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A RALLIDAE (AVES, GRUIFORMES) FROM THE PLEISTOCENE LA ESPERANZA FORMATION OF OLAVARRÍA (ARGENTINA)

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Abstract. A tarsometatarsus recovered from the lower Pleistocene levels of the La Esperanza Formation in Olavarría, Argentina, represents the first avian remains reported from this locality. Its morphology and size allow its assignment to *Aramides cajaneus* (Aves, Gruiformes), a species that still occurs in or near the area. Members of the genus *Aramides* are terrestrial birds closely associated with wetland environments, providing valuable paleoenvironmental insight into the conditions that prevailed in the region during the Pleistocene.

Key words. Neognathae. Neoaves. *Aramides*. Cenozoic. Pampean Region. Quaternary.

Resumen. UN RALLIDAE (AVES, GRUIFORMES) DEL PLEISTOCENO DE LA FORMACIÓN LA ESPERANZA DE OLAVARRÍA (ARGENTINA). Un tarsometatarso recuperado de los niveles del Pleistoceno inferior de la Formación La Esperanza, en Olavarría (Argentina), constituye el primer resto aviano reportado para esta localidad. Su morfología y tamaño permiten asignarlo a *Aramides cajaneus* (Aves, Gruiformes), una especie que aún habita en la región o en sus proximidades. Los representantes del género *Aramides* son aves terrestres estrechamente vinculadas a ambientes húmedos, lo que aporta información paleoambiental valiosa sobre las condiciones que prevalecieron en la región durante el Pleistoceno.

Palabras clave. Neognathae. Neoaves. *Aramides*. Cenozoico. Región Pampeana. Cuaternario.

INTRODUCTION

The traditional "Gruiformes" comprises diverse living and extinct bird lineages that share superficial similarities with rails or cranes and exhibit broad geographical distribution. However, recent phylogenetic analyses support the monophyly only of the more restricted “core Gruiformes” (Ericson et al., 2006; Fain et al., 2007; Hackett et al., 2008), which includes the sister taxa Gruoidea, composed of Psophiidae (trumpeters), Aramidae (limpkin), and Gruidae (cranes), and Ralloidea, constituted by Rallidae (rails), Sarothruridae (flufftails), and Heliornithidae (finfoots) (Hackett et al., 2008; Mayr, 2011; García-R et al., 2014; Prum et al., 2015).

Among them, Rallidae stands out for its high dispersal capacity and cosmopolitan distribution. This is one of the most specious clades within the order, having colonized a broad range of habitats, from marshes and grasslands to forests, which often results in convergent morphological patterns that obscure their evolutionary history (García-R et al., 2014). Despite detailed anatomical studies of some fossil species (*e.g.*, Olson, 1977, 1985; Steadman, 1995, 2006; Mayr & Smith, 2001; Mayr, 2005, 2006a, 2022), the fossil record of Rallidae provides limited insight into the early evolution of the family. Several early and middle Eocene remains previously attributed to Rallidae (Olson, 1977; Harrison & Walker, 1976, 1979; Harrison, 1984; Mlíkovský, 2002) have either been rejected due to their fragmentary preservation (Mayr, 2022) or reassigned to other groups (Cracraft, 1973a, 1973b; Olson, 1977; Mourer-Chauviré, 1992). The earliest well-supported rallid fossils correspond to *Belgirallus oligocaenus* and *B. minutu*s, both described by Mayr and Smith (2001) from the earliest Oligocene of Belgium and Germany (Mayr, 2006b, 2022) with additional indeterminate remains from Egypt (Rasmussen et al., 1987).

Subsequently, the fossil record of Rallidae becomes increasingly abundant in the Neogene of all continents, except Antarctica. It includes representatives in the early Oligo–Miocene deposits of Australia (Worthy & Boles, 2011), the Early Miocene of New Zealand (Worthy et al., 2007; Mather et al., 2019), Europe (De Pietri & Mayr, 2014;

Zelenkov et al., 2017), and Asia (Mlíkovský, 2002).

In South America, the earliest record of Rallidae dates to the Miocene; yet, despite their present-day diversity and abundance, the fossil record of the group remains relatively scarce and is mostly restricted to isolated remains. It includes the basal gruiform *Anisolornis excavatus* Ameghino, 1891 from the Early–Middle Miocene Santa Cruz Formation (see Degrange et al., 2012), as well as fragmentary Late Miocene remains from the Ituzaingó Formation referred to the extant genus *Grus* (Noriega & Agnolín, 2008), and Late Miocene of Las Flores Formation in San Juan, Argentina (Agnolín et al., 2025). Additional rallid fossils include Late Pleistocene remains of *Fulica montanei* Alarcón-Muñoz, Labarca and Soto-Acuña, 2020 from Laguna Tagua Tagua Formation in central Chile (Alarcón-Muñoz et al., 2020), various extant *Fulica* species from the Luján Formation in Buenos Aires Province (Cenizo et al., 2015), and an indeterminate species of *Porphyrio* Brisson, 1760 from Middle Pleistocene deposits at Bajo San José, in the upper basin of the Río Sauce Grande (Deschamps & Tomassini, 2016).

A new tarsometatarsus from Pleistocene levels of the La Esperanza Formation, exposed in Olavarría (Buenos Aires Province, Argentina), is here assigned to the Grey-cowled Wood-Rail *Aramides cajaneus*. A brief discussion of paleoenvironmental implications derived from this finding is provided below.

MATERIALS AND METHODS

The specimen, collected by one of the authors (MDIR), is housed in the paleontological collection of Cementos Avellaneda (CCA), Olavarría, Buenos Aires Province, Argentina, under the acronym CCA-165. It consists of a right tarsometatarsus. Comparative material is housed in the Ornithological Section (MLP-Or) of the Vertebrate Zoology Division at the Museo de La Plata (Argentina), the Ornithological Section of the Museo Nacional de Historia Natural (MNHN) of Montevideo (Uruguay), the Division of Birds Collection (USNM) of the National Museum of Natural History, Smithsonian Institution (USA), and the Senckenberg Research Institute (SMF), Frankfurt (Germany).

Descriptions follow the osteological terminology of Baumel (1993) and the hypotarsus morphology as outlined by Mayr (2016). Measurements were taken with a vernier caliper to the nearest 0.02 mm.

Anatomical Abbreviations. fdl, sulcus/canal for tendon of *musculus flexor digitorum longus*; **fhl,** sulcus/canal for tendon of *musculus flexor hallucis longus*.

GEOLOGICAL AND GEOGRAPHICAL SETTING

The study area is located near the city of Olavarría (36° 58′ 40.06″ S; 60° 12′ 23.92″ W), Buenos Aires Province, Argentina (Pampas Region). This area (Figs. 1A–C) exposes a Neogene–Quaternary succession (Fig. 1C), which has been exposed due to mining activity. The formational units of these Cenozoic packages are from base to top, the La Alcancía, El Polvorín, La Esperanza, and El Búho formations (Poiré, 2012), which unconformably support Neoproterozoic units of the Sierras Bayas Group and the Cerro Negro Formation (Poiré & Gaucher, 2009). The La Esperanza Formation (Poiré, 2012) consists of four levels. The basal layer, from which the fossil remains studied here originate (Fig. 1C), is composed of conglomerate lenses and coarse sands that contain abundant fossil remains, most of which are disarticulated and fragmented. Within the coarse sands, lenses of black tinges of manganese oxides are deposited; fossils also acquire a dark, blackish coloration.

The stratigraphic units of the quarry exhibit prominent erosional surfaces, characteristic of a mountainous environment subject to contemporary tectonic uplift (Poiré et al., 2005; Poiré, 2012). The presence of coarse sands and conglomerates arranged in strata with decreasing grain size and lenticular structure suggests a high-energy environment with fluctuating flow. These characteristics are typical of braided fluvial systems (Bridge, 2003). The lenticular structure reflects channel migration or bar formation within these systems, while the gradual decrease in grain size may indicate stream decline or episodic events such as floods.

Specimen CCA-165 was found at the time of the excavation of a *Glyptodon* sp. carcass. Other remains of *Hippidion* sp., *Lama* sp., *Panochthus intermedius*, *Glyptodon munizi*, *Mylodon*, Glyptodontinae cf. *Doedicurus*, and Toxodontidae were excavated from the same level. This diversity of taxa would correspond to an Ensenadean Stage/Age (Gelasian–Calabrian), early Pleistocene.

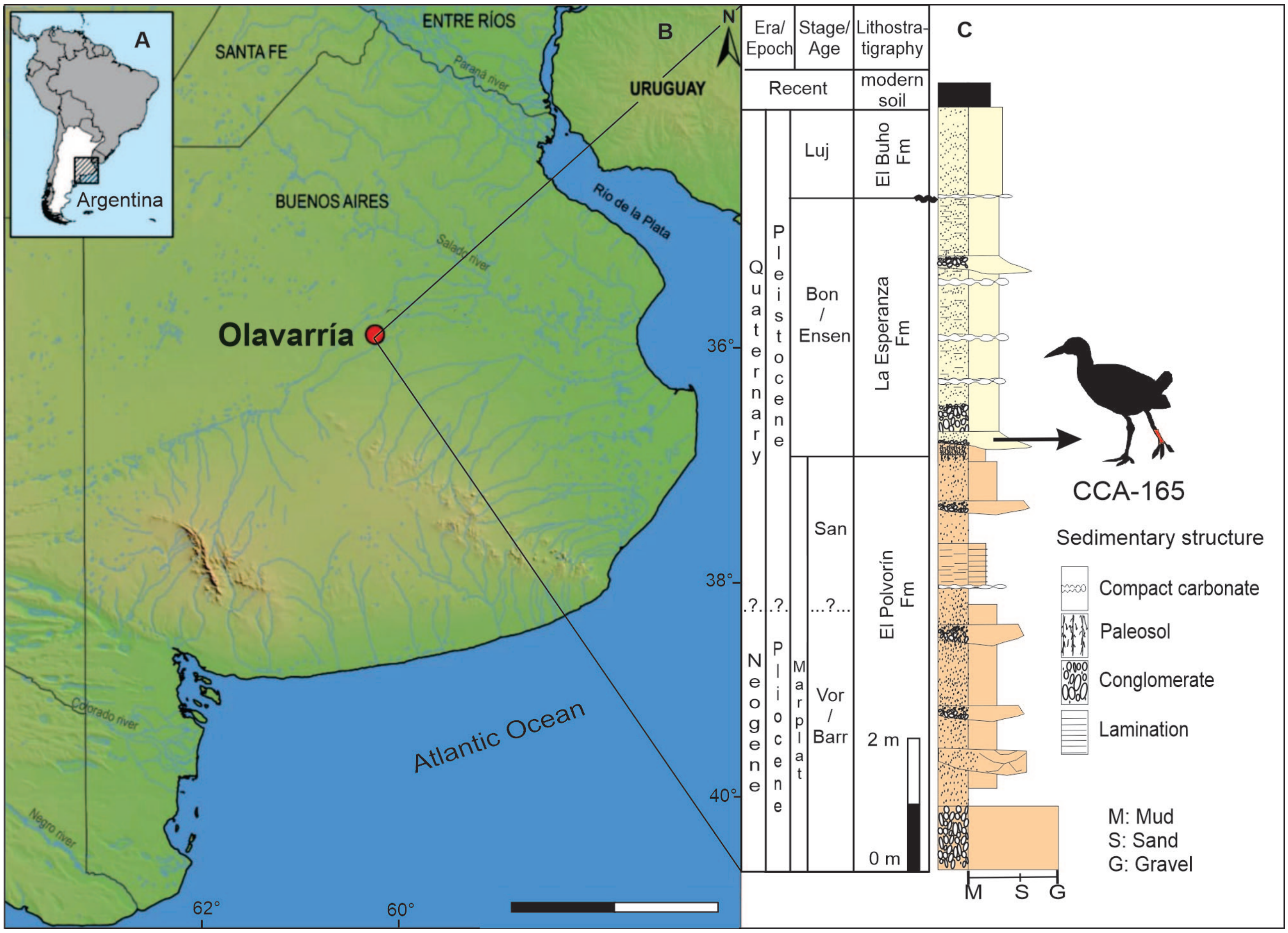

Figure 1. Geographical and stratigraphical provenance of *Aramides cajaneus* CCA-165. A, Location of Argentina in Southern South America; B, a square indicating the Buenos Aires Province and the fossiliferous locality in Olavarría (modified from Google Earth accessed December 2025; C, stratigraphic position of specimen CCA-165. Scale = 200 km. Abbreviations: Barr, Barrancalobian; Bon, Bonaerian; Ensen, Ensenadean; Luj, Lujanian; San, Sanandresian; Vor, Vorohuean.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

NEORNITHES Gadow, 1883

GRUIFORMES Bonaparte, 1854

RALLIDAE Vigors, 1825

Genus ***Aramides*** Pucheran, 1845

Type species. *Fulica cajanea* Statius Müller, 1776. Neotropical Region, Recent.

Aramides cajaneus (Statius Müller, 1776)

Figures 2A–F; 3A–G

Material. CCA-165, right tarsometatarsus.

Description. The tarsometatarsus is elongated, with a slender gracile shaft. The *eminentia intercotylaris* is pointed and projects proximally slightly beyond the medial rim of the *cotyla medialis* (Fig. 2A). The proximalmost portion of the shaft tapers both proximally and distally to the *impressio ligamentaris collateralis lateralis* (Fig. 2A). In dorsal and plantar views, the *foramen vasculare proximale mediale* opens more proximally than the *foramen vasculare proximale laterale* (Figs. 2A, E). Both foramina are elongated and pierce the diaphysis, opening on either side of the hypotarsus (Fig. 2E).

The *tuberositas musculi tibialis cranialis* forms a rounded protuberance, distal to which the *sulcus extensorius* becomes slightly deeper. The lateral and medial edges of this sulcus are delimited by raised margins that become gradually lower distally (Fig. 2A).

The *fossa metatarsi I* is shallow and elongated (Fig. 2E). The *trochlea metatarsi II* ends more proximally than *the incisura intertrochlearis lateralis*; the trochlea is relatively more distally projected and plantarly deflected, with the medial margin projecting even farther plantarly. The *trochlea metatarsi III* is the most symmetrical in terms of plantar projection and the development of its trochlear margins.

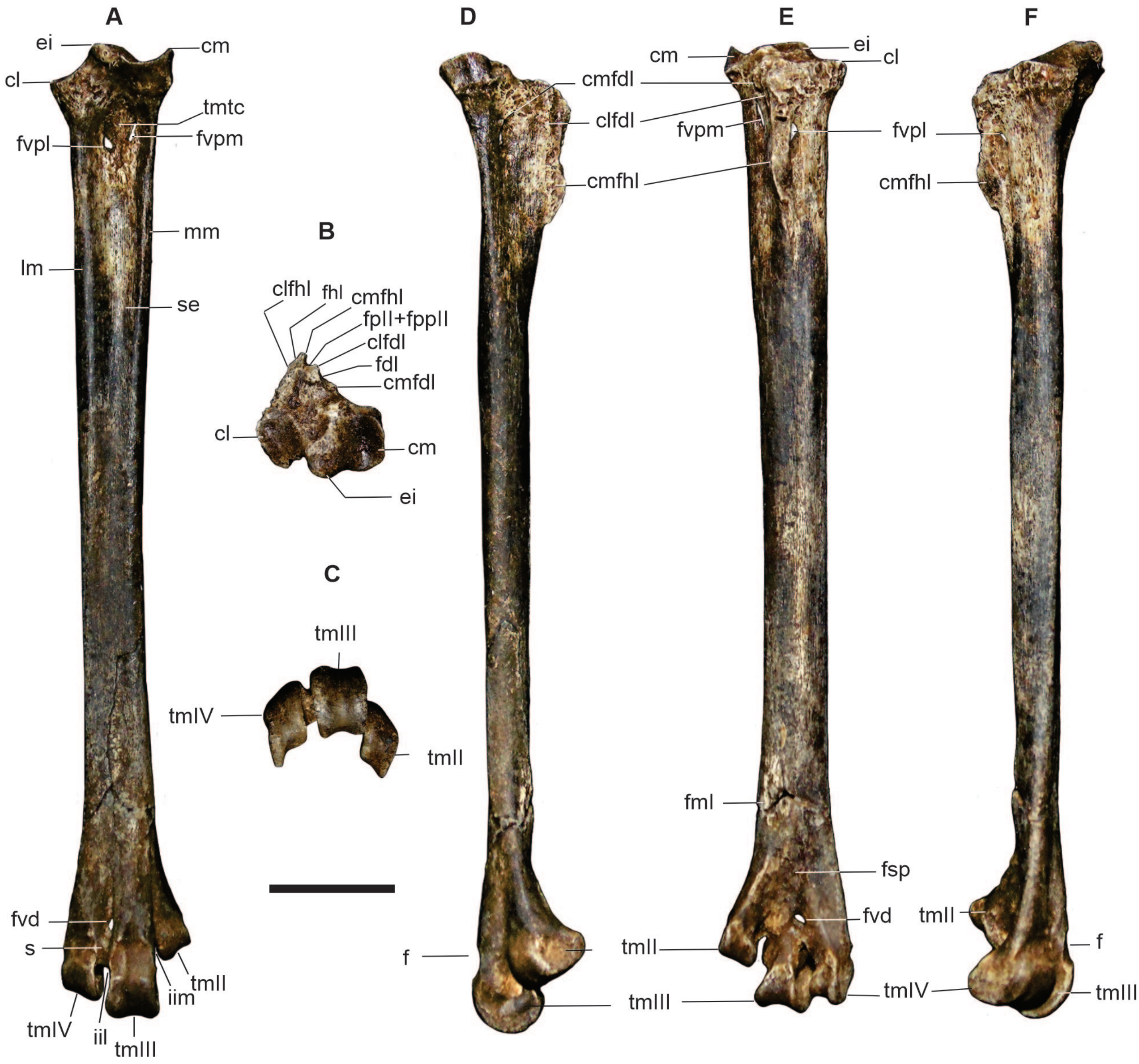

Figure 2. *Aramides cajaneus* CCA-165, right tarsometatarsus. A, dorsal; B, proximal; C, distal; D, medial; E, plantar; F, lateral views. Scale = 10 mm. Abbreviations: cl, *cotyla lateralis*; clfdl, *crista lateralis* sulcus/canal for tendon of *musculus flexor digitorum longus*; clfhl, *crista lateralis* sulcus/canal for tendon of *musculus flexor digitorum longus*; cm, *cotyla medialis*; cmfdl, *crista medialis* sulcus/canal for tendon of *musculus flexor digitorum longus*; cmfhl, *crista medialis* sulcus/canal for tendon of *musculus flexor hallucis longus*; ei, *eminentia intercotylaris*; f, fossa; fdl, sulcus/canal for tendon of *musculus flexor digitorum longus*; fhl, sulcus/canal for tendon of *musculus flexor hallucis longus*; fmI, *fossa* metatarsal *digiti* I; fpii+fppii, sulcus/canal for tendon of *musculus flexor perforatus digiti* II + sulcus/canal for tendon of *musculus flexor perforans et perforatus digiti* II; fsp, *fossa supratrochlearis plantaris*; fvd, *foramen vasculare distale*; fvpl, *foramen vasculare proximale laterale*; fvpm, *foramen vasculare proximale mediale*; iil, *incisura intertrochlearis lateralis*; iim, *incisura intertrochlearis medialis*; lm, lateral margin; mm, medial margin; s, sulcus; tmII, *trochlea metatarsalis* for *digiti* II; tmIII, *trochlea metatarsalis* for *digiti* III; tmIV, *trochlea metatarsalis* for *digiti* IV; tmtc, *tuberositas musculi tibialis cranialis*.

It is also the most dorsally positioned and is slightly displaced medially relative to the shaft axis. The *trochlea metatarsi IV* shows an intermediate degree of plantar deflection (Figs. 2C, F). Its margins are symmetrical in dorsal view, although the lateral margin is more expanded plantarly than the medial one (Figs. 2A, C, E).

The *foramen vasculare distale* is large and opens on both the plantar and dorsal surfaces, well separated from the *incisura intertrochlearis lateralis*. A deep sulcus extends proximally from this foramen along the shaft but does not reach the *sulcus extensorius* (Figs. 2A, E). Well-defined pits or rounded fossae are developed along the margins *of trochleae metatarsalia III* and *IV* (Figs. 2A, D, E). The *fossa supratrochlearis plantaris* is triangular and contains two foramina of unequal size at its proximal portion (Fig. 2E).

The hypotarsus is slightly eroded, and the canal for the tendon of the *musculus* fdl is broken, appearing as an open sulcus bounded by the *crista medialis* fdl and the *crista lateralis* fdl. The *crista medialis* of the canal for the tendon of fhl is the most prominent. It is inclined medially and separates the sulcus for the tendons of *musculus flexor perforatus digiti II* and *musculus flexor perforans et perforatus digiti II* from that of the fhl. The *crista lateralis* fhl is barely developed. The *fossa parahypotarsalis medialis* is absent (Fig. 2B).

Geographic and Stratigraphic Occurrence. Near the city of Olavarría (36° 58′ 40.06″ S; 60° 12′ 23.92″ W), Buenos Aires Province, Argentina. Ensenadean Stage/Age (Gelasian–Calabrian), early Pleistocene (Figs. 1A–C).

Remarks. The genus *Aramides*, with an exclusively Neotropical distribution, comprises eight species (*A. ypecaha*, *A. wolfi*, *A. mangle*, *A. saracura*, *A. calopterus*, *A. cajaneus*, *A. albiventris*, and *A. axillaris*), which are similar to each other and are mainly distinguished by throat, breast, and belly coloration, along with certain differences in size and proportions (Winkler et al., 2020). *A. mangle* (Little Wood-Rail) is the smallest species, whereas *A. ypecaha* (Giant Wood-Rail) is the largest. The remaining species vary in size within this range, with some differences attributable to sexual dimorphism, as males tend to be slightly larger, measuring approximately 27–29 cm in *A. mangle* to 41–45 and possibly 53 cm in *A. ypecaha* (Marcondes, 2013). This variation is also reflected in tarsometatarsal length (Marcondes, 2013; Marcondes & Silveira, 2015).

The three species that reach the highest latitudes and extend to, or near, the discovery area are *A. cajaneus, A. saracura*, and *A. ypecaha*. The fossil tarsometatarsus CCA-165 measures 83.2 mm in length, smaller than *A. ypecaha* MNHN 6327 (92.3 mm) and slightly larger than *A. saracura* SMF 2153 (72.7 mm) and falls within the size range of the Gray-cowled Wood-Rail *A. cajaneus* (MLP-Or 2156 from Argentina: 90 mm; USNM 612267 from Panamá: 80 mm). In addition, *A. cajaneus* (and specimen under study) differs in tarsometatarsal proportions, being slightly more robust than *A. saracura* and *A. ypecaha*, particularly in the shaft (Figs. 3A–G).

According to published data, *A. cajaneus* ranges from 33 to 40 cm in height and 320 to 480 g in weight (Pagano & Salvador, 2017), with the largest individuals being up to 21% taller and 50% heavier than the smallest.

DISCUSSION

The La Esperanza Formation in Olavarría has long been recognized for its contributions to the understanding of Pleistocene faunas. However, no avian remains had been reported from this locality until now. This study documents the first occurrence of rails (Aves, Gruiformes, Rallidae) in the formation, expanding the known diversity of its Pleistocene vertebrate assemblage. As previously noted, and in contrast to the present-day abundance and diversity of the group, the fossil record of Rallidae in Argentina is limited to a few fragmentary remains.

The specimen described here is assigned to *Aramides* based on a combination of features that also distinguish it from other rallids with a similar tarsometatarsal morphology, such as *Fulica* and *Pardirallus*. In *Aramides*, as in the specimen CCA-165, the *trochlea metatarsi II* terminates more proximally than the *incisura intertrochlearis lateralis*. The tarsometatarsus is elongated with a slender shaft, shorter than those of *A. saracura* and *A. ypecaha* (Figs. 3A–G), including a proximally projected and sharply defined *eminentia intercotylaris* (rounded and blunt in *Fulica*), and gracile trochleae that are moderately divergent. In CCA-165, like in *A. cajaneus*, the trochlear divergence is slightly less pronounced than in the other species of *Aramides* compared (Figs. 3A–G). The shaft narrows more abruptly immediately distal to the cotylae than in *Pardirallus*, and the *sulcus*

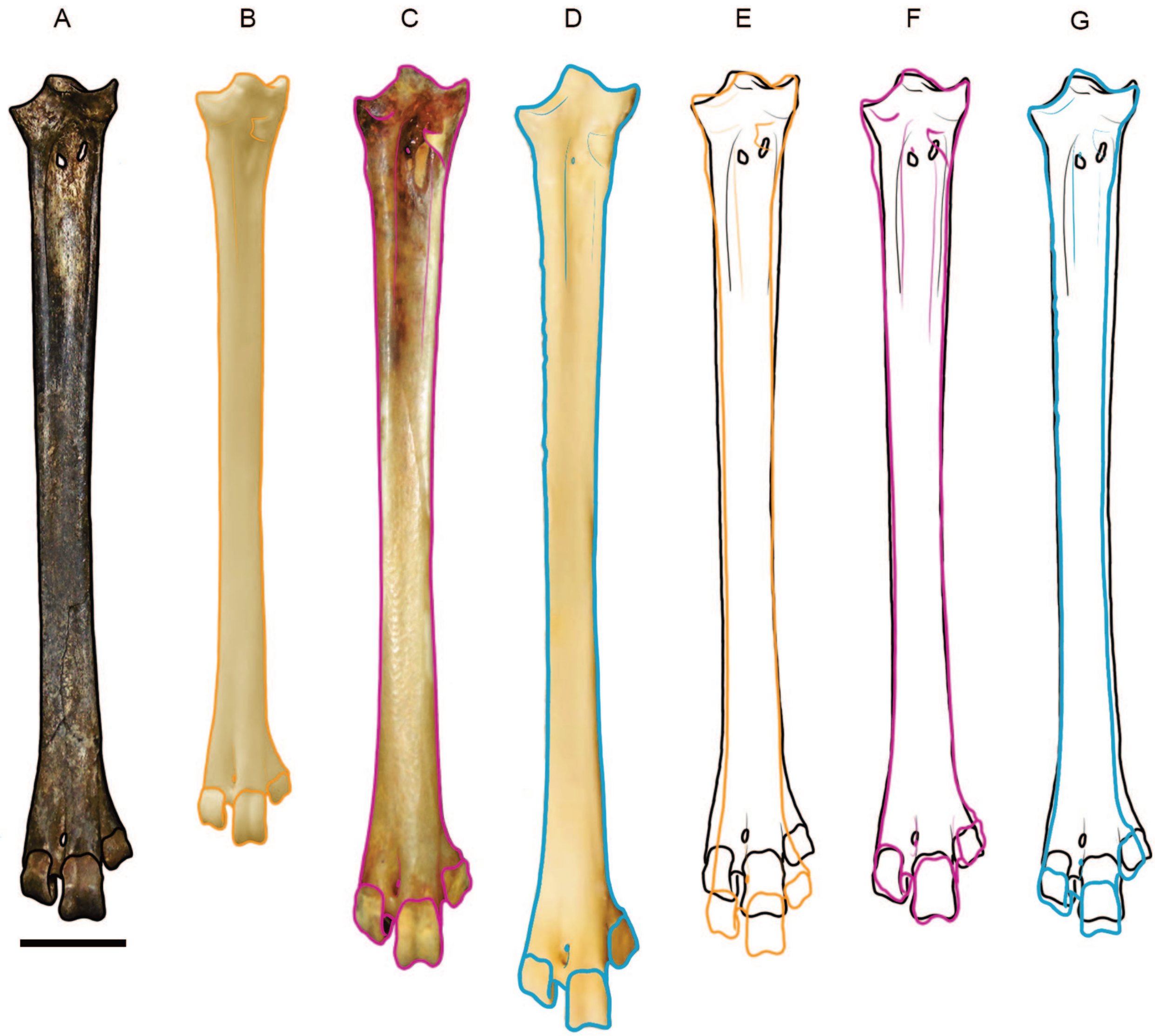

Figure 3. Schematic drawings illustrate the differences in the tarsometatarsal proportions between the fossil specimen *Aramides cajaneus* CCA-165 (black outline) and the most austral modern species of *Aramides* in dorsal view. A, *A. cajaneus* CCA-165; B, *A. saracura* SMF 2153 (yellow outline); C, *A. cajaneus* MLP-Or 2156 (pink outline); D, *A. ypecaha* MNHN 6327 (mirrored, light blue outline); E, outlines of CCA-165 and *A. saracura*; F, outlines of CCA-165 and *A. cajaneus*; G, outlines of CCA-165 and *A. ypecaha*. Scale = 10 mm (outlines were scaled for comparisons).

extensorius that hosts two large *foramina vascularia* is delimited by well-defined edges. The hypotarsus configuration matches that of other rallids (see Mayr, 2016, fig. 4, Mayr, 2019; De Mendoza et al., 2024, fig. 2), with a well-developed and medially inclined *crista medialis* for the *flexor hallucis longus*, a weakly developed *crista lateralis* fhl, and a sulcus for the tendon of *musculus flexor digitorum longus*, likely modified (from a canal) by taphonomic processes.

The presence of *Aramides* provides valuable paleoenvironmental information about the conditions that prevailed in the region during the Pleistocene. Although the genus comprises terrestrial species, they are consistently linked to wetland environments. Of the two species currently occurring in or near the area where specimen CCA-165 was recovered, only *A. cajaneus* matches it in size.

Aramides cajaneus is the most widely distributed rallid in the Americas, ranging from southwestern Central America to central Argentina, reaching just north of Olavarría. It typically inhabits riparian and swampy environments, including forested wetlands, stream banks, and marsh margins. Although it generally remains concealed in dense vegetation, it occasionally forages in open areas. Nests are constructed above the ground, often over water, using twigs and grasses, and placed in shrubs or trees up to three meters high. Due to its ecological flexibility, *A. cajaneus* inhabits a wide range of moist habitats, including seasonal wetlands, reedbeds, and humid scrublands adjacent to wooded zones (Taylor, 2020; Winkler et al., 2020).

The occurrence of *A. cajaneus* in the La Esperanza Formation suggests that wooded or semi-wooded wetlands were present in the area during the Pleistocene. This is consistent with the information derived from the sedimentary structures observed in the collecting site, which indicate fluvial environments. This finding helps reconstruct local paleoenvironments and provides a foundation for further research on avian biogeography and environmental change in southern South America, particularly in the Pampean Region during the Pleistocene.

CONCLUSIONS

The tarsometatarsus CCA-165 is confidently assigned to *Aramides cajaneus* (Rallidae, Gruiformes), a modern species with a broad distribution across the Neotropics, extending as far south as areas near the discovery site. This record constitutes not only the first occurrence of *A. cajaneus* in the fossil record of Argentina, but also the first avian remains recovered from the Pleistocene deposits of the La Esperanza Formation (Olavarría, Argentina). Beyond its taxonomic importance, the presence of this species provides valuable paleoenvironmental insights. The ecological preferences of extant *A. cajaneus* indicate that the area was likely characterized by seasonal wetlands and/or humid scrublands during the early Pleistocene. Additionally, the nesting behavior of the species, which requires vegetated and wooded areas, suggests the existence of forested patches in the landscape. Taken together, this evidence contributes to refining paleoenvironmental reconstructions for the region and underscores the relevance of avian fossils as indicators of past habitats.

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