

The first Cenozoic fossil bird from Venezuela

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with 4 figures

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Abstract: The first Cenozoic avian remains from Venezuela are described. The material comprises an associated right tarsometatarsus and tibiotarsus from the earliest Pliocene of the Codore Formation, northwestern Venezuela. The fossil-bearing horizon represents a deltaic paleoenvironment. The elements are long and narrow, and the presence of a circular incisura intercondylaris bordered proximally by a prominent and centrally-situated tuberculum m. tibialis anticus on the tibiotarsus, allows confident referral to the Ciconiidae (storks). The elements are a close match in morphology and size to the extant *Jabiru mycteria* (Jabiru Stork), although the presence on the distal tibiotarsus of a well-defined caudal sulcus, a narrower sulcus extensorius and shallower angled pons supratendineus, and on the tarsometatarsus of a narrower and deeper sulcus on the plantar surface and a less prominent ridge laterally bordering the fossa supratrochlearis plantaris indicate that this is a new species, *Jabiru codorensis* n. sp. *Jabiru mycteria*, the only living species, still occurs in Venezuela, where it is found mostly in grassy wetlands. These specimens represent the first fossil record of *Jabiru*, as well as the first pre-Pleistocene record of fossil birds from Venezuela.

Keywords: Stork • *Jabiru* • Venezuela • Codore Formation • Pliocene

Kurzfassung: Die ersten fossilen Nachweise von Vögeln aus dem Tertiär Venezuelas werden beschrieben. Bei dem Material handelt es sich um einen assoziierten rechten Tarsometatarsus und Tibiotarsus aus der unterpliozänen Codore-Formation, nordwestliches Venezuela. Die fossilführenden Horizonte entsprechen einem deltaischen Paläoenvironment. Die Fossillemente sind lang und dünn. Das Vorhandensein einer kreisförmigen Incisura intercondylaris, an welche proximal ein prominenter, zentraler Tuberculum m. tibialis anticus auf dem Tibiotarsus grenzt, ermöglicht eine zuverlässige Einordnung dieser Fossilien in die Ciconiidae (Störche). Die Elemente sind morphologisch und in ihrer Größe der lebenden Art *Jabiru mycteria* (Jabiru-Storch) sehr ähnlich, obwohl das Vorhandensein eines klar abgegrenzten kaudalen Sulcus am distalen Tibiotarsus, eines schmaleren Sulcus extensorius und flacheren abgewinkelten Pons supratendineus des Tibiotarsus, sowie eines schmaleren und tieferen Sulcus auf der plantaren Oberfläche des Tarsometatarsus und einer weniger prominent ausgebildeten Kante, welche lateral die Fossa supratrochlearis plantaris begrenzt, am Tarsometatarsus auf eine neue Art, *Jabiru codorensis* n. sp., hindeuten. *Jabiru mycteria*, die einzige lebende Art der Gattung, kommt heute noch in Venezuela vor, wo sie hauptsächlich in grasbewachsenen Feuchtgebieten zu finden ist. Die hier beschriebenen Fossilien sind sowohl die ersten fossilen Nachweise von *Jabiru* als auch die ersten präpleistozänen Nachweise fossiler Vögel aus Venezuela.

Schlüsselwörter: Storch • *Jabiru* • Venezuela • Codore-Formation • Pliozän

Introduction

Bird species form an important part of most modern ecosystems, with 9,700 avian species estimated to be in existence today (STATTERSFIELD et al. 1998). Many bird species are restricted to specific environments and are consequently susceptible to environmental change. Avian extinction rates are thus increasingly being used

as indicators of the progression of global warming (e.g., CANTERBURY et al. 2000). How the high avian diversity of neotropical regions will be affected by future environmental change has particularly been the focus of a significant research effort in recent years (HUNTLEY et al. 2006). An important aspect of understanding how distribution and diversity patterns of living species may be affected by future environmental change lies in gain-

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ing an understanding of how those patterns developed over time. Direct evidence of former taxic distribution is, however, only available through the fossil record.

That the fossil record of birds is depauperate is a common misconception. In fact, bird bones are not uncommon in many geological deposits, despite their apparent fragility (OLSON 1976, 1985; UNWIN 1996). South America has a particularly diverse avian fossil record, although most Cenozoic reports come from particularly productive deposits in Argentina (e.g., VUILLEUMIER 1984; ALVARENGA & HÖFLING 2003). Tertiary fossil birds have also been reported from Brazil, Chile and Peru (e.g., CHENEVAL 1993; WALSH & HUME 2001; ALVARENGA & GUILHERME 2003), but, to our knowledge, no pre-Pleistocene avian fossils have been recorded from Colombia, Venezuela, Guyana, Suriname, or French Guiana. This seems surprising, considering that today almost 1400 endemic or migratory bird species are known in Venezuela alone (HILTY 2003). This absence of data on Cenozoic avian diversity is a major impediment to our understanding of the evolution of modern avifaunas in the Neotropics.

Here we provide the first description of Tertiary fossil avian remains from Venezuela. The material comprises a right tarsometatarsus and tibiotarsus that were recovered in association by one of us (RS) from the early Pliocene of the Codore Formation, north western Venezuela. The specimens are referable to the extant genus *Jabiru*, although they clearly represent a new species. The material is accessioned to the collections of the Alcaldía del Municipio Urumaco.

Institutional abbreviations: AMU-CURS, Alcaldía del Municipio Urumaco; BMNH, Natural History Museum, London.

Anatomical nomenclature follows BAUMEL & WITMER (1993), with some English modifications.

Geology and paleoenvironment

The type section of the Codore Formation crops out along the Codore river, 3.5 km north of El Mamón, and the formation can be recognized from the northeast and north-central Falcón region to the Zazárida river in the west, and close to Coro in the east (MINISTERIO de ENERGÍA y MINAS 1997) (Fig. 1). In the type locality the formation comprises around 757 m of fine sandstones, siltstones, and limestones. The formation can be divided into three successive lithostratigraphic units (Fig. 1); the basal El Jebe Member (301–398 m thick), the Chiguaje Member (approximately 72 m thick) and the overlying Algodones Member (298–303 m thick; not shown here) (MINISTERIO de ENERGÍA y MINAS 1997). The sediments of the El Jebe Member were deposited in a dry to subhumid climate (indicated by palynomorphs) on an distal alluvial flood plain with small meandering fluvial channels to the west, larger distal river systems in the central region, and with no channel development to the east. The overlying late early Pliocene marine Chiguaje Member demonstrates a subsequent marine transgression (LINARES 2004), which does not appear to have affected the more easterly parts of the formation (MINISTERIO de ENERGÍA y MINAS 1997). The Algodones Member represents a return to an alluvial plain environment with meandering river systems, indicating a relative drop in sea level. The greater channel development in the Algodones Member, compared with that of the El Jebe Formation, suggests that the sea level may have been slightly lower than during the deposition of the El Jebe Member.

The Codore Formation overlies the Urumaco Formation, which has one of the most diverse vertebrate faunas of the Tertiary Neotropics (AGUILERA 2004). Vertebrate fossils from the lower and middle levels of the El Jebe Member of the Codore Formation are also

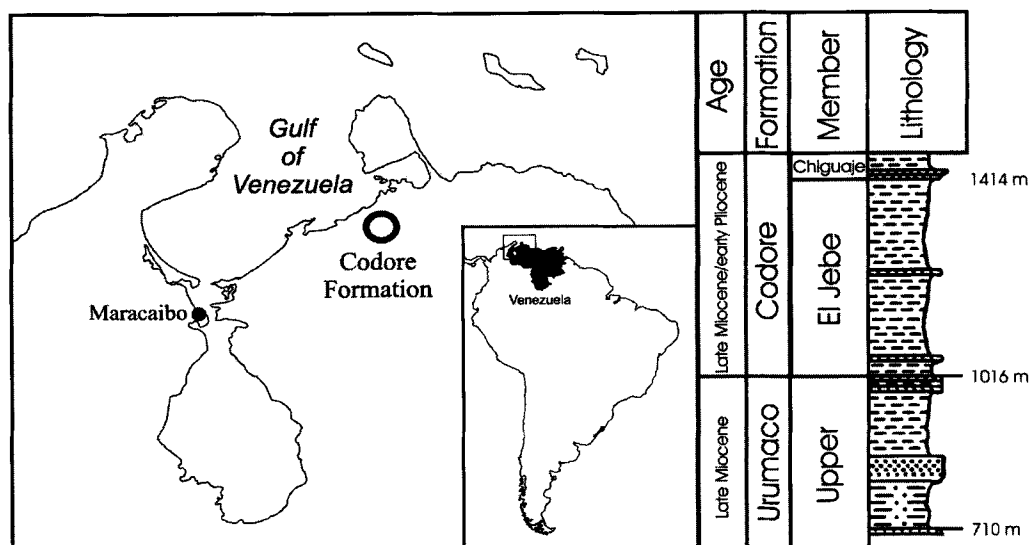


Fig. 1. Collection locality of AMU CURS 130-5, with stratigraphy of the Codore Formation (excluding the Algodones Member). Stratigraphic log modified after LINARES (2004).

becoming increasingly known, and include mammals, reptiles and fish (LINALES 2004; CARLINI et al. 2006; SÁNCHEZ-VILLAGRA & AGUILERA 2006). The two specimens reported here (AMU CURS 130-5) come from a middle level (earliest Pliocene) of the El Jebe Member. The observation that both elements are from the right hind limb, their discovery in association with each other, their consistency in size and similarity in preservation, strongly support derivation from the same individual. Furthermore, these observations indicate that the specimens are very unlikely to have been reworked from underlying strata. However, we choose to designate only the tibiotarsus as the holotype, in order to simplify any future revision that may arise in the unlikely event that the two specimens prove not to be referable to a single taxon.

Systematic paleontology

Aves LINNAEUS, 1758
 Ciconiiformes GARROD, 1874
 Ciconiidae SUNDEVALL, 1836
 Mycteriini MAYR & COTTRELL, 1979
Jabiru HELLMAYR, 1906

Jabiru codorensis n. sp.

Figs. 2–4

Etymology: Species name in recognition of the provenance of this jabiru stork from the Codore Formation of Venezuela.

Holotype: AMU CURS 130-5; right tibiotarsus lacking the proximal-most region and exhibiting slight cranial-caudal/dorsal-plantar post-diagenetic compression (Figs. 2A–B).

Paratype: AMU CURS 130-5; right tarsometatarsus, also lacking the proximal-most region and exhibiting slight cranial-caudal/dorsal-plantar post-diagenetic compression (Figs. 2C–D), recovered with the right tibiotarsus and believed to be from the same individual.

Locality and distribution: Middle level of the El Jebe Member of the Codore Formation, Early Pliocene, Urumaco region, Venezuela.

Diagnosis: The tibiotarsus and tarsometatarsus of this taxon are almost identical in size and morphology to the extant *Jabiru mycteria*, but the holotype tibiotarsus primarily differs from that species by possessing a narrower sulcus extensorius, a shallower angled pons supratendineus, a sulcus on the distal caudal surface and a shorter sulcus extensorius. The paratype tarsometatarsus differs from *Jabiru mycteria* by a narrower and deeper sulcus on the plantar surface and a less prominent ridge laterally bordering the fossa supratrochlearis plantaris.

Description

Tibiotarsus (Figs. 3A–D)

The element is long and slender (length 248.5 mm), tapering distally from its proximal extremity (maximum diaphyseal width at proximal end 17 mm), and widening at the distal epiphysis (maximum width of epiphysis 21.5 mm) (Figs. 2A–B). The proximal region does not

preserve evidence of the proximal articular surface, and is probably missing around 90 mm of its total length (reconstructed length approximately 340 mm). The diaphysis is rounded in section caudally, becoming much flatter on the cranial surface. Slight cranial-caudal burial compaction is evident from visible compression cracks, mostly on the lateral and medial surfaces, and is more severe at the proximal end.

In cranial view (Fig. 3A), the sulcus extensorius extends along the medial margin of the distal cranial surface, and is narrow and well defined (width of the sulcus represents 28 % of the total width of the diaphysis in that region), similar in relative width to *Mycteria ibis* (Yellow-Billed Stork). The pons supratendineus is angled as it protrudes cranially more shallowly than in *Jabiru mycteria*, and is more similar to that of *M. leucocephala* (Painted Stork). The cranial surface of the pons supratendineus slopes toward the lateral margin unlike in *Mycteria* (SW pers. obs.) or *Ciconia*, but like *Ephippiorhynchus* (BOLES 2005) or *Jabiru* (SW pers. obs.). Distally the pons supratendineus terminates in an almost perfectly round exit for the canalis extensorius, the relative width of which is approximately 50 % larger than in *J. mycteria*, and larger than most other Ciconiidae examined, including *E. senegalensis* (Saddle-Billed Stork). The incisura intercondylaris is a large, deep and perfectly circular rounded pit bordered proximally by a prominent and centrally situated tuberculum m. tibialis anticus. The presence of this condition allows confident referral to the Ciconiidae (e.g., BOLES 2005). The incisura intercondylaris is slightly laterally compressed in many ciconiid taxa, due to the narrower width of the epiphysis. However, the incisura lacks the slightly notched medial margin of the lateral condyle, considered by OLSON (1991; SUAREZ & OLSON 2003) as characteristic of *Mycteria* and absent in *Ciconia*, and is larger and more regular than in *Ephippiorhynchus*.

The distal extension of the lateral and medial condyles is approximately equal. In lateral (Fig. 3C) and medial views the outline of the condyles is oval rather than circular; the distal border of the lateral condyle is distinctly flattened and notched and is most similar to *J. mycteria*. In distal view (Fig. 3D) the sulcus intercondylaris is broad, as in *Ciconia*, *Jabiru* and *Ephippiorhynchus*, and unlike *Mycteria* (OLSON 1991). The tuberositas retinaculi m. fibularis is broad, flattened and does not form an elongate ridge, as in *Ciconia*, or a distinct papilla, as in *Ephippiorhynchus* (see BOLES 2005). The distal caudal surface is flattened to the extent that distinct angles are formed between the caudal surface and the lateral and medial surfaces. In *Ciconia*, *Leptoptilus* and *Mycteria* the junction between the caudal and medial, and caudal and lateral surfaces are much more rounded; only in *Jabiru mycteria* and *Ephippiorhynchus asiaticus* (Black-Necked Stork) are the junctions observed to be as angular. A distinct sulcus is developed (maximum width 8.5 mm) on the caudal surface, and extends distally approximately 40 mm until it is delimit-

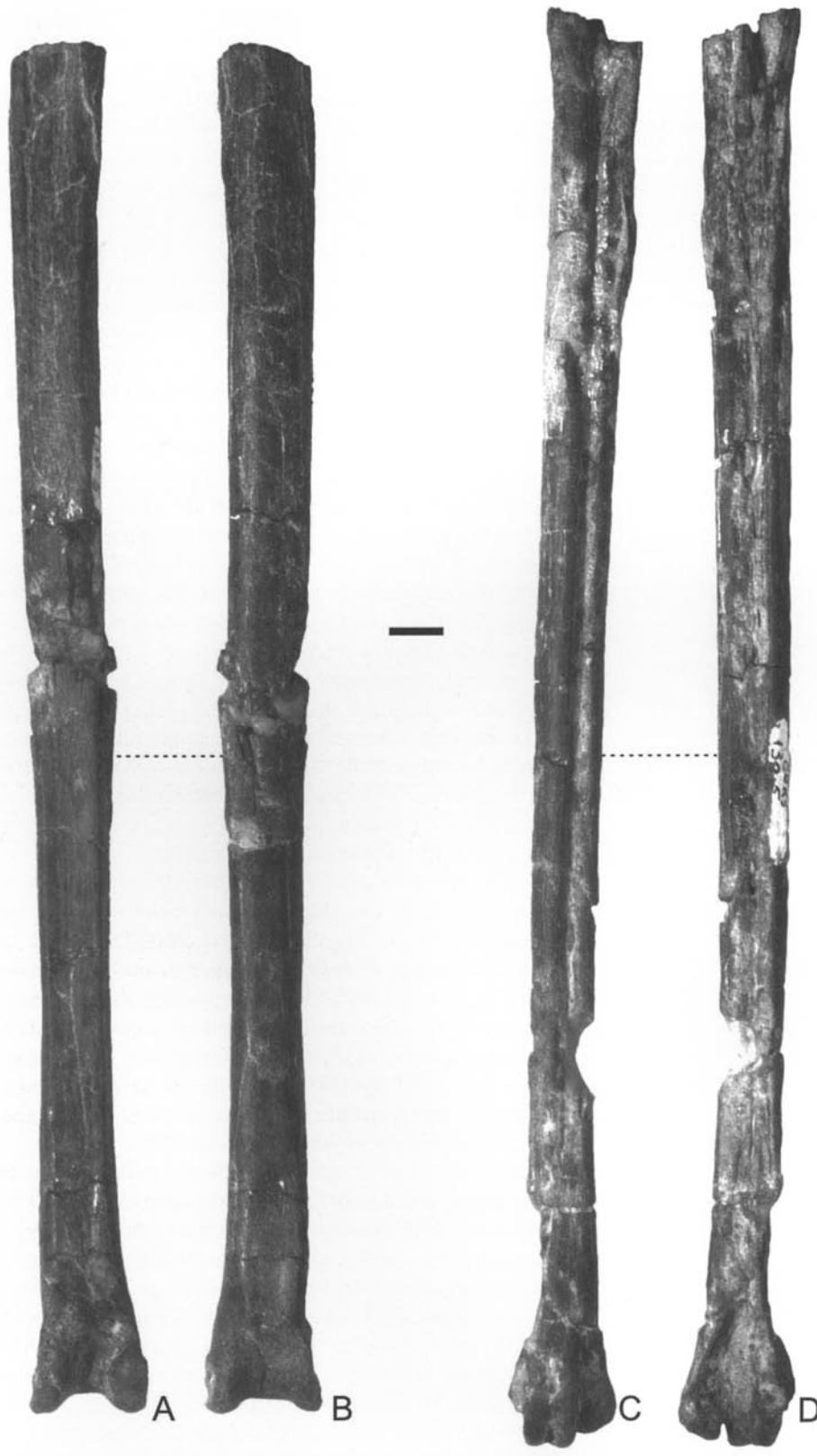


Fig. 2. Holotype material of *Jabiru codorensis* (AMU CURS 130-5). **A–B:** Tibiotarsus in A, cranial and B, caudal views; **C–D:** Tarsometatarsus in C, dorsal and D, plantar views. – Scale bar = 10 mm.

ited by the proximal border of the articular surface (Fig. 3B). The presence of the sulcus on the least compressed portion of the element, the evenness of this feature and the complete absence of compression fissures indicates that this linear depression is not related to burial compaction. A similar sulcus is absent in *J. mycteria*.

Tarsometatarsus (Figs. 4A–C)

The tarsometatarsus is also long and slender, but, with a preserved length of 280 mm, is slightly longer than the tibiotarsus. Based on the position of the two cristae hypotarsi, the missing portion represented approximately 20 mm, indicating a probable original length of 300 mm.

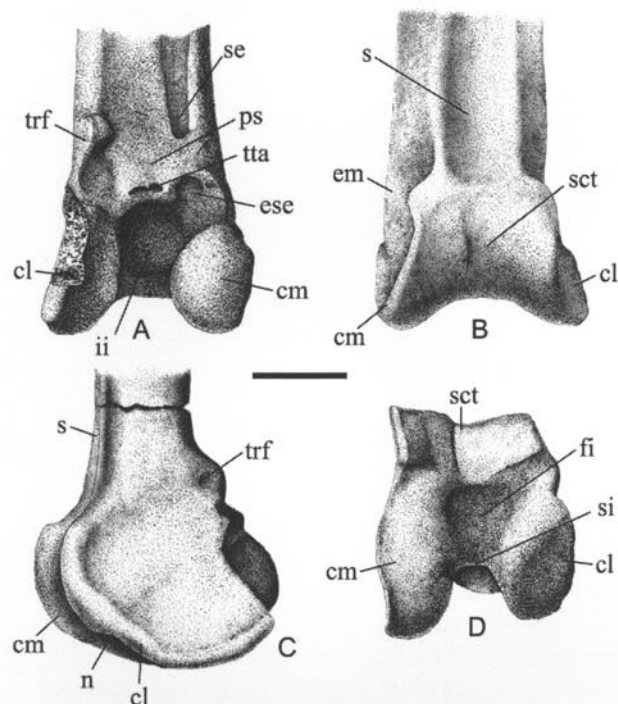


Fig. 3. Detail of the distal region of the holotype tibiotarsus of *Jabiru codorensis* n. sp. (AMU CURS 130-5) in A, cranial; B, caudal, C, lateral and D, distal views. – Abbreviations are as follows: cl, condylus lateralis; cm, condylus medialis; em, epicondylus medialis; ese, exit of the sulcus extensorius; fi, fossa intercondylaris; ii, incisura intercondylaris; n, notch on the condylus lateralis; ps, pons supratendineus; s, sulcus on the caudal surface; sct, sulcus cartilaginis tibialis; se, sulcus extensorius; si, sulcus intercondylaris; trf, tuberositas retinaculi m. fibularis. – Scale bar = 10 mm.

With its maximum width (18.5 mm) at the proximal extremity, the shaft tapers slightly up to the flaring of the distal trochleae, where it reaches a maximum width of 21 mm. The proximal extremity is damaged, and lacks evidence of the cotylae and all except for the proximal-most region of the hypotarsus. The preserved region is in shape and relative width most like that of *J. mycteria*, but the cristae hypotarsi are lightly less prominent. The shaft is slightly dorsoplantarly compressed due to burial compaction, although in most Ciconiidae the shaft cross section is approximately equant (in *Ephippiorhynchus asiaticus* the shaft is laterally compressed). The shaft is noticeably broader than in *Jabiru* tarsometatarsi of comparable length, although this may be mostly due to burial compaction noted above. The plantar surface of the shaft possesses a shallow sulcus which extends almost from the apex of the hypotarsus to slightly short of the trochlear region. In *Ephippiorhynchus* the sulcus is much narrower and shallower, in *Jabiru* it is wider and shallower, and in all *Mycteria* examined extends into the fossa supratrochlearis plantaris.

In dorsal view, the sulcus extensorius is narrow at approximately 5 mm wide, centrally situated, and occupies approximately 79 % of the shaft, from the proximal

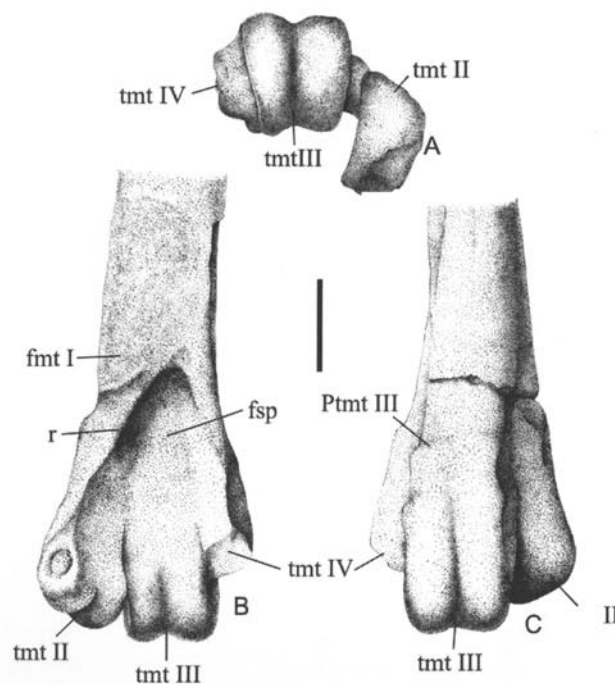


Fig. 4. Detail of the distal region of the holotype tarso-metatarsus of *Jabiru codorensis* n. sp. (AMU CURS 130-5) in A, distal; B, plantar and C, dorsal views. – Abbreviations are as follows: fmt I, fossa metatarsi I; fsp, fossa supratrochlearis plantaris; ptmt III, proximal extent of trochlea metatarsi III; r, ridge medially bordering the fossa supratrochlearis plantaris; tmt II, trochlea metatarsi II; tmt III, trochlea metatarsi III; tmt IV, trochlea metatarsi IV. – Scale bar = 10 mm.

fracture surface to approximately 40 mm short of the proximal border of the trochlea metatarsi IV (in *Ciconia* the sulcus extends to the foramen vasculare distale; BOLES 2005). The proximal-most region of the sulcus is slightly widened, as in *Jabiru*, and less so than in species of *Ciconia*, including *C. maguari* (Maguari Stork). Much of the lateral and distal regions of trochlea metatarsi IV are missing, and as a result the position of the foramen vasculare distale is difficult to determine. In the preserved trochleae, trochlea metatarsi III (maximum width 10.5 mm) extends little further distally than trochlea metatarsi II (maximum width 7.0 mm) to create what would probably have been a shallow arch. In distal view trochlea II is much deflected plantarly (although far less so than in the Phoenicopteridae), and the preserved region of trochlea IV also suggests that this trochlea was similarly deflected.

On the plantar surface of the trochlear region, a well-defined fossa supratrochlearis plantaris is bordered laterally by a well-defined ridge, which is angled proximally towards the midline. In *Leptoptilus*, *Ephippiorhynchus* and *Ciconia* this ridge is less well-developed or absent, and, in *Mycteria* and *Jabiru*, it is broader than in AMU CURS 130-5. The proximal portion of the ridge forms the medial border of the fossa metatarsi I, which is broad and triangular, but otherwise is flattened and

poorly-defined. The shape of this attachment is identical to that in *J. mycteria* (in *Ciconia* and *Mycteria* the attachment is more elongate).

Discussion

Based on their narrow and elongate form and their recovery from continental strata, we initially suspected that these specimens would be referable to one of the gracile species of the Phorusrhacidae. This extinct family of terrestrial predeaceous birds is well known in other parts of South America, and would be expected in Venezuela. However, the presence of a circular incisura intercondylaris bordered proximally by a prominent and centrally situated tubercle for the m. tibialis anticus instead confirms referral to the Ciconiidae (BOLES 2005).

Although the absence of the proximal regions of the tarsometatarsus and tibiotarsus preclude precise determination of the length ratio between the elements, it is very likely that the tarsometatarsus was around 90 % of the length of the tibiotarsus. The tibiotarsus is not referable to *Mycteria* based on the angle of the pons supratendineus, absence of a notch on the medial margin of the lateral condyle, broad sulcus intercondylaris and the angular junction between its caudal and lateral surfaces. The presence of an angled pons supratendineus combined with the angular junction of the caudal and lateral surfaces also preclude referral to *Ciconia*. The broad and flattened tuberositas retinaculi m. fibularis also precludes referral to *Ciconia*. A rounded junction of the caudal and lateral surfaces is also a feature of *Leptoptilus*. *Ephippiorhynchus* can be excluded based on its possession of a less regular incisura intercondylaris and a distinct papilla for the tuberositas retinaculi m. fibularis. Although only the distal regions are preserved in AMU CURS 130-5, BOLES (2005) noted that the proximal region has limited utility for distinguishing extant stork genera.

The tarsometatarsus differs from *Mycteria* in that the sulcus on the plantar surface does not extend into the fossa supratrochlearis plantaris, and the attachment for os metatarsale I is much less elongate. The less elongate shape of that attachment also excludes referral to *Ciconia*, as does the narrower proximal widening of the sulcus extensorius, the failure of the sulcus to extend to the foramen vasculare distale, and the poorer development of the ridge laterally bordering the fossa supratrochlearis plantaris. Poor development of this ridge is also characteristic of *Leptoptilus* and *Ephippiorhynchus*, which is also excluded based on its narrower and shallower sulcus on the plantar surface.

By comparison the elements are a very close match in overall morphology to *Jabiru mycteria*, although the genus does not possess clear apomorphies in the regions of the tibiotarsus and tarsometatarsus that are preserved in AMU CURS 130-5. Consequently, referral to *Jabiru* is based mostly on overall morphological similarity and

the presence of several characters that preclude referral to other living ciconiid genera. The minor differences observed between these specimens and the same elements in *J. mycteria* indicate that this taxon is sufficiently different from *J. mycteria* to justify erection of a new species. The elements are also a close match in size with *J. mycteria*, and clearly came from an individual well within the size range of the larger living stork species (KAHL 1973).

With a fossil record extending at least as far as the early Oligocene, several Cenozoic species of fossil stork are known from deposits as widely spaced as western and eastern Europe (France, Romania and the Ukraine), North and sub-Saharan Africa (Egypt, Tunisia and Kenya), Asia (India, Pakistan, Mongolia), and North America (Arizona, California, Carolina, Florida, Idaho, Oregon and Texas; e.g., BRODKORB 1961; SHORT 1966; PHILLIPS 1968; HILL & WALKER 1979; OLSON 1985a, 1991; BECKER 1987; HAARHOPP 1988; MILLER et al. 1997; BRUNET & M. P. F. T. 2000). Only a few fossil ciconiid species allow comparison with AMU CURS 130-5. OLSON (1991) showed that the type material of the mid-Miocene *Dissouroides milleri* SHORT from Nebraska belongs in *Mycteria*, primarily on the basis of the presence of a notched medial margin of the lateral condyle of the tibiotarsus. As mentioned above, the absence of this notch in AMU CURS 130-5 (among other characters) precludes its referral to any species of *Mycteria*, including *M. milleri* and the much younger (Pleistocene) *M. wetmorei*.

Records for fossil *Jabiru* include an extinct species, *J. weillsi* (SELLARDS 1916), which WETMORE (1931) subsumed in the extant *J. mycteria*. WETMORE (1928, 1931) also recorded *Jabiru mycteria* from the Pleistocene of Florida and Cuba. However, in a thorough revision of the North American fossil ciconiid material, HOWARD (1942) reassigned all specimens referred to *Jabiru* to the extinct *Ciconia maltha*, a large species spanning the Upper Pliocene to Pleistocene. *C. maltha* apparently enjoyed a wide distribution from Nebraska to Cuba and is very similar in its postcranial osteology to *J. mycteria* (FEDUCCIA 1973). It seems possible that *C. maltha* may have extended into the early Pliocene of Venezuela. Nonetheless, although AMU CURS 130-5 is within the size range of this highly variable species, the specimens are not referable to *C. maltha*, as in that taxon the sulcus extensorius of the tarsometatarsus extends into the foramen vasculare distale (for instance, compare Fig. 2C of this work with MILLER 1932: 213, fig. 23b). VUILLEUMIER (1984) listed *Jabiru* from the late Pleistocene of Peru, but provided no source or reference for this record. The validity of identifications for the taxa listed in this work was severely questioned by OLSON (1985b), and consequently this record cannot be regarded at face value. The material described in the present work therefore constitutes the only fossil record of *Jabiru*, and confirms the presence of *Jabiru* storks in Venezuela at least as long ago as the earliest Pliocene.

Jabiru mycteria breeds from Honduras to northern Argentina in the south, and has been reported in most South American countries east of the Andean Cordillera, and even as far north as Texas (KAHL 1971). Breeding populations of *J. mycteria* occur in Venezuela, and the possibility exists that *J. codorensis* n. sp. also nested in the region during the early Pliocene, although these adult specimens obviously provide no direct evidence for this. *Jabiru mycteria* today inhabits swamps and wetlands, and is known to hunt fish, amphibians, snakes, gastropods, insects, and other invertebrates (KAHL 1971). The environments suggested for the El Jebe Member from sedimentological evidence (MINISTERIO de ENERGÍA y MINAS 1997) are fully consistent with the ecological preferences of the modern species. It therefore seems highly likely that *J. codorensis* n. sp. had very similar environmental requirements to *J. mycteria*. If *J. codorensis* n. sp. was indeed nesting in the region, the former local presence of tall trees within the Codore Formation wetland habitat is indicated.

Considering the El Jebe Member paleoenvironment it seems entirely unsurprising that a wetland bird should be the first avian species to be recovered from these sediments. However, considering the abundance and diversity of bird species in the wetlands of Venezuela today, and the abundance of vertebrate material in these sequences – particularly in the Urumaco Formation – it is presently unclear why avian material is apparently so rare. One reason may relate to the preservation potential of bird bones in the largely uncemented sediments of the formation, where burial compaction appears to be commonplace. On the other hand, the observed burial compaction in AMU CURS 130-5 is by no means severe, and one would expect even small avian bones to be preserved, albeit in a crushed state. An alternative possibility is that such crushed material is normally simply not collected due to its poor condition. Whatever the case, the type material of *Jabiru codorensis* n. sp. demonstrates that avian material is indeed present in the Venezuelan Neogene formations, and suggests that future prospecting from fossiliferous localities may result in the collection of further avian specimens. In addition to the considerable environmental information provided by bird remains, avian fossils from these Venezuelan sequences will provide crucial data on the development of modern Neotropical avifaunas.

Conclusions

The specimens described here represent the first avian fossils described from the Cenozoic of Venezuela, the first fossil record of *Jabiru*, and the only other species of *Jabiru* currently known. They provide important data on avian diversity in the Neotropics during the Neogene, and indicate the possibility of finding further avian material in the formation. Modeling the development of modern environmentally sensitive Neotropical avifaunas

cannot be achieved without such avian diversity data from the Cenozoic of Venezuela and adjacent countries.

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