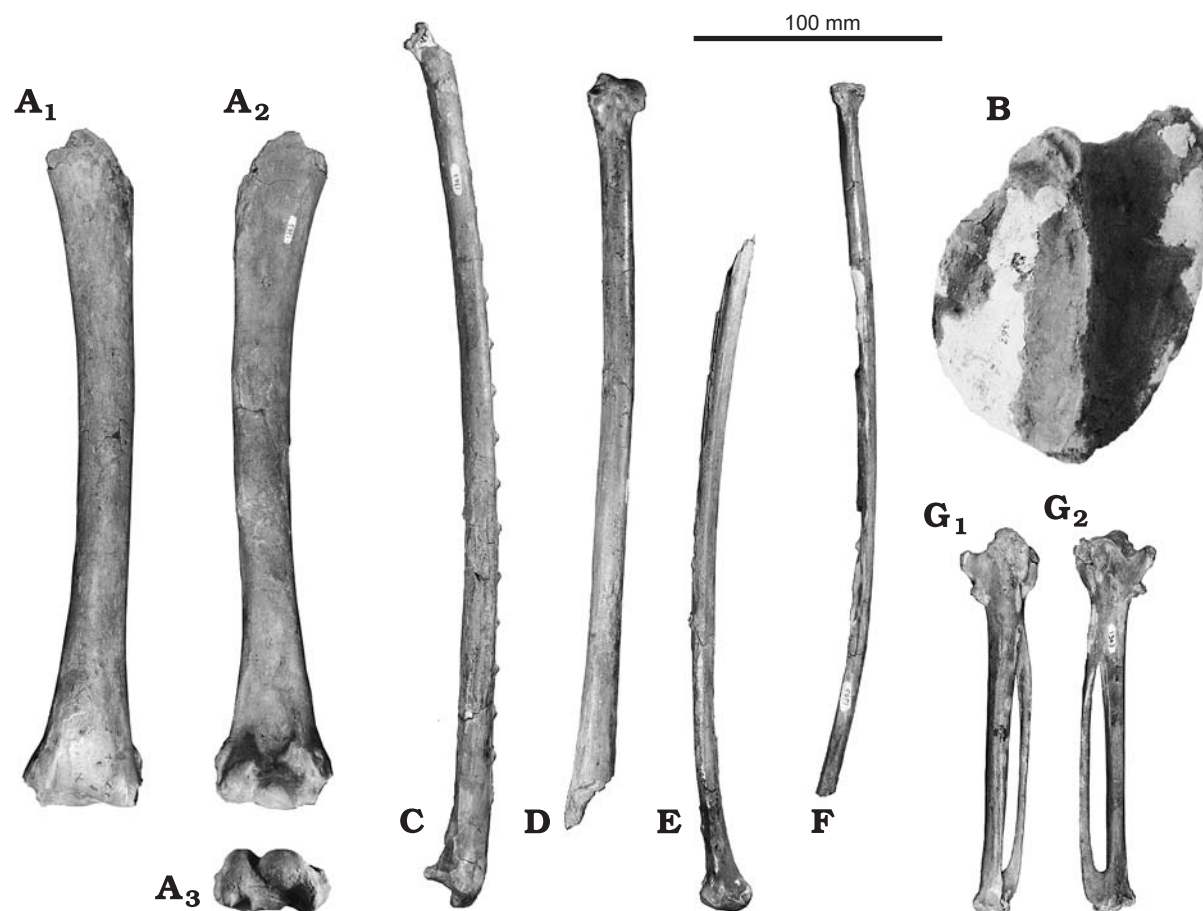


Fig. 2. The marabou stork *Leptoptilos patagonicus* sp. nov., specimen MEF-1363 (holotype) from the Puerto Madryn Formation (late Miocene), Punta Buenos Aires, Península Valdés, Chubut Province, Patagonia, Argentina. A. Right humerus in anconal (A<sub>1</sub>), palmar (A<sub>2</sub>), and distal (A<sub>3</sub>) views. B. Sternum in lateral aspect. C, D. Right (C) and left (D) ulnae in palmar and anconal views. E, F. Left (E) and right (F) radii, in palmar views. G. Left carpometacarpus in internal (G<sub>1</sub>) and external (G<sub>2</sub>) views.

**Diagnosis.**—Larger than the living *Leptoptilos javanicus*, but overlapping with the largest individuals of *L. crumeniferus* and *L. dubius*, and smaller than the extinct *L. falconeri*. Hindlimbs larger than forelimbs compared with extant species of the genus, similar to the condition observed in *L. falconeri*. *Leptoptilos patagonicus* differs from *L. crumeniferus*, *L. dubius*, and *L. javanicus* by having ventral and dorsal lips of sulcus articularis coracoideus of sternum wider; humeral scars for M. pronator profundus and M. flexor carpi ulnaris larger and deeper; processus flexorius more strongly projected; epicondylus ventralis less protrudent medio-distally; internal rim of trochlea carpalis less rounded, merging with os metacarpale minus more distally; proximal surfaces of tibiotarsal condyles more extended up the shaft; ala ischii more expanded ventrally with its lower border more curved.

Description

**Humerus.**—The humerus is larger than in *Ephippiorhynchus senegalensis* and *Jabiru mycteria*, but shorter than in *L. dubius* and *L. crumeniferus* (Table 1; Fig. 2A). The width of distal end of shaft at the level of the tuberculum supracondylare dorsale, just proximal to the epiphysis, is greater than in most of the storks compared (Table 1). However, the distal end width is proportionally smaller in comparison to other mea-

surements of the bone. The distal epiphysis is moderately flexed antieriad as in *Jabiru*. The tuberculum supracondylare dorsale is well developed proximally, angling moderately relative to shaft as in *Ciconia*, and not projected laterally as observed in the remaining genera compared. The epicondylus ventralis is less protrudent medio-distally than in *Jabiru*, *Ephippiorhynchus*, *Leptoptilos*, and *Mycteria*; similar to those of *Ciconia*. The scars for M. pronator profundus and M. flexor carpi ulnaris are larger and deeper than those of the species compared, giving a pronounced excavation to the area of the ventral side distal to the epicondylus ventralis and undercutting the latter more markedly. The processus flexorius is more strongly projected distally than in all genera compared. The tuberculum supracondylare ventrale is similar to that of *Ephippiorhynchus* and *Leptoptilos*, i.e., elongated vertically and flattened, whereas it is more transverse and rounded in the remaining species compared. The impression of M. brachialis is large and deep, being well excavated medially and shallower laterally, with its proximal end forming a marked ridge along the lateral edge of the shaft as in *Jabiru*. The fossa olecrani is broad and deeper than in the comparative species.

**Ulna.**—The ulna is slightly more robust and longer than in the species used in comparison with the exception of *L. dubius* and *L. crumeniferus* (Table 1; Fig. 2C, D). The cotyla ventralis is shallow and subelliptical as in *Jabiru*, *Ephippiorhynchus*, and *Leptoptilos*; whereas it is deeper and more rounded in

Table 1. Measurements (in mm) of the humerus and the ulna of Leptoptilini. Humerus: greatest preserved length measured from the proximal margin of insertion of M. latissimus dorsi caudalis through the midpoint of the condylus medialis (L.h); transverse width at midshaft (W-s.h); depth at midshaft (D-s.h); transverse width of distal end from the tuberculum supracondylare dorsale to the epicondylus ventralis (W-d.h). Ulna: greatest length measured from the olecranon through the condylus ventralis ulnaris (L.u); width of proximal end through cotyles (W-p.u); width of midshaft (W-s.u); depth of midshaft (D-s.u); width of distal end through condyles (W-d.u).

|                                                | Humerus |       |       |                   | Ulna  |       |       |       |       |
|------------------------------------------------|---------|-------|-------|-------------------|-------|-------|-------|-------|-------|
|                                                | L.h     | W-s.h | D-s.h | W-d.h             | L.u   | W-p.u | W-s.u | D-s.u | W-d.u |
| <i>Leptoptilos patagonicus</i> MEF-1363        | c.250   | 23.2  | 15.9  | 46.2              | 351   | 28.8  | 14.5  | 12.2  | 22.9  |
| <i>Leptoptilos dubius</i> LAC-MNHN1993-16      | 265     | 26.4  | 19.7  | 53.4              | 458   | 37.0  | 16.0  | 14.4  | 27.2  |
| <i>Ephippiorhynchus senegalensis</i> MHNT 1742 | 238.5   | —     | —     | 36.1 <sup>a</sup> | 276.0 |       |       |       |       |
| <i>Jabiru mycteria</i> CICYTTP-ACI-73          | 218.6   | 19.4  | 16.9  | 43.6              | 341.2 | 28.0  | 13.8  | 11.4  | 17.6  |

<sup>a</sup> Walter Boles (personal communication 2004).

Table 2. Measurements (in mm) of the radius and the carpometacarpus of Leptoptilini. Radius: greatest length from cotyla humeralis to facies articularis radiocarpalis (L.r; estimated by summing both right and left partial radii of MEF-1363); width of proximal end from facies articularis ulnaris to head (W-p.r); width of distal end (W-d.r). Carpometacarpus: greatest length from the most proximal portion of the trochlea carpalis through facies articularis digitalis minor (L.c); transverse width of proximal end from the ventral rim of the trochlea carpalis through processus extensorius (Cc); depth of proximal end from ventral to dorsal rims of trochlea carpalis (D-p.c); length of the os metacarpale alulare I from processus extensorius to processus alularis (L-McI); depth at midshaft of os metacarpale majus (D-s.c); transverse width of midshaft of os metacarpale majus (W-s.c); greatest depth of distal end, measured across the dorsal edge of facies articularis digitalis major (D-d.c); transverse width of distal end from edge of facies articularis digitalis major through facies articularis digitalis minor (W-d.c).

|                                                | Radius |       |       | Carpometacarpus |      |       |       |       |       |       |       |
|------------------------------------------------|--------|-------|-------|-----------------|------|-------|-------|-------|-------|-------|-------|
|                                                | L.r    | W-p.r | W-d.r | L.c             | Cc   | D-p.c | L-McI | D-s.c | W-s.c | D-d.c | W-d.c |
| <i>Leptoptilos patagonicus</i> MEF-1363        | c.310  | 16.1  | 20.8  | 151.7           | 31.8 | 14.9  | 19.1  | 10.7  | 7.6   | 12.0  | 17.0  |
| <i>Leptoptilos dubius</i> LAC-MNHN1993-16      | 438.6  | 18.5  | 25.7  | 187.8           | 37.8 | 17.3  | 23.0  | 13.0  | 9.7   | 13.6  | 21.6  |
| <i>Ephippiorhynchus senegalensis</i> MHNT 1742 |        |       |       | 119.2           |      |       |       |       |       |       |       |
| <i>Jabiru mycteria</i> CICYTTP-ACI-73          | 300.3  | 14.6  | 19.0  | 137.5           | 29.5 | 14.5  | 18.5  | 10.0  | 8.0   | 12.0  | 17.2  |

*Ciconia* and *Mycteria*. The impressio brachialis is less deep than in *Jabiru*, with its bordering bony ridges less marked, as in *Leptoptilos*, *Ephippiorhynchus*, *Ciconia*, and *Mycteria*. The impression of *M. scapulotriceps* is more distal and elongated. The condylus dorsalis is proportionally greater, more protruding medially than in the living species compared.

**Radius.**—The cotyla humeralis is quadrangular as in *Jabiru*, *Leptoptilos*, and *Ephippiorhynchus*, whereas it is more subelliptical in *Ciconia*. The facies articularis ulnaris is prominent. The tuberculum bicipitalis radialis is more distally extended than in *Jabiru*, similar to those of *Leptoptilos*, *Ephippiorhynchus*, and *Ciconia*. The pneumatic foramina at proximal and distal ends are absent, as in *Ephippiorhynchus* and *Ciconia*, unlike the conspicuous pneumatization shown by *Jabiru* and *Leptoptilos*. The facies articularis radiocarpalis is more elongated transversally and the sulcus tendinosus is larger than in the species compared, making distal end wider. The tuberculum aponeurosis ventralis is less bulbous than in *Jabiru* and *Leptoptilos*, as in *Ephippiorhynchus* and *Ciconia* (Fig. 2E, F).

**Carpometacarpus.**—The internal rim of the trochlea carpalis is less rounded and less protruding posteriorly, merging with the shaft more distally than in all the species compared. The proximal and distal metacarpal symphyses are similar to those of *Leptoptilos*, proportionally larger than in the remaining species compared (Fig. 2G; Table 2).

**Sternum.**—The size and robustness of the sternum is slightly greater than those of *Jabiru mycteria*. The sulcus articularis coracoideus is wider than those of *Ephippiorhynchus* and *Ciconia*, similar in width to that of *Jabiru* and *Leptoptilos*. The ventral and dorsal lips of the sulcus articularis coracoideus are wider than in all the species compared, more similar to those of *Jabiru* and *Leptoptilos*. The pila coracoidea is wider than in *Ephippiorhynchus* and *Ciconia*, with its medial edge more rounded as in *Jabiru* and not clear-cut as in the former (Fig. 2B).

**Pelvis.**—The foramen ilioischadicum is bigger and less elliptical than in *Ephippiorhynchus* and *Jabiru*, its shape being considerably more similar to those of *Leptoptilos* and *Ciconia*. The ala ischii is more expanded ventrally with its lower border curved, not straight as in the species compared (Fig. 3C).

**Tibiotarsus.**—The shape of the facies articularis medialis is quadrangular, similar to that of *Ephippiorhynchus* and *Leptoptilos*, with its medial and posterior borders forming a close to 90° angle; the junction of these borders is rounded in *Jabiru*, *Mycteria*, and *Ciconia*. The crista fibularis is proportionally shorter and more spread outwards than in *Ephippiorhynchus* and *Jabiru*. The condylus medialis and the condylus lateralis are less projected anteriorly, but their cranial surfaces are more developed proximally than in all the species compared. The distal width through condyles is similar to that measured in *L. dubius*, larger than those of *Ephippiorhynchus*, *Jabiru*, and *Mycteria* (Tables 3, 4), with the condylus medialis and the

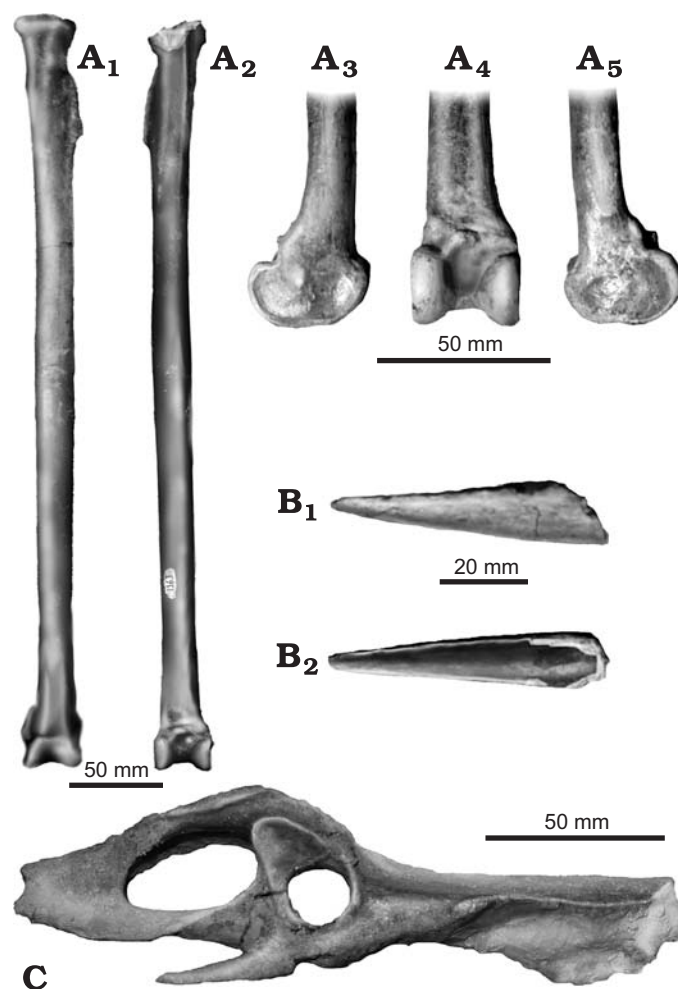


Fig. 3. The marabou stork *Leptoptilos patagonicus* sp. nov., specimen MEF-1363 (holotype) from the Puerto Madryn Formation (late Miocene), Punta Buenos Aires, Península Valdés, Chubut Province, Patagonia, Argentina. **A.** Right tibiotarsus in posterior ( $A_1$ ) and anterior ( $A_2$ ) views. Details of the distal end of right tibiotarsus in medial ( $A_3$ ), anterior ( $A_4$ ), and lateral ( $A_5$ ) views. **B.** Tip of mandible in lateral ( $B_1$ ) and dorsal ( $B_2$ ) views. **C.** Pelvis in lateral view.

condylus lateralis more or less parallel and aligned to the respective borders of the shaft; the width of the distal end of tibiotarsus is proportionately broader in *Ciconia* than in *L. patagonicus* due to its more pronounced mediolateral expansion. The pons supratendineus is covered by a matrix which hides its morphology (Fig. 3A).

**Skull fragments.**—The tip of the mandibular symphysis is robust, with the edges of the tomial shelf sharp and high. The fragmentary state of the ramus mandibulae and the os articulare make it difficult to recognize morphological features on both of them (Fig. 3B).

## Discussion and conclusions

The traditional systematic arrangement divides the Ciconiidae in the tribes Mycteriini, Ciconiini, and Leptoptilini on the ba-

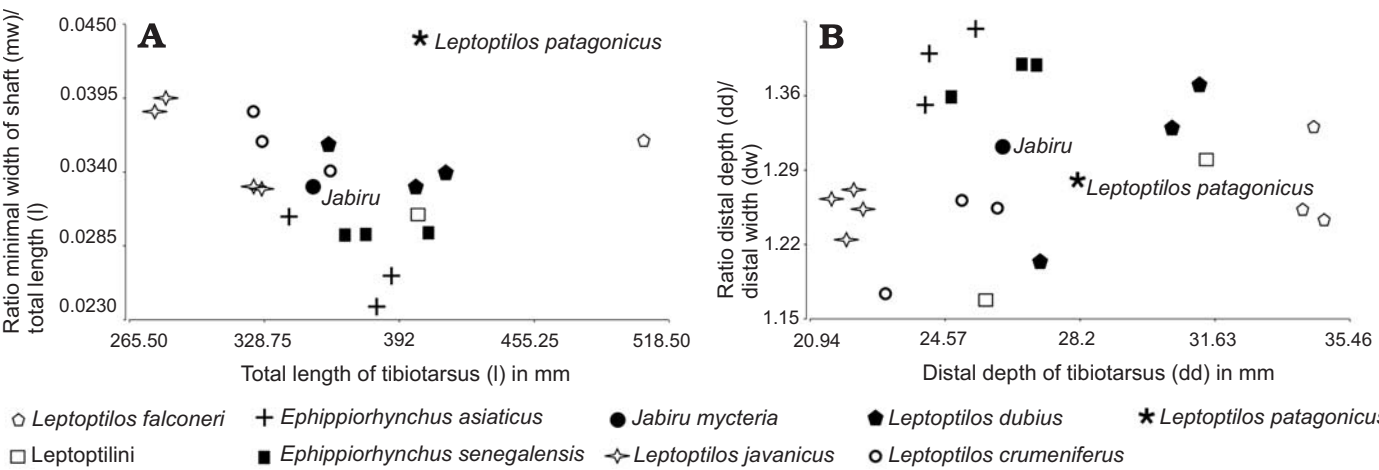


Fig. 4. Tibiotarsus ratios in the living Leptoptilini, fossil *Leptoptilos*, and *L. patagonicus* sp. nov., specimen MEF-1363 (holotype) from the Puerto Madryn Formation (late Miocene), Punta Buenos Aires, Península Valdés, Chubut Province, Patagonia, Argentina. **A.** Minimum shaft width to total length ratio. **B.** Distal depth to distal width ratio. Modified from Louchart et al. (2005).

sis of external morphology (Kahl 1972, 1979). The tribe Leptoptilini comprises three genera (*Ehippiorhynchus*, *Jabiru*, and *Leptoptilos*), with six living species distributed in the Neotropics, Africa, the Oriental Region, SE of Asia, New Guinea, and Australia. These storks are distinctive by their large size and massive bills. The genus *Jabiru* is sometimes included in *Ehippiorhynchus* due to its resemblance in feeding and display behaviour (Wood 1984), but seems to be morphologically intermediate between this genus and *Leptoptilos* (Elliott 1992).

The classification derived from DNA hybridization studies recognizes only the Ciconiinae under the family level (Sibley and Monroe 1990). A more recent cladistic approach, based on molecular evidence, suggests that the Leptoptilini is probably a paraphyletic group which comprises basal species of storks (Slikas 1997). Osteological characters are not commonly used in ornithology to discriminate groups within the family level and, indeed, there are only a few discrete characters that are useful in separating the tribes of Ciconiidae (e.g., Cheneval 1984; Haarhoff 1988; Olson 1991; Louchart et al. 2005). Thus, diagnoses combining external and molecular

characters with those of the skeleton will be necessary in the future for sound systematic revision of the subordinated natural groups of storks. Because this phylogenetic task largely exceeds the goal of our contribution, we adopt provisionally the traditional classification scheme, referring the specimen to the Leptoptilini due to its phenetic similarities with the genera compared in this tribe in overall morphology, robustness, size, and inter-segment proportions of limb bones (Louchart et al. 2005). The similarities of the specimen MEF-1363 with Leptoptilini are clearly observed in the sternum, humerus, ulna, radius, tibiotarsus, and by having the limb bones larger and more robust than in Mycteriini and Ciconiini (Louchart et al. 2005).

We adopt the criteria of Louchart et al. (2005) for generic identification of the specimen MEF-1363 within the Leptoptilini. The proportions of the tibiotarsus in *Leptoptilos* are similar to those in *Jabiru*, being the tibiotarsus more robust in the former than in *Ehippiorhynchus* (Table 4; Fig. 4A). The carpometacarpus in *Leptoptilos* and *Ehippiorhynchus* is more slender than in *Jabiru*. The same conditions of the tibiotarsus and carpometacarpus, similar to *Leptoptilos*, are also observed on the specimen MEF-1363. Moreover, the

Table 3. Measurements (in mm) of the pelvis and the tibiotarsus of Leptoptilini. Pelvis: length from the anterior end of ala preacetabularis ilii to the posterior end of ala postacetabularis ilii (Tl); least width of ala preacetabularis ilii measured from the constriction of its lateral free edge to crista spinosa synsacri (Pf); width measured from the lateral edge of antitrochanter to crista spinosa synsacri (Ph); length from the anterior end of ala preacetabularis ilii to the anterior end of pubis, just ventral to foramen acetabuli (Pt); length of foramen ilioischadicum at its long axis (Lif); tibiotarsus: total length from facies articularis at proximal end to distal portion of condyles (L); depth at midshaft (D-s.t); minimal width of shaft medio-laterally (Mw); width of distal articular end medio-laterally (Dw); depth of distal articular end cranio-caudally (Dd); greatest depth of condylus lateralis (D-l.con).

|                                               | Pelvis |      |      |       |      | Tibiotarsus |       |      |                   |                   |                   |
|-----------------------------------------------|--------|------|------|-------|------|-------------|-------|------|-------------------|-------------------|-------------------|
|                                               | Tl     | Pf   | Ph   | Pt    | Lif  | L           | D-s.t | Mw   | Dw                | Dd                | D-l.con           |
| <i>Leptoptilos patagonicus</i> MEF-1363       | 175.0  | 39.4 | 39.8 | 106.8 | 35.0 | 403.0       | 14.1  | 16.9 | 22.5              | 28.9              | 28.1              |
| <i>Leptoptilos dubius</i> LAC-MNHN1993-16     | 194    | 42.3 | 48.6 | 107.7 | 33.7 | 436.5       | 14.3  | 14.6 | 22.5              | 29.8              | 28.2              |
| <i>Ehippiorhynchus senegalensis</i> MHNT 1742 |        |      |      |       |      | 352.0       | —     | —    | 18.1 <sup>a</sup> | 25.4 <sup>a</sup> | 25.0 <sup>a</sup> |
| <i>Jabiru mycteria</i> CICYTTP-ACI-73         | 167.8  | 32.3 | 40.1 | 91.8  | 29.4 | 368.6       | 11.8  | 13.3 | 19.6              | 30.8              | 24.7              |

<sup>a</sup> Walter Boles (personal communication 2004).

Table 4. Measurements (in mm) of the tibiotarsus of extinct and living Leptoptilini, modified from Louchart et al. (2005: 555; Table 2). Abbreviations: L, total length; dw, width of distal articular end medio-laterally; dd, depth of distal articular end cranio-caudally; mw, minimal width of shaft medio-laterally. Most values are single measurements; means are in bold, with the sample sizes (n) at right.

|                                                                                                                                        | L                   | dw           | dd           | mw           | dd/dw       | mw/L         |
|----------------------------------------------------------------------------------------------------------------------------------------|---------------------|--------------|--------------|--------------|-------------|--------------|
| <i>Leptoptilos falconeri</i> MNH-39735                                                                                                 |                     | 28.0         | 34.8         |              | 1.24        |              |
| <i>Leptoptilos falconeri</i> CNAR-KB3.97.161                                                                                           | 507                 |              |              | 17.5         |             | 0.035        |
| <i>Leptoptilos falconeri</i> NME-OMO-1222-76-367                                                                                       |                     | 27.4         | 34.2         | 17.2         | 1.25        |              |
| cf. <i>Leptoptilos falconeri</i> NME-SAG-VP-1/19                                                                                       |                     | 26.0         | 34.5         |              | 1.33        |              |
| Leptoptilini indet. Previously <i>Leptoptilos siwalicensis</i> (Harrison 1974), BMNH-39734                                             |                     | 24.4         | 31.6         | 15.3         | 1.30        |              |
| Leptoptilini indet. Previously <i>Criptomiconia indica</i> , BMNH-48444                                                                |                     | 22.0         | 25.6         |              | 1.16        |              |
| <i>Leptoptilos</i> sp. indet. Previously <i>Leptoptilos</i> sp., KNM-BN-002                                                            | 403.0               | 23.0         |              | 12.0         |             | 0.030        |
| <i>Ehippiorhynchus asiaticus</i> IRSN 12386                                                                                            | 388.0               | 17.9         | 24.1         | 10.2         | 1.35        | 0.026        |
| <i>Ehippiorhynchus asiaticus</i> IRSN 42167                                                                                            | 382.0               | 18.0         | 25.4         | 9.35         | 1.42        | 0.024        |
| <i>Ehippiorhynchus asiaticus</i> LAC-MNHN 1 specimen, USNM 346193                                                                      | <b>339.75</b> n = 2 | 17.3         | 24.2         | <b>10.27</b> | 1.40        | <b>0.030</b> |
| <i>Ehippiorhynchus senegalensis</i> IRSN 1922, MVZ 140361                                                                              | <b>407.5</b> n = 2  | <b>19.5</b>  | <b>27.0</b>  | <b>11.87</b> | <b>1.39</b> | <b>0.029</b> |
| <i>Ehippiorhynchus senegalensis</i> IRSN 55843                                                                                         | 367.5               | 18.2         | 24.8         | 10.60        | 1.36        | 0.029        |
| <i>Ehippiorhynchus senegalensis</i> LAC-MNHN 1869-89, LAC-MNHN 1935-193, LAC-MNHN 1882-421, LAC-MNHN 1909-62, MRAC 91056A01, UCBL 1974 | <b>376.5</b> n = 6  | <b>19.2</b>  | <b>26.7</b>  | <b>10.7</b>  | 1.39        | 0.029        |
| <i>Jabiru mycteria</i> MVZ 133932                                                                                                      | 352.0               | 20.0         | 26.2         | 11.30        | 1.31        | 0.032        |
| <i>Leptoptilos javanicus</i> IRSN 12392                                                                                                | 324.0               | 17.5         | 22.2         | 10.30        | 1.27        | 0.032        |
| <i>Leptoptilos javanicus</i> IRSN 12391                                                                                                | 327.0               | 18.0         | 22.5         | 10.40        | 1.25        | 0.032        |
| <i>Leptoptilos javanicus</i> UCBL 1975                                                                                                 | 277.0               | 17.1         | 21.6         | 10.40        | 1.26        | 0.037        |
| <i>Leptoptilos javanicus</i> MVZ 137570                                                                                                | 282.5               | 18.1         | 22.0         | 10.50        | 1.22        | 0.038        |
| <i>Leptoptilos dubius</i> IRSN 12395                                                                                                   | 400.0               | 23.0         | 30.7         | 13.10        | 1.33        | 0.032        |
| <i>Leptoptilos dubius</i> FMNH 104387                                                                                                  | 415.0               | 23.0         | 31.5         | 13.15        | 1.37        | 0.033        |
| <i>Leptoptilos dubius</i> IRSN 60379                                                                                                   | 359.0               | 22.6         | 27.2         | 12.40        | 1.20        | 0.035        |
| <i>Leptoptilos crumeniferus</i> IRSN 12396                                                                                             | <b>323.75</b> n = 2 | <b>20.9</b>  | <b>26.05</b> | <b>11.85</b> | <b>1.25</b> | <b>0.037</b> |
| <i>Leptoptilos crumeniferus</i> MRAC 98025A01                                                                                          | 327.5               | 19.6         | 23           | 11.40        | 1.17        | 0.035        |
| <i>Leptoptilos crumeniferus</i> LAC-MNHN 1884-215, LAC-MNHN 1909-21, LAC-MNHN 1997-232, MVZ 134058                                     | <b>360.15</b> n = 4 | <b>20.15</b> | <b>25.04</b> | <b>12</b>    | <b>1.27</b> | <b>0.033</b> |
| <i>L. patagonicus</i> MEF-1363                                                                                                         | 403.0               | 22.5         | 28.9         | 16.9         | 1.28        | 0.042        |

proportions of the distal end of the tibiotarsus are typical in *Leptoptilos* in comparison to *Ehippiorhynchus* and *Jabiru*, the ratio of its depth to its width being less in the former than in the later two (Miller et al. 1997; Louchart et al. 2005). The distal end of the tibiotarsus MEF-1363 exhibits a ratio similar to that of *Leptoptilos* (Table 4; Fig. 4B). Consequently, we establish that the fossil specimen herein described belongs to *Leptoptilos*.

A comparison with the truly giant fossil *L. falconeri* and the largest individuals of extant species of *Leptoptilos* shows that *L. patagonicus* was a large stork. The tibiotarsus of *L. patagonicus* is shorter in length than those referred to *L. falconeri* (Table 4). The largest living *L. crumeniferus* and *L. dubius* have tibiotarsi of similar length or slightly shorter than that of *L. patagonicus* (Table 4), but the inter-segment proportions between wing and leg bones are quite different among them; wing elements of *L. patagonicus* are considerably smaller than those of the former.

Finally, as noted in the diagnosis and description, MEF-1363 exhibits a combination of morphological characters which, together with the presence of short wings relative to the legs, merit the recognition of a new species.

Leptoptilini have a rich temporal and spatial distribution in the Palearctic, Oriental, Ethiopian, and Australasian re-

gions (Louchart et al. 2005: 561; Table 5), with *Jabiru mycteria* as the only Neotropical species with the fossil record restricted to the Late Pleistocene of Peru (Campbell 1979). Fossils assignable to the Leptoptilini have previously been unknown from the Tertiary of South America. Therefore, *Leptoptilos patagonicus* constitutes not only the first record for the genus in the Neogene of South America, but it also reveals the presence of an old lineage of the tribe in this continent. The paleobiogeographic significance of this find cannot be fully determined until the phylogenetic relationships of *L. patagonicus* to the remaining extinct and living storks are elucidated. This will also provide tools to link the natural history of this Patagonian marabou stork with those of Eurasia, Africa or Australasia.

## Acknowledgments

We thank Jorge Genise and Edgardo Ortiz Jaureguizar (Museo Paleontológico Egidio Feruglio, Trelew, Argentina) for allowing us to study the material; Eric Buffetaut (CNRS, Paris, France), Jean Le Loeuff (Musée des Dinosauriens, Espéraza, France), Florencio G. Aceñolaza (Programa de Biodiversidad del Litoral-SECYT), PEI 6083 (CONICET), PICT 11928 (ANPCYT), and Armando Brizuela (CICYTTP-Diamante) for provid-

ing financial support to assist the 6<sup>th</sup> SAPE Meeting and to develop this work, Brenda Ferrero and Jorge González (both of CICYTTP, Diamante, Argentina) for making the figures, and Walter Boles (Australian Museum, Sidney, Australia) for providing unpublished data about characters and measurements. Rosendo Fraga, Nacho Areta (both of CICYTTP, Diamante, Argentina) and Steve Emslie (University of North Carolina, Wilmington, USA), and anonymous reviewers provided very useful criticism. Christian de Muizon and Christine Lefèvre (both Muséum national d'Histoire naturelle, Paris, France) allowed access to palaeontological and osteological (LAC) collections, respectively.

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