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### THE WING OF TITANIS WALLERI (AVES:PHORUSRHACIDAE) FROM THE LATE BLANCAN OF FLORIDA

#### Robert M. Chandler<sup>1</sup>

Titanis walleri Brodkorb (1963:113) is the only known member of the South American avian family Phorusrhacidae to have successfully emigrated north during the Great American Interchange at the end of the Tertiary about 2.5 Ma (i.e., late Pliocene; Webb 1991:266). Titanis and its closest relatives in the subfamily Phorusrhacinae were flightless ground predators from one and one half to two meters tall. Their skulls were laterally compressed for shredding their prey. The holotype tarsometatarsus (UF 4108) and the first phalanx of Digit III (UF 4109) of this remarkable bird remain the only published fossils. Field crews from the Florida Museum of Natural History, led by Vertebrate Paleontology curators Clayton Ray and later by S. David Webb, continued to work the type locality (Santa Fe River 1A and 1B) through the 1960s. Santa Fe 1A is a mid-channel deep-water basin where the fossils accumulate. Santa Fe 1B contains inplace sediments from which the fossils are eroding. Additional fossils of Titanis were collected by these field crews, but were not identified as such until recently.

Carr (1981:91-94) identified 47 species, including *T. walleri*, from the early Pleistocene avifauna of Inglis 1A, Citrus County. Among the referred material for *Titanis* were several skeletal elements including a left carpometacarpus, which has not been found at the Santa Fe River. Inglis 1A is an early Irvingtonian sinkhole deposit (Webb 1974:29; Meylan 1982:3-4). The only other locality in Florida where *Titanis* has been found is Port Charlotte, Charlotte County, on a canal spoil pile. This record is based on a digit II, phalanx 2 (UF 124228).

In 1993, with the financial support of the Philip M. McKenna Foundation, field crews from the Florida Museum of Natural History began diving at the type locality of *Titanis* in search of additional phorusrhacoid fossils. I have relocated

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Santa Fe 1B, the in-place sediments, and found that it is a bone bed. The most significant new fossil recovered to date is the proximal end of a left humerus (UF 137839) of *Titanis walleri*. This is the first *Titanis* humerus known. Also, it is the first humerus correctly identified for the group of phorusrhacines (*Andrewsornis*, *Andalgalornis*, and *Phorusrhacus*), which are the closest relatives of *Titanis* (Chandler MS).

The left proximal humerus (UF 137839, Santa Fe River 1B) is broken just distal to the external tuberosity and the head is missing (Fig. 1 A-D). It is very large and robust with a palmoaconally flattened shaft. The deltoid crest is perpendicular to the trailing edge of the shaft on the palmar surface. The shaft is not hollow, but it has a greatly reduced pneumatic network of bone extending from below the head distad through the shaft and also into the deltoid crest. The leading edge of the shaft is densely packed bone. The raised bicipital surface is distinctly demarcated and the bicipital furrow is broad and deep.

The left carpometacarpus (UF 30003, Inglis 1A) is robust but short relative to the depth of the proximal end (Fig. 2 A-E). The carpal trochlea is broad and almost vertical in orientation not extending distad below metacarpals I and II. Metacarpal I is rounded and the facet for the pollex is a ball joint about 7mm in diameter. Metacarpals II and III are both slightly bowed. An enlarged tubercle below the proximal symphysis provides insertion for the M. ulni-metacarpalis dorsalis.

Recently, I have studied the phorusrhacoids in the collections at the American Museum of Natural History and the Field Museum of Natural History and have discovered that the long-standing ideas about phorusrhacine wing structure are incorrect. In the past, the wings of these large ground predators have been modelled after the smaller psilopterine sister group because more complete skeletons of psilopterines are known. The shaft of the humerus of psilopterines is curved and rod-like in cross section. The humerus and carpometacarpus show that *Titanis* and its closest relatives have a strong, robust wing instead of a small, paedomorphic wing like ratites (e.g., rheas and ostriches) or a rod-like humerus as in the psilopterines. The almost vertical carpal trochlea of the carpometacarpus of *Titanis* shows that the manus was held extended, as in penguins, and could not be folded under the ulna as in other birds.

Popular accounts illustrate these large phorusrhacines using their small wings for balance like ratites (Marshall 1978; 1994). It is now clear that *Titanis* had a much stronger wing architecture possibly equipped with a large claw. The claw hypothesis is based on the presence of a ball joint for the facet of Metacarpal I (Fig. 3A, B), which is unique in birds. This ball joint would allow the pollex to be very moveable and more useful. The claws could have been used to keep struggling prey, which may have had horns or antlers, from injuring the attacker.

Another intriguing discovery from the Santa Fe River includes two quadratojugals. Both are from large adult (completely ossified) phorusrhacines, but they have different qualitative articular characters and differ in size. The

larger right quadratojugal (UF 57585) is from an individual the size of Titanis, whereas, the left quadratojugal (UF 57580) is significantly smaller. elements are evidence for either sexual dimorphism in Titanis or that there is a second undescribed species represented by the smaller individual. dimorphism has not been proven to be present in the smaller psilopterine phorusrhacoids, which are more abundant in collections.

The skeletal material of Titanis now represented in the Vertebrate Paleontology collection at the Florida Museum of Natural History includes cranial pieces, vertebrae, and portions of the wings and legs. Hopefully with the continued success of this Santa Fe River project we will achieve a more comprehensive view of Titanis and its relationship to other phorusrhacoids.

#### **ACKNOWLEDGMENTS**

I thank the Philip M. McKenna Foundation for supporting this project. I want to thank the owners and the management of Ginnie Springs, particularly Wes Skiles, for their cooperation and interest in this project. I received travel awards from the American Museum of Natural History and the Field Museum of Natural History to study fossils in those collections. Scott Lanyan (Birds) and John Bolt (Vertebrate Paleontology), Field Museum; and Larry Martin, Museum of Natural History, The University of Kansas, loaned important specimens to me for this study. Janis Brown, an enthusiastic volunteer diver, made the significant find of the humerus of Titanis. Early versions of this manuscript were improved by critical comments by Linda Dryden Chandler, Steven D. Emslie, S. David Webb, and W. Mark Whitten. The drawings were skillfully done by Linda Dryden Chandler. This is University of Florida Contribution to Paleontology Number 443.

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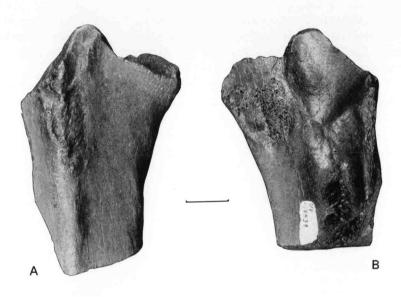
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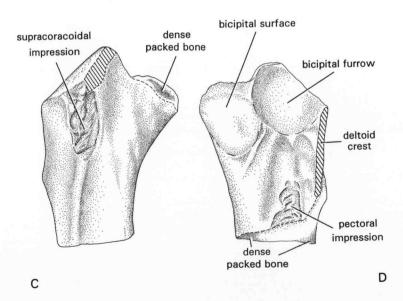


Figure 1. Proximal left humerus of *Titanis walleri*, UF 137839. (A and C) Anconal view. (B and D) Palmar view. Scale equals 2 cm.

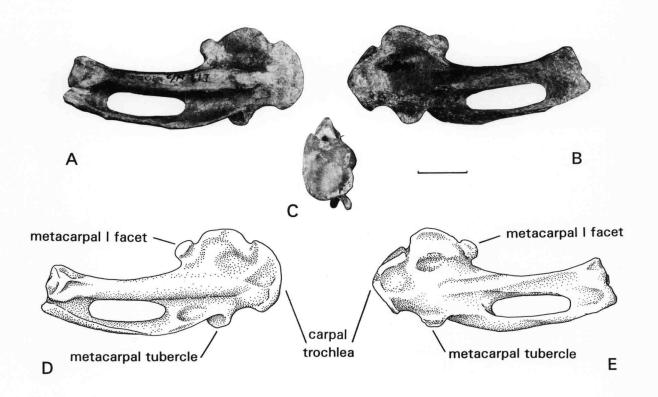


Figure 2. Left carpometacarpus of Titanis walleri, UF 30003. (A and D) External view. (B and E) Internal view. (C) Proximal view. Scale equals 2 cm.

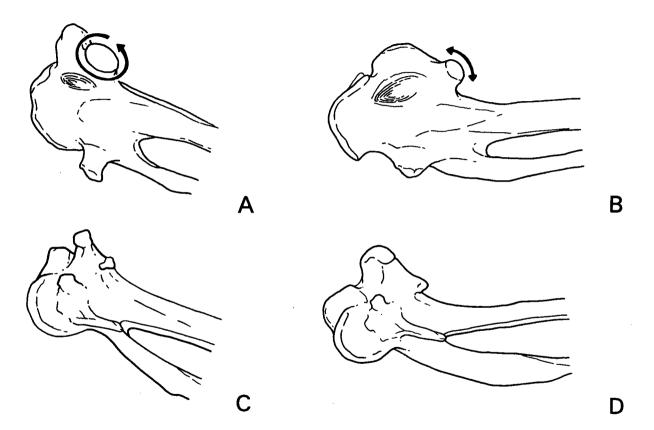


Figure 3. The range of motion for the pollex of the left carpometacarpi with a ball-joint (A and B), *Titanis walleri*, UF 30003; and with a flat facet (C and D), the modern Red-legged Seriema, *Cariama cristata*, FMNH 105635. The carpometacarpi in this figure are drawn to approximately equal size.

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