

The first Eocene bird from Northwestern Argentina

SARA BERTELLI^{1,2,3} NORBERTO PEDRO GIANNINI^{1,3,4} DANIEL ALFREDO GARCÍA-LÓPEZ^{4,5} VIRGINIA DERACO^{4,5} IUDITH BABOT^{1,2} CECILIA DEL PAPA⁶ MATIAS ALBERTO ARMELLA^{4,5,7} CLAUDIA HERRERA^{4,5} GERALD MAYR⁸

1. Unidad Ejecutora Lillo (UEL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Fundación Miguel Lillo (FML). Miguel Lillo 251, 4000 San Miguel de Tucumán, Tucumán, Argentina.

2. Fundación Miguel Lillo (FML). Miguel Lillo 251, 4000 San Miguel de Tucumán, Tucumán, Argentina.

3. American Museum of Natural History (AMNH). 200 Central Park West, NY 10024-5102, New York, USA.

4. Facultad de Ciencias Naturales e Instituto Miguel Lillo (IML), Universidad Nacional de Tucumán (UNT). Miguel Lillo 205, 4000 San Miguel de Tucumán, Tucumán, Argentina.

5. Instituto Superior de Correlación Geológica (INSUGEO), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Tucumán (UNT). Av. Presidente Perón S/N, 4107 Yerba Buena, Tucumán, Argentina.

6. Centro de Investigaciones de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Córdoba (UNC). Av. Vélez Sarsfield 1611, X5016GCA Córdoba, Córdoba, Argentina.

7. Facultad de Ciencias Exactas y Naturales (FaCEN), Universidad Nacional de Catamarca (UNCa). Belgrano 300, 4700 San Fernando del Valle de Catamarca, Catamarca, Argentina.

8. Ornithologie, Senckenberg Forschungsinstitut. Senckenberganlage 25, 60325 Frankfurt am Main, Germany.

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Asociación Paleontológica Argentina Maipú 645 1º piso, C1006ACG, Buenos Aires República Argentina Tel/Fax (54-11) 4326-7563 Web: www.apaleontologica.org.ar



THE FIRST EOCENE BIRD FROM NORTHWESTERN ARGENTINA

SARA BERTELLI^{1,2,3}, NORBERTO PEDRO GIANNINI^{1,3,4}, DANIEL ALFREDO GARCÍA-LÓPEZ^{4,5}, VIRGINIA DERACO^{4,5}, JUDITH BABOT^{1,2}, CECILIA DEL PAPA⁶, MATIAS ALBERTO ARMELLA^{4,5,7}, CLAUDIA HERRERA^{4,5}, AND GERALD MAYR⁸

¹Unidad Ejecutora Lillo (UEL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Fundación Miguel Lillo (FML). Miguel Lillo 251, 4000 San Miguel de Tucumán, Tucumán, Argentina. *sbertelli@lillo.org.ar*, *ngiannini@amnh.org*, *mjbabot@lillo.org.ar*

²Fundación Miguel Lillo (FML). Miguel Lillo 251, 4000 San Miguel de Tucumán, Tucumán, Argentina.

³American Museum of Natural History (AMNH). 200 Central Park West, NY 10024-5102, New York, USA.

⁴Facultad de Ciencias Naturales e Instituto Miguel Lillo (IML), Universidad Nacional de Tucumán (UNT). Miguel Lillo 205, 4000 San Miguel de Tucumán, Tucumán, Argentina. dgarcialopez@csnat.unt.edu.ar, virginiaderaco@gmail.com, matiasarmella@yahoo.com.ar, claucordoba@hotmail.com

⁵Instituto Superior de Correlación Geológica (INSUGEO), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Tucumán (UNT). Av. Presidente Perón S/N, 4107 Yerba Buena, Tucumán, Argentina.

⁶Centro de Investigaciones de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Córdoba (UNC). Av. Vélez Sarsfield 1611, X5016GCA Córdoba, Córdoba, Argentina. delpapacecilia@yahoo.com https://orcid.org/0000-0001-5645-849X

⁷Facultad de Ciencias Exactas y Naturales (FaCEN), Universidad Nacional de Catamarca (UNCa). Belgrano 300, 4700 San Fernando del Valle de Catamarca, Catamarca, Argentina.

⁸Ornithologie, Senckenberg Forschungsinstitut. Senckenberganlage 25, 60325 Frankfurt am Main, Germany. Gerald.Mayr@senckenberg.de

SB: https://orcid.org/0000-0001-7096-2940; NPG: https://orcid.org/0000-0002-8402-0126; DAGL: https://orcid.org/0000-0001-9588-9225;
VD: https://orcid.org/0000-0002-5819-5846; JB: https://orcid.org/0000-0003-1810-7634; CDP: https://orcid.org/0000-0001-5645-849X;
MAA: https://orcid.org/0000-0001-8870-3891; CH: https://orcid.org/0000-0002-7589-3363; GM: https://orcid.org/0000-0001-9808-748X

Abstract. A new fossil bird is described from the Upper Lumbrera Formation of Northwestern Argentina. *Lumbrerornis rougieri* gen. et sp. nov. is represented by three-dimensionally preserved elements of the hindlimb of a single individual. Morphological comparative studies and particular characters of the tibiotarsus suggest that the new species might be related to the extinct clades Palaeotididae and Geranoididae of the Northern Hemisphere, which were recently hypothesized to be Paleogene palaeognathous birds. However, the fragmentary preservation of the new fossil prevents a confident systematic position. The Upper Lumbrera Formation is a widely recognized fossiliferous unit with a very rich fauna of mammals and other vertebrates (*e.g.*, fishes, crocodilians, turtles, snakes). This is the first record of a three-dimensionally preserved fossil bird from the Eocene of northwestern Argentina and thus provides fresh evidence of the Eocene faunas from the area and improves our understanding of the poorly known early Paleogene avifaunas from South America.

Key words. Aves. Eocene. Paleogene. Upper Lumbrera Formation.

Resumen. PRIMER AVE DEL EOCENO DEL NOROESTE DE ARGENTINA. Se describe una nueva ave fósil de la Formación Lumbrera Superior del Noroeste de Argentina. *Lumbrerornis rougieri* gen. et sp. nov. está representada por elementos del miembro posterior de un único individuo que se ha preservado tridimensionalmente. Estudios de morfología comparada y caracteres del tibiotarso sugieren que la nueva especie se relacionaría con los clados extintos Palaeotididae y Geranoididae del hemisferio norte, grupos que han sido recientemente hipotetizados como relacionados a aves paleognatas del Paleógeno. Sin embargo, la preservación fragmentaria del nuevo fósil impide una ubicación sistemática precisa. La Formación Lumbrera Superior es una unidad fosilífera ampliamente reconocida por una gran diversidad de mamíferos y otros vertebrados (ej., peces, cocodrilos, tortugas, serpientes). Éste es el primer registro de un ave preservada tridimensionalmente que constituye una nueva evidencia sobre la fauna del Eoceno del noroeste de Argentina y contribuye a un mayor conocimiento sobre la avifauna poco conocida del Paleógeno de América del Sur.

Palabras clave. Aves. Eoceno. Paleógeno. Formación Lumbrera Superior.

THE EARLY Paleogene fossil record has played a key role in our understanding of the early steps of the evolutionary history of fossil modern birds (Neornithes) (Mayr, 2022). Many of the major lineages of extant birds are represented in sediments from the early Eocene of the Northern Hemisphere (50 to 55 Ma), but Paleogene avian remains are relatively scarce and this is particularly true for South America (Mayr, 2022). In this continent, the earliest neornithine birds are known from the Eocene of Brazil and Argentina (Tambussi *et al.*, 2023). The Itaboraí Basin in Brazil (Itaborian SALMA, early Eocene) produced fossils of a palaeognathous bird (*Diogenornis* Alvarenga, 1983), a representative of the Phorusrhacidae (Paleopsilopterus Alvarenga, 1985), a small long-legged bird (*Eutreptodactylus* Baird & Vickers-Rich, 1997), an enigmatic tinamou-like taxon (Itaboravis Mayr et al., 2011) and various undetermined remains (Alvarenga, 1983, 1985; Baird & Vickers-Rich, 1997; Mayr et al., 2011). In Argentina, the sediments of the early Eocene El Fresco Formation in La Pampa Province and those of the Cañadón Hondo and Huitrera formations in Chubut Province (Patagonia), provided basal members of Anseriformes and putative Coracii (Tambussi & Noriega, 1998; Degrange *et al.*, 2021), with the affinities of the latter having recently been disputed (Mayr, 2021). In addition, the oldest fossil record of penguins from the Patagonian Atlantic coast stems from the middle Eocene of Tierra del Fuego Province, Argentina (Clarke et al., 2003; Acosta Hospitaleche & Olivero, 2016). These fossil sites provide the only available information of neornithine fossil birds from the early Paleogene in South America (Mayr, 2022; Tambussi et al., 2023).

In northwestern (NW) Argentina, the Paleogene record of vertebrates includes various well-preserved fossils mainly recovered from the Lower Lumbrera and Upper Lumbrera formations (early and middle Eocene; del Papa et al., 2022). About 30 vertebrate taxa have been described so far in these units, which belong to notoungulates, litopterns, astrapotheres, cingulates, and metatherians among mammals, in addition to fishes, crocodilians, turtles, and snakes (Pascual et al., 1981; Powell et al., 2011; Babot et al., 2017; García-López et al., 2019; Herrera et al., 2021; Fernicola et al., 2021). Recent collecting efforts in sediments of the Upper Lumbrera Formation resulted in the discovery of the first Paleogene bird from NW Argentina, which is represented by articulated elements of the left hindlimb of a hitherto unknown avian taxon. Previous records of fossil birds from the Paleogene of NW Argentina are limited to an incomplete feather impression from the Maíz Gordo Formation (latest Paleocene-early Eocene) that was assigned to Neornithes (Petrolevicius & Tambussi, 1998). Comparisons based on overall morphology and particularly characters of the tibiotarsus suggest that the new specimen shows affinities to some Paleogene long-legged birds that are currently considered members of the Palaeognathae. In this contribution, we describe this new fossil, adding fresh evidence to the bird record, and interpret the evolution of early avian taxa of the South American Paleogene.

GEOLOGICAL SETTING

Specimen IBIGEO-P 161 comes from the fossiliferous levels of the Upper Lumbrera Formation exposed at the El Simbolar locality (Guachipas, Salta Province; Fig. 1). The Upper Lumbrera Formation is here represented by a thick succession of reddish and sandy siltstones, with scarce intercalations of fine-grained sandstones and levels of carbonate and gypsum nodules (see del Papa, 2006; del Papa et al., 2010; Lapiana et al., 2016). According to Lapiana et al. (2016), the paleoenvironment of Upper Lumbrera consists of an extended vegetated plain formed by eolian sandy loess alike to the present-day Pampa region. At El Simbolar, the recovered vertebrate fossils are abundant and represented mainly by mammals (Babot et al., 2017), although some crocodilians, turtles, and snakes were also found. Almost all the fossils were found at the sandy siltstones deposited within the first 50 m of this 274 m thick sequence (del Papa et al., 2010). The age range of the



Figure 1. Map of northwestern Argentina showing location of fossil locality. Scale bar = 50 km.



formation has been estimated to be late Lutetian–early Bartonian (del Papa *et al.*, 2010; Fernicola *et al.*, 2021); specifically, the radiometric age of the upper levels of the Upper Lumbrera Formation was estimated at 39.9 ± 0.4 Ma (*i.e.*, Bartonian) from a 30 cm-thick layer of crystal-tuff located 163 m above the base of Upper Lumbrera Formation in this locality (El Simbolar) (del Papa *et al.*, 2010). The fossil here studied was obtained from beds located 35 m from the base of the formation; therefore, its age is interpreted as most likely late Lutetian.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758 NEORNITHES Gadow, 1893 cf. PALAEOTIDIDAE Peters, 1988 / GERANOIDIDAE Wetmore, 1933

Lumbrerornis gen. nov.

LSID urn:lsid:zoobank.org:act:E3EBA76A-58BD-43B7-BABB-C95CBDEF3DDB **Derivation of name.** The generic name refers to a bird (Greek *ornis*) from Lumbrera (*i.e.*, the geologic Upper Lumbrera Formation).

Diagnosis. As in the type species by monotypy.

Lumbrerornis rougieri sp. nov. Figures 2.1–4, 3, 4.1–3, 5, 6

LSID urn:lsid:zoobank.org:act:AEOCC54D-961F-43B6-8917-FA96749B69F0 **Derivation of name.** The species epithet refers to the discoverer of the holotype, Dr. Guillermo Rougier.

Diagnosis. Both *cristae cnemialis cranialis* and *lateralis* of the tibiotarsus equally projected distally, *condylus medialis* distinctly shorter than *condylus lateralis*, *sulcus extensorius* very narrow and situated far medially, and distal rims of both condyli *medialis* and *lateralis* notched.

Type material. Holotype, IBIGEO-P161, a left tibiotarsus, a left tarsometatarsus, and an indeterminate bone fragment. Type locality and horizon. El Simbolar locality, Guachipas Department, Salta Province (Fig. 1); Upper Lumbrera Formation (del Papa, 2006; del Papa *et al.*, 2010, 2017, 2022), middle Eocene, late Lutetian (Salta Group, Santa Bárbara Subgroup).

Description and comparison. A nearly complete left

tibiotarsus is preserved (Figs. 2.1-4, 3, 4.1-4). Its overall morphology resembles the tibiotarsus of long-legged Eocene taxa, which have recently been considered to be palaeognathous birds, that is, the Palaeotididae, Geranoididae, and Eogruidae (Mayr, 2019; Mayr & Zelenkov, 2021). However, some of the shared features -e.g., a notch in the distal margin of the condylus medialis of the tibiotarsus—also occur in some neognathous birds, such as the gruiform Gruidae. The proximal end is mediolaterally compressed and dissociated from the shaft (Fig. 2.1-4). On the proximal surface, both femoral articular facets (facies articularis medialis and lateralis) are visible and the area interarticularis between these facets is a wide surface (Fig. 2.1-2, 2.4). The facies articularis medialis is flat as opposed to the *facies lateralis* being developed as a more distinct subovate protuberance that projects dorsolaterally. The *fossa retropatellaris* is discernible between the *crista* patellaris and the femoral articular facets (Figs. 2.1, 2.4). In cranial view, the cristae cnemialis cranialis and lateralis are well developed, enclosing a deep sulcus intercnemialis, which probably has been emphasized by crushing (Fig. 2.1, 2.3). Both cristae are weakly projected proximally above the articular surface and are equally projected distally, extending approximately to the level of the fibular crest. The crista cnemialis cranialis is notably less prominent than in the Paleogene Lithornis and most extant Palaeognathae (Bourdon et al., 2009; Nesbitt & Clarke, 2016), in which it protrudes markedly. The evenly curved crista cnemialis *cranialis* is projecting far cranially in the Aepyornithidae and Casuariidae (Bourdon et al., 2009). This crest in the new fossil is long and forms a distinct obtuse angle with the shaft when viewed in lateral aspect. The *crista cnemialis* lateralis is thicker and longer than the crista cnemialis cranialis. The latter condition differs from the early Paleogene palaeognathous bird *Lithornis*, in which the *crista cnemialis* cranialis is slightly longer than the crista cnemialis lateralis. In most Tinamidae, the crista cnemialis cranialis is distinctly longer but less projected distally than the level of the crista fibularis (only in Tinamus and Eudromia both cristae are short and less projected distally than the level of the crista fibularis) as opposed to the condition present in the new taxon. The crista cnemialis lateralis is very poorly developed and knob-like in the Struthionidae and Rheidae (Bourdon et



Figure 2. Photograph and interpretive drawing of the proximal end of the left tibiotarsus of *Lumbreronis rougieri* gen. et sp. nov. (IBIGEO-P 161) in 1, lateral view; 2, cranial view; 3, medial view; 4, caudal view. Abbreviations: ai, *area interarticularis*; cc, *crista cnemialis cranialis*; cf, *crista fibularis*; cl, *crista cnemialis lateralis*; cr, *crista tuberositas popliteus*; ei, *foramen interosseum proximale*; fg, *facies gastrocnemialis*; ff, *fossa flexoria*; fl, *facies articularis* is, *si*, *sulcus intercnemialis*. Scale bar = 10 mm.





Figure 3. Photograph and interpretive drawing of the distal portion of the left tibiotarsus of *Lumbreronis rougieri* gen. et sp. nov. (**IBIGEO-P 161**) in cranial view. Abbreviations: **bg**, bulge; **cl**, *condylus lateralis*; **cm**, *condylus medialis*; **do**, distal opening of *sulcus extensorius*; **ic**, area *intercondylaris*; **nt**, notch; **ps**, *pons supratendineus*; **rg**, ridge; **se**, *sulcus extensorius*; **sf**, *spina fibulae*. Scale bar = 10 mm.

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Figure 4. Photograph and interpretive drawing of the distal end of the left tibiotarsus of *Lumbrerornis rougieri* gen. et sp. nov. (IBIGEO-P 161) in 1, caudal view; 2, medial view; 3, lateral view. Abbreviations: cl: *condylus lateralis*; cm, *condylus medialis*; ct, *crista trochleae*; dl, *depressio epicondylaris lateralis*; dm, *depressio epicondylaris medialis*; nt, notch; tt, trochlea *cartilaginis tibialis*. Scale bar = 10 mm.







Figure 5. Photograph and interpretive drawing of the tarsometatarsus of *Lumbrerornis rougieri* gen. et sp. nov. (IBIGEO-P 161) in dorsal view. Abbreviations: ch, *crista hypotarsi*; se, *sulcus extensorius*; tb, tubercles. Scale bar = 10 mm.

al., 2009). On the caudal surface of the proximal tibiotarsus shaft, just distal to the *facies articularis medialis*, there is a distinct crest (tuberositas poplitea) tentatively identified as the attachment of *m. popliteus* (Fig. 2.4). The lateral side of the shaft bears the proximal end of a low crista fibularis (Fig. 2.1-2, 2.4). In cranial view, the distal end of the tibiotarsus exhibits a proximodistally deep pons supratendineus that bridges a narrow and medially placed sulcus extensorius (Fig. 3). The distal opening of the sulcus extensorius is only partially visible and covered with sediment. The narrow *sulcus* distinguishes the bone from the tibiotarsus of most extant neognathous birds and corresponds to the condition in the Palaeognathae, especially the Tinamidae (Fig. 7.4) and the recently extinct Dinornithidae. A supratendinal bridge and a medially placed sulcus are also present in Palaeotis, a flightless palaeognathous bird from the Eocene of Germany (Mayr, 2019), but in this taxon both the pons supratendineus and

sulcus extensorius are mediolaterally wider (Fig. 7.1). The supratendinal bridge is absent in the early Paleogene Lithornithidae (Houde, 1988) and Diogenornis, a flightless palaeognathous bird from the early Eocene of Brazil (Alvarenga, 1983). The supratendinal bridge is also absent in most crown group Palaeognathae (except for Tinamidae and Dinornithidae). In contrast to the new fossil, the broad supratendinal bridge is not medially displaced in other long-legged Eocene birds such as the phorusrhacid Paleopsilopterus from Brazil (Alvarenga, 1985) and related Cariamae. Next to the lateral surface and at the level of the proximal end of the extensor sulcus, fragments of the fibula are preserved (Fig. 3). Lateral to the pons supratendineus, a transverse ridge runs perpendicular to the longitudinal axis of the tibiotarsus; a similar ridge was also reported in Palaeotis (Fig. 7.1; Mayr, 2019). Situated distal to this ridge is the deeply concave incisura intercondylaris, which encompassed the eminentia intercotylaris of the tarsometatarsus during





Figure 6. Photograph and interpretive drawing of the left tarsometatarsus of *Lumbrerornis rougieri* gen. et sp. nov. (IBIGEO-P 161) in plantar view. Abbreviations: cpm, crista plantaris medialis; hy, hypotarsus; sf, sulcus flexorius. Scale bar = 10 mm.

flexion of the foot. The medial condyle is distinctly shorter proximodistally than the lateral condyle. In cranial aspect, the general shape of the condyles is similar to the Eocene taxa Palaeotididae and Geranoididae (Figs.7.2-3). Even though condyli of similar proportion occur in other taxa (e.g., the cariamiform Dynamopterus from the Paleogene of Europe), these usually lack notches in the distal rims of both condyli. On the proximal margin of the latter, there is a marked bulge, which probably corresponds to the ligamental attachment of the *m. fibularis*. A small tubercle proximal to the condylus lateralis is present in the Tinamidae and seems to correspond to this bulge in *Lumbreronis*. In Palaeotis, a cranially raised bulge was also reported by Mayr (2019) but it is placed more proximolaterally to the supratendinal bridge (Fig. 7.1). On the caudal surface of the distal end, the trochlea cartilaginis tibialis is deep with welldeveloped cristae on either side (Fig. 4.1). On the medial surface, there is a well-developed medial condyle featuring a marked notch in the distal rim, whereas proximal to its distal articular surface, there is a distinct condylus epicondylaris medialis (Fig. 4.2). On the lateral surface there is also a shallow condylus epicondylaris lateralis and the distal notch is partially broken, but visible in distal view (Fig. 4.3). The caudal projection of the cristae trochleae and the distal notches give the distal end a clover-like aspect in medial and lateral views (Fig. 4.2-3). As in the new fossil, the distal rim of the *condylus medialis* of *Palaeotis* bears a deep notch (Fig. 7.5). The distal rim of the condylus medialis is also distinctly notched in other fossil taxa (e.g., Eogruidae, Palaeotididae and Geranoididae, Fig. 7.5-7) that were considered palaeognathous birds by Mayr (2016) and Mayr & Zelenkov (2021). A small notch in the distal margin of the condylus medialis of the tibiotarsus also occurs in some neognathous birds, such as the gruiform Gruidae and extant Cariamae. The distinct notches in the distal rims of both condyles that characterize the tibiotarsus of the new fossil



are absent in the Eocene *Paleopsilopterus* and other Phorusrhacidae. The overall morphology of the tibiotarsus of the new taxon resembles that of some long-legged Eocene taxa, which have recently also been considered to be palaeognathous birds, that is, the Palaeotididae, Geranoididae, and Eogruidae (Mayr, 2019; Mayr & Zelenkov, 2021). However, some of these features—*e.g.*, a notch in the distal margin of the *condylus medialis* of the tibiotarsusalso occur in some neognathous birds, such as the gruiform Gruidae, and the fragmentary representation of the fossil impedes a definitive phylogenetic placement.

The proximal end is dissociated from the shaft and damaged, making it difficult to discern anatomical details; the distal end is lacking (Figs. 5 and 6). On the plantar surface of the proximal end, a fragment of a protuberance has been tentatively identified as a piece of the hypotarsus.



Figure 7. Distal end of right tibiotarsi of the Paleogene Palaeotididae, Geranoididae, and the extant palaeognathous Tinamidae. *Palaeotis weigelti* (Palaeotididae), from the latest early or earliest middle Eocene of Germany in 1, cranial view; 5, medial view (modified from Mayr, 2019); *Palaeophasianus meleagroides* (Geranoididae) from the early Eocene of USA in 2, cranial view; 6, medial view (modified from Mayr, 2019); *Palaeogrus princeps* (?Palaeotididae) from the middle Eocene of Italy in 3, cranial view; 7, medial view (modified from Portis, 1885); and *Rhynchotus rufescens* (Tinamidae) in 4, cranial view; 8, medial view. Abbreviations: cl, *condylus lateralis*; cm, *condylus medialis*; do, distal opening of *sulcus extensorius*; ic, area *intercondylaris*; nt, notch; ps, *pons supratendineus*; rg, ridge; se, *sulcus extensorius*. Scale bar = 10 mm.

The shaft is crushed and dorsoventrally compressed. A shallow *sulcus extensorius* is marked on the dorsal surface. The lateral surface bears two tubercles that are not considered to be preservational artifacts. These tubercles project on the lateral margin of the proximal end and possibly correspond to the proximolateral insertion of the *lig. collateralis lateralis* (Fig. 5). On the plantar surface, the *crista plantaris medialis* is sharp, delimiting a narrow *sulcus flexorius*; the *crista plantaris lateralis lateralis* is damaged.

DISCUSSION

The tibiotarsus of Lumbrerornis rougieri gen. et sp. nov. exhibits a morphology present in some archaic palaeognathous taxa and putatively palaeognaths (e.g., Palaeotididae, Geranoididae, Eogruidae; Fig. 7.1-3, 7.5-7) from the early and middle Eocene of Europe and North America (Mayr, 2016, 2019), and it also resembles the condition in two taxa of extant Palaeognathae: the recently extinct Dinornithidae (moas) from New Zealand and the extant neotropical Tinamidae (Mayr, 2016, 2019; Mayr & Zelenkov, 2021) (Fig. 7.4, 7.8). The tibiotarsus of the new fossil shows features present in Palaeotis, such as the medially placed and very narrow *sulcus extensorius* bridged by a proximodistally deep pons supratendineus with a transverse ridge and a bulge that raises close to the intercondylar articular area (Fig. 7.1). In addition, the distal rim of the condylus medialis of Palaeotis also bears a distinct notch, a condition present in the distal condylar rim of the new fossil bird (Fig. 7.5). The above mentioned features are also present in some species of the North American Geranoididae (Mayr, 2016; Mayr & Zelenkov, 2021) (Fig. 7.1-3, 7.5-7). Within Neognathae, a notch in the distal margin of the condylus medialis also occurs in some taxa, such as the gruiform Gruidae.

The best represented palaeognathous bird from the Paleogene of South America is *Diogenornis fragilis* from the early Eocene of Brazil (Alvarenga, 1983), which was originally considered to be related to the Rheidae, but whose affinities within Palaeognathae remain controversial (Alvarenga, 2010; Mayr, 2022). Other fossil remains from Argentina that are possibly related to Rheidae are a poorly preserved tibiotarsus (Agnolin, 2016) and a set of pedal phalanges (Tambussi, 1995) from the middle and early

Eocene, respectively. However, the anatomy of the distal end of the tibiotarsus in the new taxon does not correspond to that of large flightless palaeognathous birds such as the species of Rheidae and most other ratites (except for Dinornithidae). For example, among several features, in Rheidae the *condylus lateralis* is sharply undercut cranially, the epicondylus medialis enlarged and plate-like, bounded distally by deep depressio epicondylaris medialis (a condition also present in the Casuariidae), as opposed to Lumbrerornis in which these conditions are absent (Bourdon et al., 2009). Furthermore, the specimen is very unlike the hindlimb of extant cursorial palaeognaths. In these large Palaeognathae, the area intercondylaris is a wide and shallow surface, so that the *condylus medialis* is continuous with the condylus lateralis (Bourdon et al., 2009). This condition is absent in the new taxa and other palaeognaths clades (Tinamidae, Dinornithidae, Lithornithidae, and basal palaeognathous fossils) in which both condyles and the intercondylar area form distinct articular surfaces (Fig. 7). Furthermore, large extant cursorial Palaeognathae lack an ossified pons supratendineus. On the other hand, it is also worth noting that the new fossil bird resembles the fossil taxa *Palaeotis* and Eogruidae, which were Eocene cursorial palaeognaths (Mayr, 2016, 2019). The new fossil resembles palaeognathous birds with regard to the narrow and medially placed *sulcus extensorius*; in neognathous birds, by contrast, the sulcus extensorius is wider and often it is more centrally situated. While many extant Palaeognathae lack a *pons supratendineus*, this structure is found in the Palaeotididae, Geranoididae, and Eogruidae, and among extant Palaeognathae it is present in the Dinornithidae and Tinamidae (also variably present in Apteryx) (Fig. 7.4).

Although *Lumbrerornis rougieri* gen. et sp. nov. shows some resemblances to the long-legged Eocene taxa Palaeotididae and Geranoididae, due to the limited material known so far, it cannot be definitely assigned to a specific clade. In any case, the new fossil bird expands our knowledge of the faunal diversity of the Eocene of northwestern Argentina, which was before mainly characterized by abundant fossil remains of mammals and other fossil vertebrates (*e.g.*, fishes, crocodilians, turtles, and snakes). Furthermore, this new three-dimensionally preserved specimen constitutes the first fossil bird from the



Eocene of northwestern Argentina, adding fresh evidence to the poorly known early Paleogene avifaunas and opening expectations of future new findings.

The paleoenvironmental framework suggests that Lumbrerornis rougieri gen. et sp. nov. lived in ephemeral settings such as ponds and related loessic plains, in which seasonal conditions favored paleosoil development (del Papa, 2006; Lapiana et al., 2016; Babot et al., 2017). Lumbrerornis shared its environment with a vertebrate fauna composed mainly by crocodiles, cingulates, and native ungulates (Powell et al., 2011; García-López et al., 2019; Herrera et al., 2021). The recorded taxa indicate a relatively high degree of endemism, considering the number of exclusive taxa and wide taxonomical differences regarding other Paleogene units from NW Argentina. Notoungulates recorded are chiefly brachydont, suggesting that the Upper Lumbrera Formation presented soft vegetation for the consumption of the predominant herbivores (García-López et al., 2019). In turn, carnivores are until now represented by sebecid crocodiles, which exhibit mainly terrestrial adaptations (Bravo et al., 2021), and small sparassodont metatherians (Babot & García-López, 2010). We conclude that the paleobiological setting for the finding of Lumbrerornis rougieri gen. et sp. nov. in the Upper Lumbrera Formation indicates conditions favorable for the presence of a rich, soft vegetation with seasonal abundance of water.

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