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The carpometacarpus of the Pliocene turkey *Meleagris leopoldi* (Galliformes: Phasianidae) and the problem of morphological variability in turkeys

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I describe the first known carpometacarpus attributable to the extinct late Pliocene (Blancan) turkey *Meleagris leopoldi* that was apparently collected with the type material at the type locality in Cita Canyon, Texas. Although known to previous workers, this specimen has never been discussed or described. The size and morphology of the carpometacarpus indicates that *M. leopoldi* may be distinct from the extant *M. gallopavo* and is similar to *Meleagris progenes* and Inglis 1A (Florida) material. However, this fossil does not clarify the relationship to and possible synonymy of *M. leopoldi* and *M. anza*, but it adds support to the idea that *M. progenes* is a junior synonym of *M. leopoldi.* The extreme morphological variation among fossil turkey specimens and recognized species obscures the phylogenetic relationships among *Meleagris* taxa. The presence of certain variable characters in geologically older *Meleagris* taxa may provide a clue to assess character polarity. Given these data, it appears that *Meleagris leopoldi* was a widely distributed late Pliocene species that was replaced in its geographic range by *M. gallopavo* during the Pleistocene.

INTRODUCTION

Turkeys are a North American clade composed of two extant species (wild turkey *Meleagris gallopavo* Linneaus 1758 and ocellated turkey *Meleagris ocellata* Cuvier 1820) that are the sister group to some partridges (*Perdix*) from Asia (Crowe et al. 2006). While there are a large number of turkey fossils that have been collected from deposits ranging in age from the Miocene through the Holocene (Steadman 1980), the exact number of extinct species and how they are related to one another phylogenetically is currently unknown. There are five extinct species (*Meleagris anza* Howard 1963, *M. californica* Miller 1909, *M. crassipes* Miller 1940, *M. leopoldi* Miller and Bowman 1956, and *M. progenes* Brobkorb 1964) that all have been placed in the genus *Meleagris*, in addition to species placed in unique genera (*Rhegminornis* and *Proagriocharis*).

Despite the availability of fossil and extant material, the great variability of the osteology of individuals within *Meleagris* confounds standard phylogenetic approaches. While the extant *Meleagris* species may exhibit distinct and consistent differences between one another, the fossil record does not provide such a luxury with some extinct species (e.g., *Meleagris californica*) that contain individuals (in varying proportions of the sample populations) that have large numbers of qualitative characters present in both extant species (Bochenski and Campbell 2006). Efforts to allocate individual specimens to particular species of *Meleagris* have focused on the use of combinations of qualitative characters and morphometric techniques (Steadman 1980, Bochenski and Campbell 2006). At present, there are no published attempts to produce a cladistic analysis of the extinct and extant taxa of *Meleagris.*

Application of standard phylogenetic coding procedures to the *Meleagris* fossils would result in those taxa (species) having multiple character states for large numbers of characters, while the extant taxa would have many characters coded with only one or few character states. The problem is analogous to examining allelic variation across populations of one species and attempting to determine their interrelatedness based on varying proportions of alleles that are present in all populations (though present in varying numbers of individuals within those populations). Bochenski and Campbell (2006) found that among variable characters within *Meleagris* individuals, *M. gallopavo* and *M. californica* share 45% of variable characters, *M. gallopavo* and *M. ocellata* share 33% of the characters, and *M. ocellata* and *M. californica* share only 9% of the characters. It would be tempting to suggest a close relationship based purely on the shared number of variable characters, but without any indication of those characters' polarity, the number of shared characters alone cannot help.

The oldest non-*Meleagris* species (*Rhegminornis calobates* Wetmore 1943 and *Proagriocharis kimballensis* Martin and Tate 1970) are known only from a partial tarsometatarsus and a coracoid (Steadman 1980). Those two specimens do not preserve what would be the outgroup (and oldest) character states for the majority of bones in the *Meleagris* skeleton. In attempting to determine to which extant species a particular extinct taxon is most closely related (or if outside the crown group of *Meleagris*), the known intraspecies variability of characters likely would obscure any phylogenetic signal among the species. Given this complex situation, additional fossil specimens generally would help to resolve the pattern of character change, but no new species or large collections of fossil *Meleagris* have been located since Steadman's (1980) work.

In the absence of clear character polarity, a researcher reasonably would turn to examining the oldest individuals within a clade. However, there are relatively few Pliocene records of *Meleagris* turkeys (in contrast to the Pleistocene record), and those fossils have been allocated to a variety of different species (Steadman 1980, Bochenski and Campbell

2006). One of those Pliocene species, *Meleagris leopoldi*, is considered distinct by some (Miller and Bowman 1956, Brodkorb 1964), although others believe that it may be synonymous with either the Pliocene *M. anza*, *M. progenes*, the extant *M. gallopavo*, or other fossil material from the Pliocene Inglis 1A site in Florida (Steadman 1980, Morgan and Hurlbert 1995). A phasianid carpometacarpus from the type locality of *M. leopoldi*, apparently collected with the holotype material, but never previously described or discussed, provides information about the status of this fossil species and the early evolution of turkeys.

Abbreviations

MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; **NCSM**, North Carolina State Museum, Raleigh, North Carolina; **PPHM**, Panhandle Plains Historical Museum, Canyon, Texas; **TAMU**, Zooarcheology collection in the Department of Anthropology at Texas A&M University, College Station; **UCLA**, University of California at Los Angeles; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

HISTORY OF THE MATERIAL

In 1937, C.S. Johnston collected the fossils that became the type series (and referred specimens) of *Meleagris leopoldi* with other bird bones at Cita Canyon, Texas. Loye Miller and Johnston (1937) assigned the turkey material from Cita Canyon (UCLA loc. V3721=UCMP loc. V3721) to *Parapavo californicus* Miller 1909. Johnston and Savage (1955) later considered the material identifiable as cf. *Meleagris*. Alden Miller and Bowman described the material (Miller and Bowman 1956) as a new species, *M. leopoldi*, designating the tarsometatarsus (UCMP 45086) as the holotype (and a paratype specimen UCMP 45087). Other paratypes were described with PPHM specimen numbers. Brodkorb (1964) transferred *M. leopoldi* to *Agriocharis*, and Steadman (1980) moved the species back to *Meleagris* (by synonymyzing the genera). Sometime prior to Steadman's work, the Cita Canyon bird material described with UCMP specimen numbers was transferred to PPHM, apparently at the request of the Texas museum. I attempted to contact PPHM to determine their current location and status without success.

Steadman (1980) did not consider the material from Cita Canyon to be very diagnostic and thought that *M. leopoldi* was potentially conspecific with *M. progenes*, *M. gallopavo*, or the Inglis 1A material. Recently, a large phasianid carpometacarpus was located in the UCMP collections from Cita Canyon (UCMP loc. V3721). It has a crossed-out UCLA vertebrate paleontology collection number (UCLA loc. VP2713), and an attached UCLA paper label identifying C.S. Johnston as its collector in 1937 (also associated was a UCMP paper label). UCLA no longer has a vertebrate fossil collection, and the UCMP became the repository for all of the non-bird fossil material in 1999. When discovered, the carpometacarpus was still in the packing material used when the UCMP collections were moved to new facilities from 1994 to 1995. This specimen appears to have resided in the UCMP collections for some time, possibly since the 1930s.

Examination of the UCLA vertebrate fossil catalogue indicates that the crossed-out UCLA specimen number on the specimen was assigned to a bird bone from Cita Canyon collected by Johnston. It is perplexing that although Loye Miller apparently knew of this carpometacarpus when it was catalogued, the specimen was not discussed in his or his son's papers on the turkey material from Cita Canyon. The *Meleagris* carpometacarpus is now catalogued as UCMP 174719 and will be discussed here.

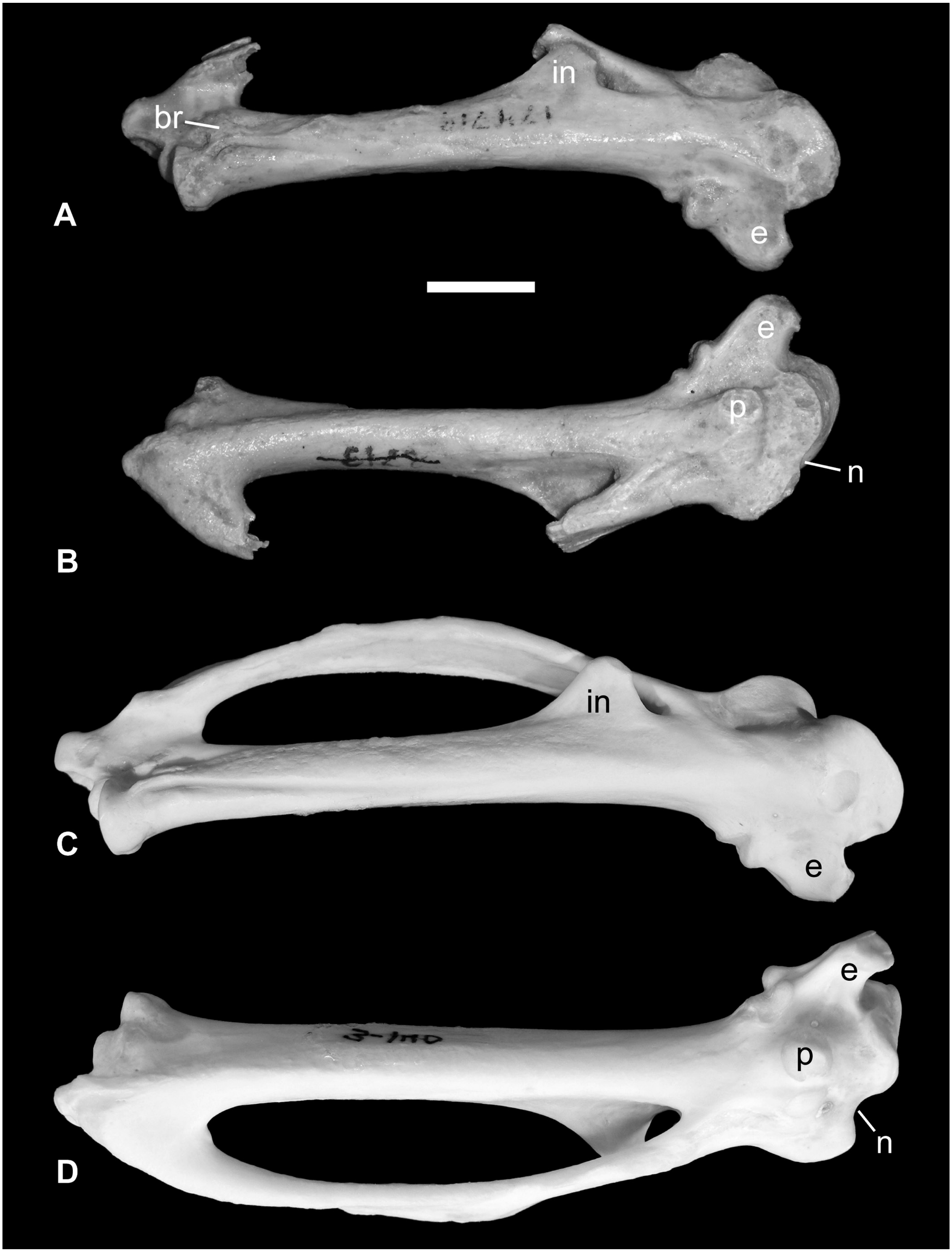
THE CARPOMETACARPUS

The carpometacarpus is from UCMP locality V3721 located in Cita Canyon, Randall County, Texas. The fauna from the site, including other birds (Miller and Bowman 1956), are part of the Blancan North American Land Mammal Age (Savage and Johnston 1955). The Cita Canyon local fauna has been placed in the Blancan V event 6 to 7 subzone (2.6 Ma to 1.9 Ma) of the Blancan North American Land Mammal Age and is late Pliocene in age (Lundelius et al. 1987), not Pleistocene as stated by Brodkorb (1964).

Description

UCMP 174719 is a nearly complete right carpometacarpus, missing most of the shaft of the minor metacarpal and the tip of the pisiform process (Fig. 1). The carpal trochlea is worn. The intermetacarpal process is large, extends to the minor metacarpal meeting it at its dorsal edge. The intermetacarpal process is not fused to the minor metacarpal. The notch in the ventral rim of the carpal trochlea is present and relatively shallow. The groove for the m. digitorum communis is deep at its distal end, and the groove for the m. interosseus passes under a short ossified bridge that is absent in almost all other *Meleagris* specimens (see below). The preserved distal end of the minor metacarpal shaft preserves a small portion of the posterior groove present in other *Meleagris* individuals. The morphology of this bone is like that of other fossil and recent turkeys except for the minor differences discussed below. The total length of the specimen is 67.6 mm, its proximal depth is 20.8 mm, the least depth of metacarpal II is 6.0 mm, and the least width of metacarpal II is 7.9 mm.

► **Figure 1.** The carpometacarpus of *Meleagris leopoldi* (UCMP 174719), **A**. dorsal view. **B**. ventral view. *Meleagris gallpavo* (TAMU 3-140), **C**. dorsal view. **D**. ventral view. Scale bar equals 1 cm. Abbreviations: **br**, bridge over canal for the m. interosseus tendon; **e**, extensor process; **in**, intermetacarpal process; **n**, notch in the ventral rim of the carpal trochlea; and **p**, pisiform process.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The length of the specimen is intermediate between that reported for male and female Inglis 1A material (Steadman 1980). However, the proximal depth, and measurements of metacarpal II (above) are within the range reported for male Inglis 1A turkeys (Steadman 1980). UCMP 174719 is larger than that of the *M. crassipes* Miller 1940 and very similar in size to that of the male *M. progenes* specimen (Steadman 1980). The size of the bone in *M. leopoldi* suggests that UCMP 174719 may be from a male.

The carpometacarpus does not appear to be a very diagnostic element among turkeys (Steadman 1980, Bochenski and Campbell 2006). The ossified bridge over the passage of part of the m. interosseus is an extremely rare character state among *Meleagris* individuals. That bridge has not been reported in any other fossil or extant specimen of *Meleagris* (Steadman 1980, Bochenski and Campbell 2006) despite relatively large collections of material from some species. However, that bridge is present in one specimen (NCSM 16094) of the extant *Meleagris gallopavo*, and what appears to be a closing bridge is present in TAMU 3-140 (Fig. 1). That ossified covering of the ligament is also present in a variety of more distantly related neognathous birds (some anseriforms, some parrots, and some coraciiforms). It is a variable (homoplastic) character among neornithines, but extremely rare among *Meleagris* individuals. At present, I am unaware of any other galliform taxon with this character. Without additional individuals from Cita Canyon, it is impossible to determine whether that character has any phylogenetic significance, relevance to species diagnosis within *Meleagris*, or if it is just the result of an aberrant individual. Despite the variability, this bridge also does not appear to be a purely ontogenetic character because the fusion of the intermetacarpal process to the minor metacarpal occurs relatively late in ontogeny, and fusion is absent in UCMP 174719.

The ventral side of the alular digit articular facet forms a more distinct flange in *M. gallopavo*, *M. occelata*, and *M. crassipes* than in *M. leopoldi.* The pisiform process is relatively closer to the extensor process in *M. gallopavo* than in *M. leopoldi.* The proximal intermetacarpal space in *M. leopoldi* is similar in its size and configuration to that in *M. gallopavo* and *M. occelata*, but not *M. crassipes.* The infratrochlear fossa is somewhat more elongate in *M. leopoldi* than in *M. gallopavo.* The infratrochlear fossa in *M. gallopavo* and *M. leopoldi* is quite different from that in *M. crassipes.* The small fossa at the distal end of the carpal trochlea (in *M. leopoldi* and *M. gallopavo*) is reduced or absent in *M. occelata.* This fossa is the deepest and most extensive in *M. crassipes.* The notch in the ventral rim of the carpal trochlea is shallow and broad in *M. ocellata*, deep and broad or deep and narrow in *M. gallopavo*, and variable in *M. californica* (Bochenski and Campbell 2006). The character state in *M. leopoldi* is shallow and broad (Fig. 1) like that in *M. ocellata* illustrated by Bochenski and Campbell (2006), and that notch most likely has the same morphology as the state in *M. progenes* (Steadman 1980).

DISCUSSION

This carpometacarpus of a turkey from the type locality for *M. leopoldi* most likely is attributable to that species because it is unlikely that multiple species of turkeys were sympatric at Cita Canyon. The *Meleagris* material from Cita Canyon includes bones from at least two individuals (Miller and Bowman 1956). The morphological and size differences (above) indicate that the carpometacarpus allocated here to *M. leopoldi* is distinct from the extant *Meleagris* species, and it maybe from the same taxon as *M. progenes* and the material from Inglis 1A in Florida. The carpometacarpus of *M. anza* is still unknown, and therefore no comparisons are possible. Brodkorb (1964) did not describe the carpometacarpus of *M. progenes* in enough detail to separate it from *M. leopoldi*, nor did he illustrate it. The measurements he presented (Brodkorb 1964) are nearly identical to those of *M. leopoldi.* However, the holotype and referred specimens of *M. progenes* currently are missing, and as a result there is no way to definitively resolve the possibility that *M. progenes* is a junior synonym of *M. leopoldi.* The synonymy of *M. leopoldi* with *M. anza* does not appear as likely as the synonymy of *M. leopoldi* and *M. progenes. M. anza* is Pleistocene, whereas *M. leopoldi* and *M. progenes* are both late Pliocene and were collected within about 250 km of each other. In addition, the morphology of the notch in the ventral rim of the carpal trochlea in UCMP 174719 is not found among extant *M. gallopavo* individuals (Bochenski and Campbell 2006) providing additional evidence that the fossil is different from the extant species. The data from this additional Pliocene carpometacarpus reinforces the previous hypothesis, based on other skeletal elements, that *M. leopoldi* and *M. progenes* are synonyms. In addition, with these data, it seems likely that the Inglis 1A turkey material is also *M. leopoldi* as Steadman (1980) suggested. However, these issues cannot be fully resolved at present until the known material of *M. leopoldi* and *M. progenes* is relocated. Without assessment (and confirmation) of the morphological characters in the holotypes, no phylogenetic hypothesis of relationships among these extinct turkeys can be proposed.

The presence of the character of having a broad shallow notch in the ventral rim of the carpal trochlea (in *M. leopoldi* and reportedly in *M. progenes*) in the Pliocene prior to the earliest occurrence of the other character states (deep and broad or very deep and narrow) in the Pleistocene in *M. californica* and *M. gallopavo* is suggestive that the state in the Pliocene individuals would be the primitive state. The shared presence of this "primitive" trait in *M. progenes* and *M. leopoldi* would not necessarily indicate any particular phylogenetic relationship, but obviously would be expected if they are from the same species. Given the probable synonymy of *M. leopoldi* and *M. progenes*, future efforts to elucidate the phylogeny of turkeys will have one less operational taxonomic unit to include. Additionally, if the Inglis 1A material, *M. progenes*, and *M. leopoldi* are all derived from one late Pliocene species, then that species would have had a broad geographic range extending from Florida through Texas to Kansas. That same geographic range has been occupied by *M. gallopavo* since the Pleistocene (Steadman 1980). The replacement of a late Pliocene species (*M. leopoldi*) in the eastern United States by a Pleistocene species in the same geographic area also is suggestive of an ancestor-descendant or sister group relationship between the extant *M. gallopavo* and extinct *M. leopoldi* species.

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