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**DOVES (COLUMBIDAE) AND CUCKOOS (CUCLIDAE) FROM  
THE EARLY MIOCENE OF FLORIDA**

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# DOVES (COLUMBIDAE) AND CUCKOOS (CUCULIDAE) FROM THE EARLY MIOCENE OF FLORIDA

David W. Steadman<sup>1</sup>

## ABSTRACT

A new genus, *Arenicolumba* (Aves: Columbiformes: Columbidae), is proposed for the fossil species *Columbina prattae* Becker and Brodkorb, 1992. This small dove is known from many hundreds of fossils, representing all major post-cranial skeletal elements, from the early Miocene (ca. 18.5 Ma; Hemingfordian land mammal age) Thomas Farm local fauna, Gilchrist County, Florida. Except for the single humerus of *Gerandia* from the Aquitanian (early Miocene; ca. 22 Ma) of France, *Arenicolumba prattae* is the oldest known member of the family Columbidae. The nearest living relatives of *Arenicolumba* appear to be the African genera *Oena* and *Turtur*. *Thomasococcyx philohippus*, new genus and species (Aves: Cuculiformes: Cuculidae), is also described from the Thomas Farm local fauna. Neotropical ground-dwelling cuckoos in the genera *Morococcyx*, *Tapera*, *Geococcyx*, and *Dromococcyx* may be the closest living relatives of *Thomasococcyx*. Along with *Cursoriococcyx* from the Hemingfordian of Colorado, *Thomasococcyx philohippus* provides evidence that the subfamily of New World ground-dwelling cuckoos (Neomorphae) existed by the early Miocene.

**Key Words:** Florida; Thomas Farm; early Miocene fossils; Hemingfordian land mammal age; Columbidae; Cuculidae.

## TABLE OF CONTENTS

Introduction .....	2
Materials and Methods.....	2
Systematic Paleontology.....	3
Order Columbiformes Family Columbidae.....	3
<i>Arenicolumba</i> n. gen.....	3
Order Cuculiformes Family Cuculidae.....	5
<i>Thomasococcyx philohippus</i> n. gen. & sp.....	5
Cuculidae, gen. uncertain.....	10
Discussion.....	10
Columbiformes.....	10
Cuculiformes.....	13
Acknowledgements.....	14
Literature Cited.....	15

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## INTRODUCTION

The Thomas Farm site (NAD 27; 29.86°N, 82.83°W, elev. 11 m) is a highly fossiliferous, sediment-filled sink-hole in Gilchrist County, Florida (Pratt 1990). The rich mammalian fauna at Thomas Farm indicates a Hemingfordian land mammal age (LMA) in the early Miocene Epoch, approximately 18.5 million years old (Hulbert 2001, MacFadden 2001). Avian fossils from Thomas Farm include at least 29 species in 25 genera and 18 families (DWS personal observation), although only seven of these species have been described until now. Five of the described species have been assigned to extinct genera, namely the accipitrids *Promilio floridanus*, *P. epileus*, and *P. brodkorbi*, the cracid *Boreortalis laesslei*, and the phasianid *Rhegminornis calobates* (Wetmore 1943, 1958, Brodkorb 1954, Olson & Farrand 1974, Steadman 1980, Becker 1987). An apparent anhinga, originally described as a cormorant *Phalacrocorax subvolans* by Brodkorb (1956), was assigned to the living genus *Anhinga* but without details by Becker (1987).

The seventh described species from Thomas Farm is a small columbid, *Columbina prattae* Becker and Brodkorb (1992). This dove is by far the most abundant species of bird at Thomas Farm. Assigning *Columbina prattae* to an extant genus sets this species apart from the rest of the avifauna, with the exception of *Anhinga subvolans*. In this paper I re-examine the osteology of *C. prattae*, and conclude that this dove is like most other birds (and all mammals; Hulbert 2001, MacFadden 2001) from Thomas Farm in being generically distinct from living species.

I also describe a new genus and species of cuckoo (Cuculidae), a family previously unreported from Thomas Farm and with a limited fossil record in North America.

## MATERIALS AND METHODS

The fossils from Thomas Farm are housed in the Division of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida. Certain of the fossils, formerly in the private collection of Pierce Brodkorb, have the catalogue prefix UF/PB. Some of the modern skeletons also were originally in the private collection of Pierce Brodkorb; these specimens have a PB catalogue number and a UF catalogue number assigned in the 1990s. Both the UF and PB numbers are listed for these specimens in the figure legends. UF is used as a prefix for both the fossils housed in the Vertebrate Paleontology Collection and for modern skeletons housed in the Ornithology Collection.

I compared the fossils with the following modern UF skeletons, supplemented by specimens from the University of Kansas Natural History Museum (KU), and the Louisiana State University Museum of Zoology (LSUMZ) — *Columbina passerina* UF 40074, 43317, *C. talpacoti* UF 41837, *C. buckleyi* UF 41837, *C. picui* UF 38965, *C. minuta* UF 38786, *C. cruziana* LSUMZ 48726, 81201, *Claravis pretiosa* UF 38787, *Scardafella inca* UF 40806, *Metriopelia melanopectera* UF 39346, *M. ceciliae* UF 38788, *Geotrygon montana* UF 33846, *G. chrysis* UF 40006, *Zenaida macroura* UF 40939, *Z. aurita* UF 40007, *Z. asiatica* LSUMZ 89696, *Leptotila verreauxi* UF 41097, *L. jamaicensis* UF 40027, and *Patagioenas* [formerly *Columba*] *leucocephala* UF 42212. In addition to these 18 species from the Americas, I also examined modern skeletons of seven Old World species of Columbidae — *Oena capensis* UF 38785, *Turtur chalcospilos* UF 38782, *Streptopelia capicola* UF 38781, *Columba guinea* UF 38769, *Ducula pistrinaria* UF 40186, *Geopelia cuneata* UF 32379, and *Gallicolumba jobiensis* UF 41460.

For the Cuculidae (sequence and subfamilial classification follow Payne 2005), I examined modern skeletons of these New World species: Crotophaginae — *Guira guira* UF 38969, *Crotophaga major* KU 32390, *C. ani* UF 40013, 42473, *C. sulcirostris* UF 33855, 40789; Neomorphae — *Tapera naevia* UF 38735, *Dromococcyx phasianellus* KU 91388, *D. pavoninus* LSUMZ 101257, *Morococcyx erythropygus* UF 16796, 26250, 26251, 38737, *Geococcyx californianus* UF 26238, *G. velox* UF 38729, *Neomorphus rufipennis* KU 86604, *N. geoffroyi* LSUMZ 106946; Cuculinae — *Coccyzua* (*Piaya*) *minuta* UF 26232, *Piaya cayana* UF 40787, *P. melanogaster* KU 88663, *Coccyzus americanus* UF 40346, *C. minor* UF 40029, *Coccyzus* (*Hyetornis*) *pluvialis* UF 26233, and *Coccyzus* (*Saurothera*) *merlini* UF 42489. Skeletons of these Old World species also were examined: Centropodinae — *Centropus superciliosus* UF 33856; Cuculinae — *Zanclostomus* (*Phaenicophaeus*) *javanicus* UF 42704, *Phaenicophaeus* (*Rhopodytes*) *viridirostris* UF 26237, *Clamator jacobinus* UF 38730, *Eudynamis scolopacea* UF 41473, *Chrysococcyx lucidus* UF 39450, and *Cuculus canorus* UF 35289. For the Musophagidae, I examined skeletons of *Corythaëola cristata* UF 38728, *Corythaixoides concolor* UF 38719, *Crinifer piscator* UF 38718, *Musophaga rossae* UF 38727, and *Tauraco corythaix* UF 38726.

Measurements were taken with digital calipers, read to the nearest 0.01 mm. Specimens were examined with a Leica MZ8 stereomicroscope, and photo-

graphed with a Sony DSC-R1 camera. Osteological terminology is from Howard (1929) and Baumel et al. (1993). Character polarities were not proposed because of a lack of strong, consistent evidence of which families would be appropriate as outgroups for the Columbidae or Cuculidae.

SYSTEMATIC PALEONTOLOGY  
Order Columbiformes (Latham 1790)  
Family Columbidae (Illiger 1811)

Six of the seven characters (based on three skeletal elements) that Becker and Brodkorb (1992) used to assign the species *prattae* to the genus *Columbina* are, in fact, found in many living genera of Columbidae worldwide. Their seventh character [“the dorsal surface of trochlea IV extending dorsad (in distal view) past the level of trochlea III”] does distinguish the tarsometatarsus of *Columbina* sensu lato (i.e., including *Claravis*, *Scardafella*, and *Metriopelia*) from that of *Geotrygon*, *Zenaida*, *Leptotila*, and *Patagioenas* but not from that in Old World genera such as *Turtur* and *Ducula*.

In the diagnosis of the new genus, I will begin with the tarsometatarsus since that is the holotype (UF 106594) of *Columbina prattae* as well as the skeletal element with the largest number of diagnostic characters.

*Arenicolumba* n. gen.

Diagnosis.—A small columbid (Table 1) that differs from other genera (especially *Columbina*, *Claravis*, *Scardafella*, *Metriopelia*, *Geotrygon*, *Zenaida*, *Leptotila*, and *Patagioenas*) as follows. Tarsometatarsus (Fig. 1B, C): 1, in acrotarsial aspect, intercotylar knob with flatter proximal surface (less rounded, less pointed); 2, facet for hallux located more proximad than in all genera except *Patagioenas*; 3, larger foramen vasculare distale; 4, crista plantare lateralis more distinct than in all genera except *Geotrygon*; 5, in both plantar and acrotarsial aspect, the articulating surface of trochlea metatarsi III shorter than in all genera except *Patagioenas*; 6, in distal aspect, trochlea metatarsi III wide relative to its depth; 7, central groove in trochlea metatarsi III deeper. Tibiotarsus (Fig. 2B): 8, inci-

Table 1. Measurements (in mm) of *Arenicolumba prattae* (Hemingfordian LMA, Thomas Farm, Florida) compared with those of adult skeletons of two widespread, living North American species, *Columbina passerina* and *Zenaida macroura* (F = female, M = male).

	Coracoid: depth of processus acrocoracoideus	Tibiotarsus: distal width	Tarsometatarsus: distal width (without medio-plantar process)
<i>Arenicolumba prattae</i>	2.47	3.39	4.09
Thomas Farm fossils	2.08–2.69	3.33–3.42	4.02–4.22
	18	3	3
<i>Columbina passerina</i> F	2.05	2.83	3.28
Florida	1.86–2.13	2.65–2.97	3.12–3.50
	12	12	12
<i>Columbina passerina</i> M	2.15	2.82	3.35
Florida	1.96–2.28	2.48–3.20	3.17–3.50
	14	14	14
<i>Zenaida macroura</i> F	3.11	3.97	4.53
Florida	2.92–3.32	3.80–4.22	4.29–4.77
	20	20	20
<i>Zenaida macroura</i> M	3.30	4.08	4.66
Florida	3.07–3.63	3.79–4.27	4.38–4.95
	20	20	20



Figure 1. The tarsometatarsus of columbids in acrotarsial (upper row) and plantar (lower row) aspects. A. *Columbina passerina* UF 40074. B. *Arenicolumba prattae* UF 62093. C. *Arenicolumba prattae* UF 219393. D. *Oena capensis* UF 38785 [PB 39624]. E. *Turtur chalcospilos* UF 38782 [PB 36021]. Scale = 10 mm.

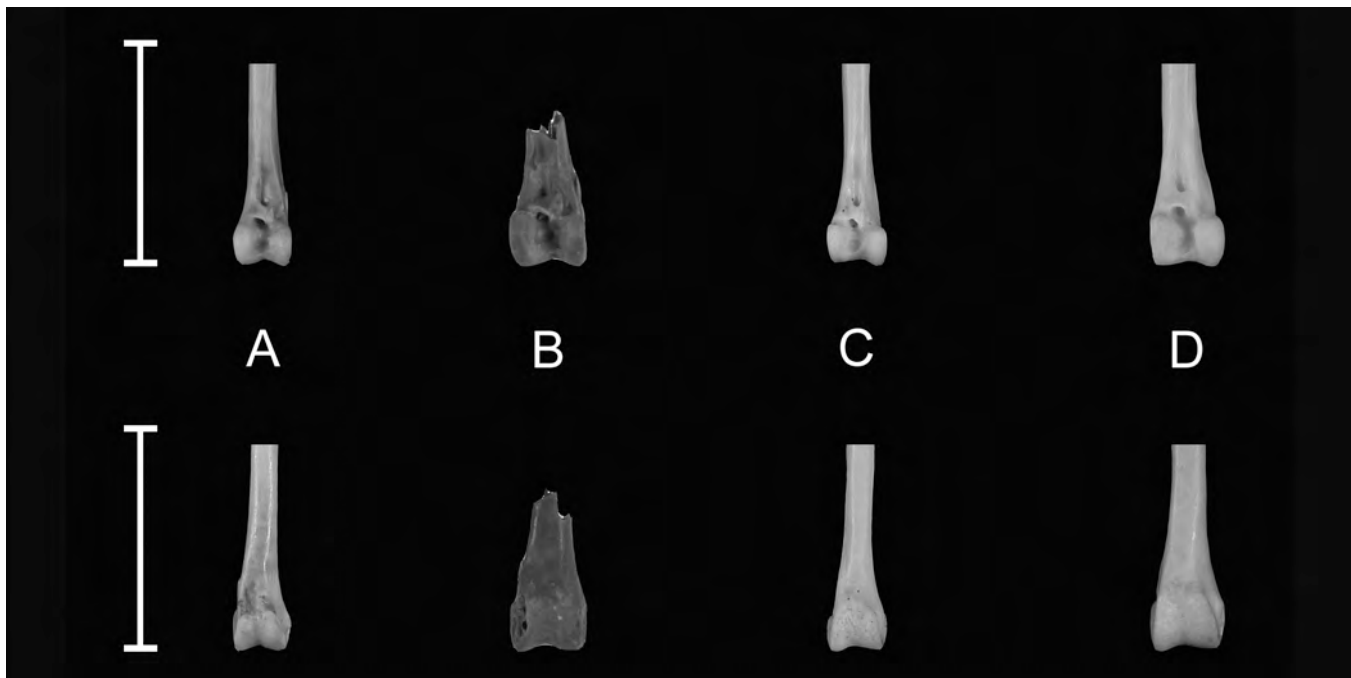


Figure 2. The tibiotarsus of columbids in dorsal (upper row) and ventral (lower row) aspects. A. *Columbina passerina* UF 40074. B. *Arenicolumba prattae* UF 96296. C. *Oena capensis* UF 38785 [PB 39624]. D. *Turtur chalcospilos* UF 38782 [PB 36021]. Scale = 10 mm.

surra intercondylaris relatively wide (condylus medialis and condylus lateralis relatively narrow). Sternum (Fig. 3B): 9, rostrum sterni (manubrium) more elongate. Coracoid (Fig. 4B, C): 10, in dorsal aspect, processus procoracoideus extends farther sternally. Humerus (Fig. 5B, C): 11, incisura capitis extends farther dorso-ventrally to wrap around the ventral margin of tuberculum ventral and separate it more from corpus humeri.

Type species.—*Arenicolumba prattae* is the type and only known species in the genus.

Etymology.—From the Latin *arena*, a feminine word that means “sand, sandy place” (Brown 1956:678) and the Latin *columba*, a feminine word meaning “dove, pigeon” (Brown 1956: 278). The second *a* in *arena* becomes a linking *i* because it looks and sounds better this way (Winston 1999: 163). The name *Arenicolumba* refers to the sandy sediment at Thomas Farm (see Pratt 1990) in which fossils of this dove and other small vertebrates are commonly found.

Remarks.—The 11 diagnostic characters of *Arenicolumba* also distinguish it from the seven Old World genera of Columbidae (see MATERIALS AND METHODS) except for agreement with *Oena* in characters 1, 3, 5, 9, and 10, with *Turtur* in characters 2, 3, 5-7, and 10, with *Streptopelia* in character 4, with *Columba* in characters 4 and 10, with *Ducula* in characters 2 and 4, with *Geopelia* in characters 4 and 10, and with *Gallicolumba* in characters 4-6 and 10.

Note in the diagnosis that *Arenicolumba* differs in all 11 diagnostic characters from all four New World genera/subgenera (depending on classification) of small columbids, namely *Columbina*, *Claravis*, *Scardafella*, and *Metriopelia*. Agreement with *Oena* and *Turtur* in

five and six of these 11 characters, respectively, suggests that *Arenicolumba* may be more closely related to these genera than to any extant New World genus of Columbidae. Today, the single species of *Oena* and the five species of *Turtur* are confined to Africa (Gibbs et al. 2001).

#### Order CUCULIFORMES (Wagler 1830)

##### Family CUCULIDAE Vigors 1825

A set of 12 fossils representing five skeletal elements is referred to the Cuculidae because of this combination of characters. Tarsometatarsus: two hypotarsal canals; intercotylar knob prominent; in plantar aspect, fused area of cristae hypotarsi short; in proximal aspect, cotyla medialis square; corpus tarsometatarsi relatively uniform in width, and much wider than deep; trochlea lateralis greatly elevated, dorso-ventrally expanded, and antero-posteriorly compressed. Coracoid: facies articularis sternalis developed on both dorsal and ventral surfaces; facies articularis sternalis evenly developed on dorsal surface. Scapula: facies articularis humeralis well elevated from corpus scapulae; acromion blunt in dorsal aspect; corpus scapulae of uniform depth through much of its length. Humerus: distal end greatly expanded ventrad, yielding an elongated processus flexorius and epicondylus ventralis; fossa musculo brachialis distinct and oval. Mandibular ramus: similar in thickness, curvature, and overall proportions to that in *Tapera* and *Morococcyx*.

##### *Thomasococcyx philohippus* n. gen. & sp.

Holotype.—Proximal end of right tarsometatarsus, UF 96268 (Fig. 6A), Thomas Farm local fauna

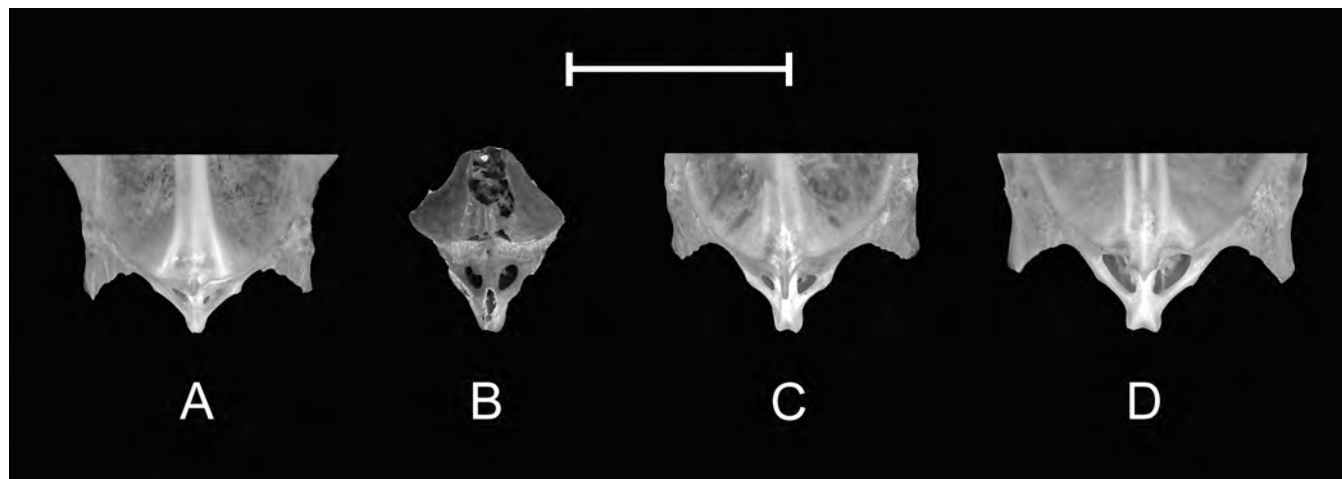


Figure 3. The sternum of columbids in ventro-anterior aspect. A. *Columbina passerina* UF 40074. B. *Arenicolumba prattae* UF 219359. C. *Oena capensis* UF 38785 [PB 39624]. D. *Turtur chalcospilos* UF 38782 [PB 36021]. Scale = 10 mm.

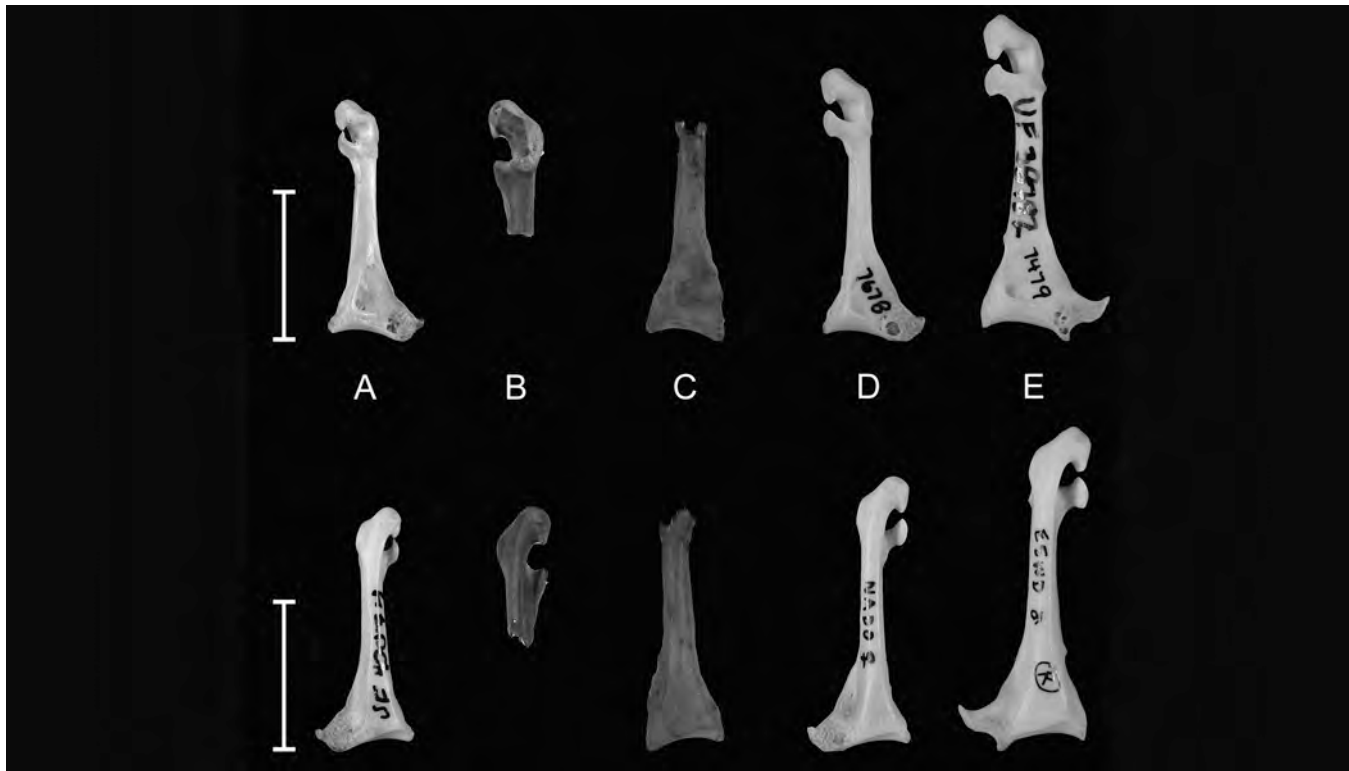


Figure 4. The coracoid of columbids in dorsal (upper row) and ventral (lower row) aspects. A. *Columbina passerina* UF 40074. B. *Arenicolumba prattae* UF 223384. C. *Arenicolumba prattae* UF/PB 6503. D. *Oena capensis* UF 38785 [PB 39624]. E. *Turtur chalcospilos* UF 38782 [PB 36021]. Scale = 10 mm.

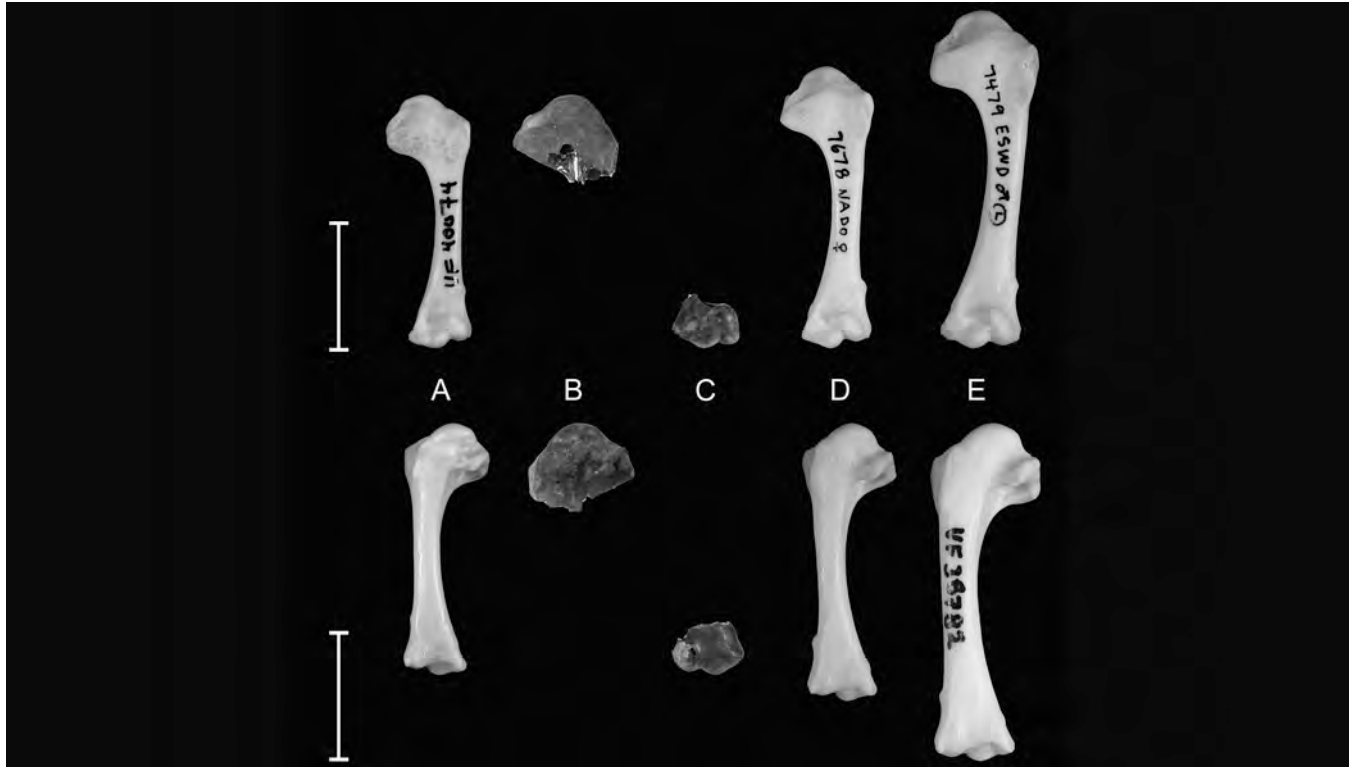


Figure 5. The humerus of columbids in palmar (upper row) and anconal (lower row) aspects. A. *Columbina passerina* UF 40074. B. *Arenicolumba prattae* UF 223471. C. *Arenicolumba prattae* UF 223408. D. *Oena capensis* UF 38785 [PB 39624]. E. *Turtur chalcospilos* UF 38782 [PB 36021]. Scale = 10 mm.

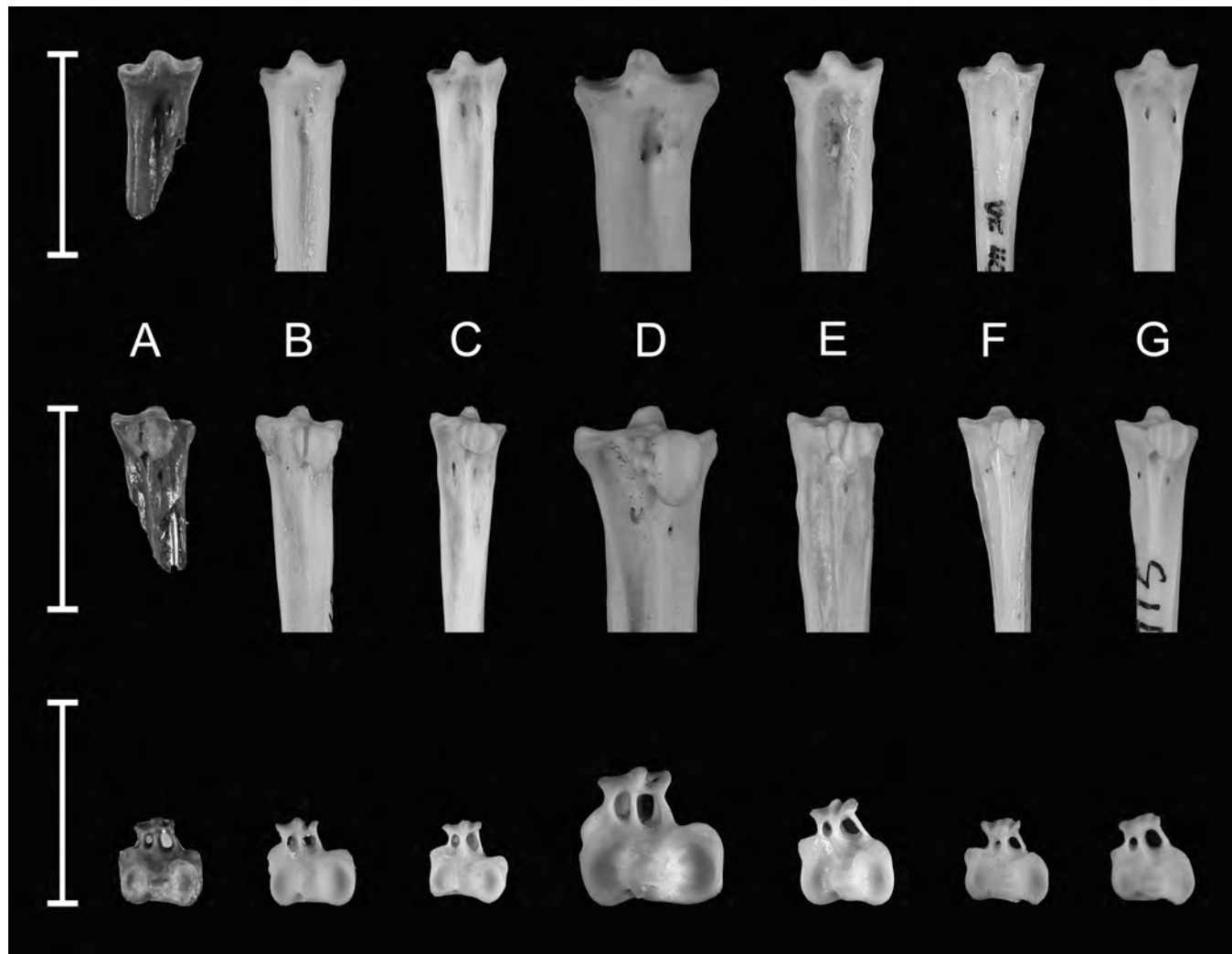


Figure 6. The proximal end of the tarsometatarsus of cuculids in acrotarsial (upper row), plantar (middle row), and proximal (lower row) aspects. A. *Thomasococcyx philohippus* UF 96268 (Neomorphinae). B. *Morococcyx erythropygus* UF 38737 [PB 29340] (Neomorphinae). C. *Tapera naevia* UF 38735 [PB 22915] (Neomorphinae). D. *Geococcyx velox* UF 38729 [PB 17647] (Neomorphinae). E. *Crotophaga sulcirostris* UF 40789 (Crotophaginae). F. *Coccyzus americanus* UF 40346 (Cuculinae). G. *Clamator jacobinus* UF 38730 [PB 27715] (Cuculinae). Scale = 10 mm.

(Hemingfordian LMA), Gilchrist County, Florida.

Paratypes.—Distal ends of tarsometatarsi UF 96268, 106406, 106595, 106735, 223532 (Fig. 7A), mandibular rami UF 219354, 219355, sternal end of coracoid UF 106422 (Fig. 8A), coracoidal ends of scapulae UF 106451, 106638 (Fig. 9A), distal end of humerus UF 223499 (Fig. 10A), all from the Thomas Farm local fauna (Hemingfordian LMA), Gilchrist County, Florida.

Diagnosis.—A medium-sized, presumably ground-dwelling cuckoo defined by the following combination of characters. Tarsometatarsus: cotyla lateralis more anconally protrudent than in *Cursoricoccyx*; foramina hypotarsi relatively larger than in *Cursoricoccyx*; hypotarsus extends more mediad than in *Cursoricoccyx*;

sulcus extensorius relatively deeper than in *Cursoricoccyx*, *Geococcyx*, *Neomorphus*, *Coccyzus*, *Clamator*, *Chrysococcyx*, or *Cuculus*; sulcus extensorius relatively narrower than in *Guira*, *Crotophaga*, *Dromococcyx*, *Geococcyx*, *Neomorphus*, *Coccyzus*, *Piaya*, *Centropus*, *Phaenicophaeus*, *Clamator*, *Eudynamys*, *Chrysococcyx*, or *Cuculus*; combined depth and width of sulcus extensorius most similar to the condition in *Tapera* and *Morococcyx*; corpus tarsometatarsi narrower relative to its depth than in any other genus, this difference being most pronounced compared to specimens of Old World genera; foramen vasculare distale larger than in all other genera. Coracoid: resembles that in *Crotophaga*, *Morococcyx*,



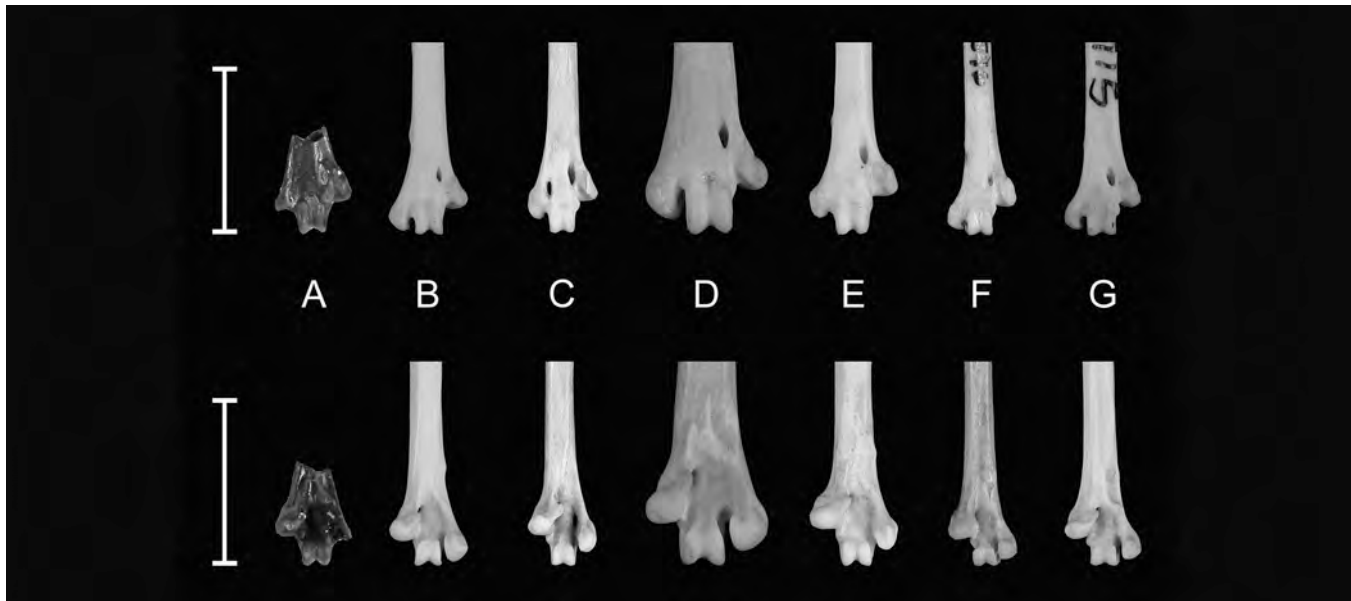


Figure 7. The distal end of the tarsometatarsus of cuculids in acrotarsial (upper row) and plantar (lower row) aspects. A. *Thomasococcyx philohippus* UF 223532 (Neomorphinae). B. *Morococcyx erythropygus* UF 38737 [PB 29340] (Neomorphinae). C. *Tapera naevia* UF 38735 [PB 22915] (Neomorphinae). D. *Geococcyx velox* UF 38729 [PB 17647] (Neomorphinae). E. *Crotophaga sulcirostris* UF 33855 (Crotophaginae). F. *Coccyzus americanus* UF 40346 (Cuculinae). G. *Clamator jacobinus* UF 38730 [PB 27715] (Cuculinae). Scale = 10 mm.

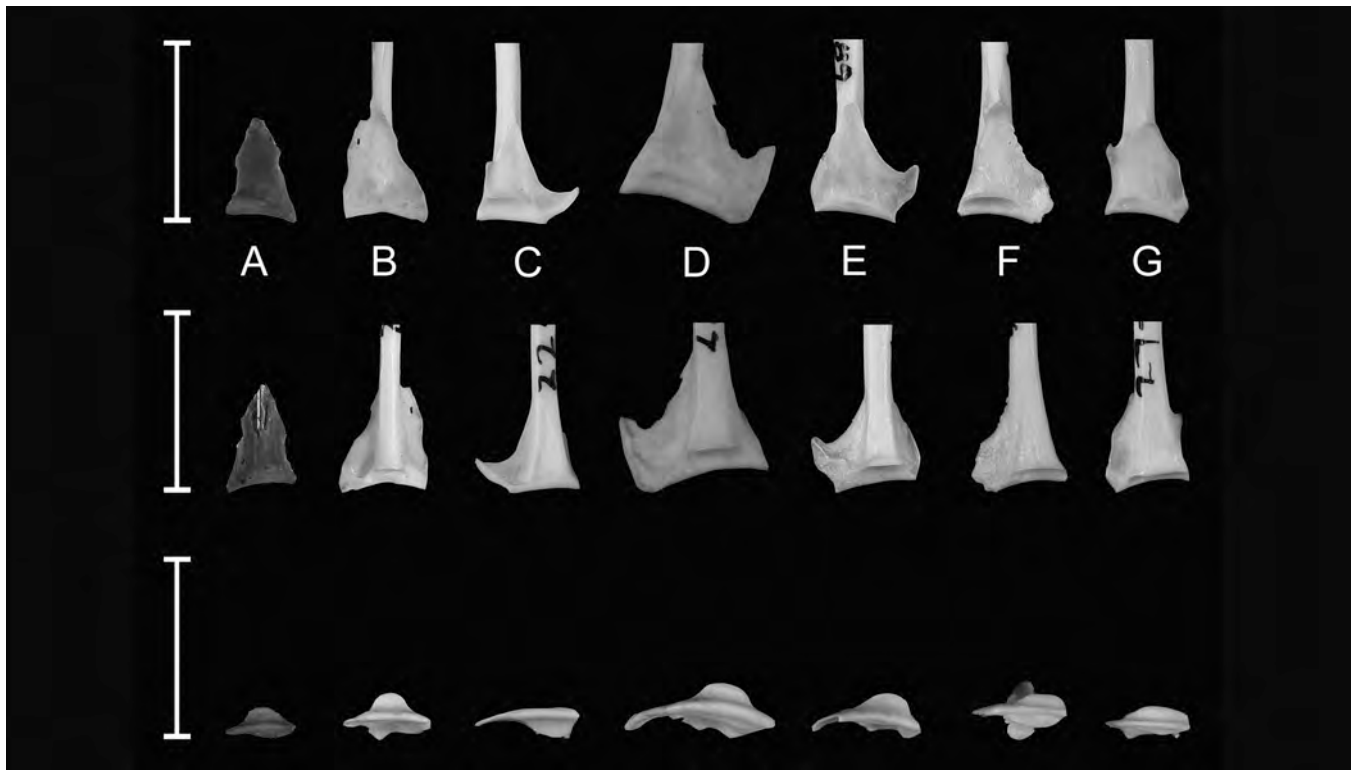


Figure 8. The coracoid of cuculids in dorsal (upper row), ventral (middle row), and sternal (lower row) aspects. A. *Thomasococcyx philohippus* UF 106422 (Neomorphinae). B. *Morococcyx erythropygus* UF 38737 [PB 29340] (Neomorphinae). C. *Tapera naevia* UF 38735 [PB 22915] (Neomorphinae). D. *Geococcyx velox* UF 38729 [PB 17647] (Neomorphinae). E. *Crotophaga sulcirostris* UF 40789 (Crotophaginae). F. *Coccyzus americanus* UF 40346 (Cuculinae). G. *Clamator jacobinus* UF 38730 [PB 27715] (Cuculinae). Scale = 10 mm.



Figure 9. The scapula of cuculids in dorsal aspect. A. *Thomasococcyx philohippus* UF 106638 (Neomorphinae). B. Cuculidae sp. UF/PB 6487. C. *Morococcyx erythropygus* UF 38737 [PB 29340] (Neomorphinae). D. *Tapera naevia* UF 38735 [PB 22915] (Neomorphinae). E. *Geococcyx velox* UF 38729 [PB 17647] (Neomorphinae). F. *Crotophaga sulcirostris* UF 40789 (Crotophaginae). G. *Coccyzus americanus* UF 40346 (Cuculinae). H. *Clamator jacobinus* UF 38730 [PB 27715] (Cuculinae). Scale = 10 mm.

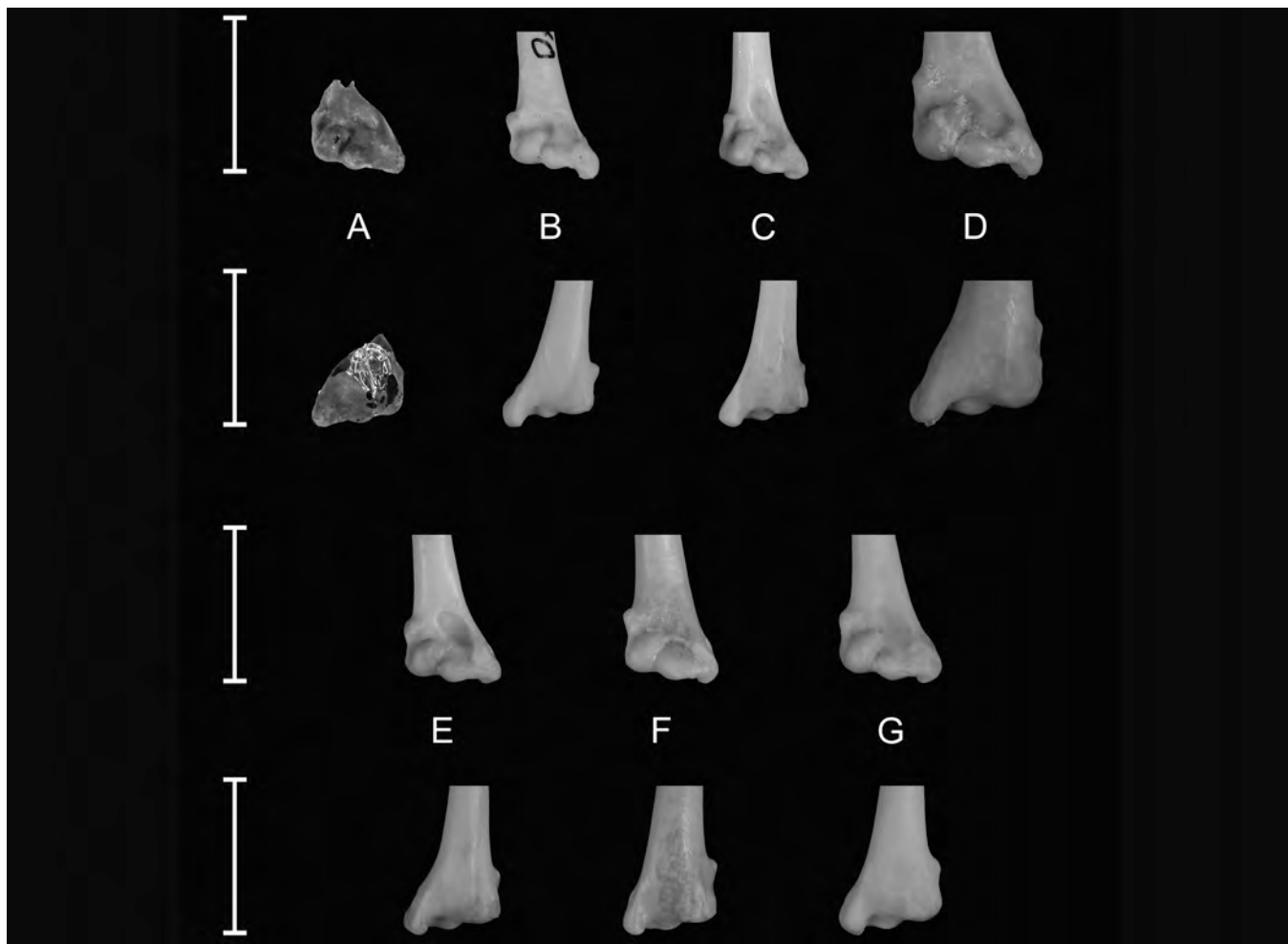


Figure 10. The humerus of cuculids in palmar (upper row) and anconal (lower row) aspects. A. *Thomasococcyx philohippus* UF 223499 (Neomorphinae). B. *Morococcyx erythropygus* UF 38737 [PB 29340] (Neomorphinae). C. *Tapera naevia* UF 38735 [PB 22915] (Neomorphinae). D. *Geococcyx velox* UF 38729 [PB 17647] (Neomorphinae). E. *Crotophaga sulcirostris* UF 40789 (Crotophaginae). F. *Coccyzus americanus* UF 40346 (Cuculinae). G. *Clamator jacobinus* UF 38730 [PB 27715] (Cuculinae). Scale = 10 mm.

*Geococcyx*, and *Neomorphus* more than in other genera in the medial-lateral placement of, and great dorsal-ventral depth of, the ventral shelf of facies articularis sternalis (and resulting bulge of corpus coracoidei); agrees with that in *Tapera*, *Morococcyx*, and *Geococcyx*, but differs from that in other genera, in having a shallow but sterno-humerally expanded dorsal component of facies articularis sternalis. Scapula: relative to overall size of the bone, facies articularis humeralis smaller than in all other genera, and less elongate than in all New World genera; acromion less elongate than in *Guira*, *Crotophaga*, *Tapera*, *Dromococcyx*, and *Neomorphus*; facies lateralis of corpus scapulae, between facies articularis clavicularis and facies articularis humeralis, more concave than in all New World genera except *Guira* and *Neomorphus*. Humerus: processus flexorius smaller (less expanded posteriorly) than in all genera except *Dromococcyx* and *Geococcyx*.

Etymology.— *Thomasococcyx* is from Thomas, referring to the Thomas Farm locality, and *coccyx* (from the Greek *kokkyx*, m., cuckoo; Brown 1956:216, 241). The Thomas family still cultivates much of the land surrounding the fossil site. *Thomasococcyx* is masculine. *philohippus* is from *philos* (Greek, m., dear one, friend; Brown 1956:355) and *hippos* (Greek, m., horse; Brown 1956:423), an allusion to the three genera and species of three-toed horses (see MacFadden 1992, 2001) that shared the northern Florida landscape with this cursorial cuckoo in the early Miocene. One of these horses, *Parahippus leonensis*, is particularly common at Thomas Farm (Hulbert 1984, 2001). The name *philohippus* is a masculine noun in apposition.

Remarks.— *Thomasococcyx philohippus* is the type and only known species in the genus. The tarsometatarsus of *Thomasococcyx* is most similar qualitatively to that in *Tapera* and *Morococcyx* among living genera of cuckoos, whereas the coracoid and scapula are most similar qualitatively to those in *Morococcyx* and *Geococcyx*. The humerus of *Thomasococcyx* is most similar qualitatively to that in *Dromococcyx* and *Geococcyx*. Thus, *Thomasococcyx* is, as far as can be determined now, a mosaic of living genera of Neomorphinae.

The coracoid, scapula, humerus, and tarsometatarsus of *Thomasococcyx philohippus* are all about the size of the same elements in *Morococcyx erythropygus* (Table 2), and therefore I interpret these four skeletal elements to belong to the same extinct species. I am somewhat less confident about referral of the two mandibular rami (UF 219354, 219355) to *Thomasococcyx*, given the great variation in bill depth among living genera of cuckoos. Nevertheless, these

two fossils respectively represent 8.5 mm (left) and 11.5 mm (right) lengths of the fused prearticular, articular, and dentary of what is likely to have been a single mandibular ramus that was similar in size to that of *Morococcyx* (as well as *Tapera* and *Dromococcyx*).

#### Cuculidae, gen. uncertain

Material.—Scapula lacking distal end, UF/PB 6487 (Fig. 9).

Description.— This scapula compares closely in overall size to that of *Guira guira*, *Crotophaga ani*, *Coccyzus (Saurothera) merlini*, and *Piaya cayana*. It is much too large to pertain to *Thomasococcyx philohippus* (Table 2), from which it differs further by having a much more dorsally flared facies articularis clavicularis as in *Tapera* or *Crotophaga*. UF/PB 6478 is approximately the right size for *Cursoriococcyx gertrudae* (Hemingfordian of Colorado; Martin and Mengel 1984), based on extrapolation from the size of the coracoid and carpometacarpus in the latter. More material of this large cuckoo from Thomas Farm is needed before it can be characterized further.

## DISCUSSION

### COLUMBIFORMES

Compared to many other non-passerine orders of birds, the Columbiformes (traditionally but probably erroneously considered to consist of Pteroclididae + Columbidae) has a poor fossil record in the Tertiary. The Pteroclididae (sandgrouse) is represented by several Paleogene (late Eocene – early Oligocene) fossils from Europe that represent two extinct genera with no apparent links to the Columbidae (*Archaeoganga*, *Leptoganga*; Mourer-Chauviré 1992, 1993). I see no characters in *Arenicolumba* that would link it more than any other columbid to the Pteroclididae or any other family.

The Columbidae has no Paleogene fossil evidence at all, even among the very rich European and North American avifaunas of the Eocene and Oligocene, where the first evidence of many if not most living orders and families of non-passerine birds is found (James 2005, Mayr 2005). Nothing in the fossil record of columbids or of birds in general supports the Cretaceous origin of Columbiformes proposed by Pereira et al. (2007) from mitochondrial and nuclear genetic sequences. Because the Columbiformes almost certainly did not exist in the Cretaceous, one need not invoke the breakup of Gondwana as an essential part of their historic biogeography. Nevertheless, the Columbiformes may have originated in the Southern hemisphere (Olson 1989), an idea supported by their absence in the rich Paleogene fossil

Table 2. Measurements (in mm) of *Thomasococcyx philohippus*, new genus and species (Hemingfordian LMA, Thomas Farm, Florida) compared to those of *Cursoriococcyx gertrudae* (Hemingfordian LMA, Martin Canyon, Colorado), an indeterminate cuculid from Thomas Farm, and adult skeletal elements of modern species of Cuculidae.

Species	Mandible: depth at junction of dentary and surangular	Coracoid: sternal width and depth	Coracoid: length through scapular and glenoid facets	Scapula: length and width of		Humerus: distal width	Carpometacarpus: proximal width	Tarsometatarsus: proximal width	Tarsometatarsus: proximal depth	Tarsometatarsus: minimum depth of corpus tarsometatarsi
				facies articularis humeralis	scapulae					
<i>Thomasococcyx philohippus</i> , new species	2.15 (UF 219355) 2.18 (UF 219354)	4.03, 1.90 (UF 106422)	---	2.48, 1.91 (UF 106451) 2.47, 1.69 (UF 106638)	1.89 (UF 106451) 1.67 (UF 106638)	6.30 (UF 223499)	---	4.22 (UF 96268)	4.51 (UF 96268)	1.14 (UF 106406)
<i>Cursoriococcyx gertrudae</i> KUVVP 25629-25631	---	---	5.51 (KUVVP 25630)	---	---	---	6.03 (KUVVP 25631)	5.68 (KUVVP 25629)	5.57 (KUVVP 25629)	---
Cuculidae sp. Thomas Farm UF/PB 6487	---	---	---	3.18, 2.29	2.12	---	---	---	---	---
<i>Gaira guira</i> UF 38969	3.58	5.84, 2.62	5.51	3.49, 2.28	2.10	7.96	5.86	5.49	5.71	1.48
<i>Crotophaga major</i> KU 32390	5.32	7.64, 2.20	5.30	3.83, 2.32	2.26	9.56	---	6.10	6.73	1.49
<i>Crotophaga ani</i> UF 42473	4.53	5.71, 2.38	4.48	3.41, 2.51	1.95	7.62	5.48	5.58	5.58	1.47
<i>Crotophaga sulcirostris</i> UF 40789	3.81	4.91, 1.94	3.64	2.59, 1.89	1.67	6.17	4.63	4.21	4.78	1.23
<i>Tapera naevia</i> UF 38735	2.33	3.92, 1.63	3.37	2.52, 1.48	1.48	5.76	4.29	4.00	3.84	0.99
<i>Dromococcyx phasianellus</i> KU 91388	2.28	5.91, 2.23	4.62	3.04, 2.48	2.00	8.42	---	4.59	5.06	1.25
<i>Dromococcyx pavoninus</i> LSUMZ 101257	2.04	4.03, 1.71	---	2.50, 1.71	1.53	7.25	---	3.98	4.29	---
<i>Morococcyx erythropygus</i> UF 38737	2.64	4.59, 1.54	3.55	2.34, 1.85	1.60	5.71	3.87	4.20	4.14	1.25
<i>Geococcyx californianus</i> UF 26238	4.90	8.78, 3.49	6.27	3.60, 2.70	2.50	9.74	7.26	8.24	8.33	2.41

Table 2. (Cont.)

Species	Mandible: depth at junction of dentary and surangular	Coracoid: sternal width and depth	Coracoid: length through scapular and glenoid facets	Scapula: length and width of facies articularis humeralis	Scapula: width of corpus scapulae	Humerus: distal width	Carpometacarpus: proximal width	Tarsometatarsus: proximal width	Tarsometatarsus: proximal depth	Tarsometatarsus: minimum depth of corpus tarsometatarsi
<i>Geococcyx velox</i> UF 38729	4.14	7.32, 2.18	5.09	3.86, 2.45	2.40	8.43	6.07	7.07	6.68	2.13
<i>Neomorphus rufipennis</i> KU 86604	4.77	7.79, 2.36	5.96	4.07, 2.54	2.37	9.19	---	8.44	8.49	2.31
<i>Neomorphus geoffroyi</i> LSUMZ 106946	5.41	8.73, 2.32	---	4.67, 3.40	2.83	10.54	---	9.41	9.23	2.62
<i>Coccyzus (Piaya) minuta</i> UF 26232	1.98	3.42, 1.48	3.14	1.86, 1.52	1.20	5.38	3.82	3.53	3.50	0.92
<i>Piaya cayana</i> UF 40787	3.32	5.56, 1.51	4.10	2.93, 2.08	2.00	7.77	5.76	5.43	5.56	1.43
<i>Piaya melanogaster</i> UF 40787	3.53	6.50, 1.80	4.26	2.87, 2.28	2.13	7.56	---	5.72	5.23	1.87
<i>Coccyzus americanus</i> UF 40346	2.90	4.66, 1.82	4.03	2.43, 1.85	1.63	6.04	5.14	4.25	4.11	1.19
<i>Coccyzus minor</i> UF 40029	3.00	5.43, 2.00	3.91	2.46, 1.90	1.61	6.24	5.10	4.69	4.63	1.18
<i>Coccyzus (Hytornis) pluvialis</i> UF 26233	---	7.17, 2.33	5.25	3.79, 2.81	2.43	9.29	---	---	---	---
<i>Coccyzus (Saurorhina) merlini</i> UF 42489	4.90	5.96, 1.81	4.31	3.21, 2.26	2.23	7.45	5.56	6.40	6.24	1.68
<i>Centropus superciliosus</i> UF 33856	4.02	6.62, 3.25	5.25	3.84, 2.43	2.13	8.25	6.41	6.46	6.70	2.00
<i>Zanclus (Phaenicochaetus) javanicus</i> UF 42704	3.08	5.56, 1.70	3.70	2.87, 1.94	1.67	7.11	5.26	4.68	4.78	1.19
<i>Clamator jacobinus</i> UF 38730	2.46	4.27, 1.56	3.75	2.41, 1.86	1.53	6.38	5.08	3.98	4.36	1.09

record of Europe and North America.

The abundant specimens of *Arenicolumba prattae* from Thomas Farm represent the New World's earliest record of Columbidae. The only earlier fossil assigned to the Columbidae is the single humerus of *Gerandia calcaria* from the early Miocene (Aquitanian; ca. 22 ma) of Saint Gérard-le-Puy, France (Lambrecht 1933, Brodkorb 1971, Olson 1985). Continental fossils of columbids that are younger than *Arenicolumba*, mainly from the northern hemisphere, seem to represent modern genera (Olson 1985, Becker and Brodkorb 1992). Columbids do have an extensive Quaternary fossil record, especially on tropical oceanic islands where considerable anthropogenic extinction of species and even genera is documented (Steadman 1992, 2006, Pregill et al. 1994).

The family Columbidae is broadly distributed in temperate and tropical regions today. Its greatest generic and species-level diversity is in the Australian-Papuan-Oceanic region (Steadman 2006), where the substantial morphological and ecological diversity of pigeons and doves stands in marked contrast to the more uniform morphology and ecology of New World columbids.

In eight genetically-based cladograms of living columbid genera by Pereira et al. (2007), *Oena* and *Turtur* (the two living genera most similar to the extinct *Arenicolumba*) are rather derived although often with low posterior probabilities or bootstrap support. Should the phylogeny hypothesized by Pereira et al. (2007) be valid, it would suggest that *Arenicolumba* is not a basal columbid. In having its proposed closest living relatives confined to Africa, *Arenicolumba* resembles the primitive crane *Balearica* (Gruidae), which occurs in Africa today but is common in the North American Neogene (Olson 1985, Feduccia and Voorhies 1992).

Of the nine osteological characters regarded by Livezey & Zusi (2006) to be diagnostic or supportive for defining the Columbidae, only seven (their characters number 1307, 1356, 1369, 1417, 1723, 2036, 2119) could potentially be evaluated in *Arenicolumba*. I found only one of these characters (number 1723) to be valid and diagnostic of columbids; the remaining six characters are either highly generalized (apply to numerous families of birds and are unlikely to represent homologies) or cannot be interpreted.

At the time of its description in 1992, at least 375 specimens of *Arenicolumba prattae* had been recovered. Subsequent field and laboratory work at Thomas Farm has increased this number to more than 700, which make up 75% to 80% of the site's identifiable bird fossils. It is noteworthy that, among these numerous specimens, only the ulnare, manus phalanges, and pedal pha-

langes are ever complete. The consistent breakage of other skeletal elements supports the thesis of Pratt (1989) that most breakage of bones in doves (and other small vertebrates) within the Thomas Farm sinkhole was due to damage by avian and mammalian predators at or just before the time of deposition.

## CUCULIFORMES

Traditionally (i.e., Mayr & Amadon 1951, Wetmore 1960), the Cuculiformes was considered to comprise two families, the Cuculidae and Musophagidae. Endemic to Africa today, musophagids (turacos and plantain-eaters) are known as fossils from the Oligocene of Africa and the Oligocene and Miocene of Europe; Ballmann 1970, Feduccia 1996, Mayr 2005). The strictly cuculid characters of the five skeletal elements available for *Thomasococcyx philohippus* (tarsometatarsus, coracoid, scapula, humerus, and mandible) support the hypothesis that the Musophagidae is only distantly related to the Cuculidae and does not belong in the Cuculiformes. This agrees with the proposals of Sibley & Ahlquist (1990), Mindell et al. (1997), Sorenson et al. (2003), Mayr & Ericson (2004), and perhaps Cracraft et al. (2004). I should note, however, that the early Eocene *Foro panarium* (known from a complete, associated skeleton, Green River Formation, Wyoming) was placed in an extinct family of Cuculiformes with characters suggestive of musophagids, cuculids, and the enigmatic *Opisthocomus hoazin* (Olson 1992). Furthermore, Hughes (2000) classified the Opisthocomidae (consisting of the living *Opisthocomus hoazin* and the middle Miocene fossil *Hoazinoides magdalenae* from Colombia; A. H. Miller 1953) and Musophagidae together to make up the Opisthocomiformes, this order being sister to the Cuculiformes, consisting only of the Cuculidae.

Whether the Cuculidae originated in the New World versus Old World, or Northern Hemisphere versus Southern Hemisphere, awaits the discovery of more Paleogene fossils. The Tertiary fossil record of cuckoos is poor. Nearly all of the supposed Eocene and Oligocene cuckoos from Europe are either not referable to the Cuculidae or are of questionable identity; *Dynamopterus velox* from the Eo-Oligocene Quercy fauna of France may be a cuckoo but is based only on a humerus (Olson & Feduccia 1979, Martin & Mengel 1984, Olson 1985, Mayr 2005, Mayr & Mourer-Chauviré 2005).

In North America, *Eocuculus cherpinae* is based on a partial associated skeleton from the late Eocene (early Chadronian LMA; ca. 37-36 Ma) of Colorado (Chandler 1999). *Eocuculus* was much smaller than *Thomasococcyx* and had relatively short legs suggesting that it was arboreal rather than ground-dwelling.

Chandler (1999) classified *Eocuculus* not only in the Cuculidae but in the subfamily Cuculinae, with its closest affinities to *Cuculus* (Old World) among living genera. Mayr (2006) reported *Eocuculus* from the early Oligocene (ca. 30 Ma) of France, excluded it from crown group Cuculidae, and was justifiably tentative about referring it to the Cuculidae. *Neococcyx mcorquodalei* is based only on the distal end of humerus from the early Oligocene (late Chadronian LMA; ca. 34 Ma; Prothero & Emry 2004) of Saskatchewan (Weigel 1963). I agree with Olson (1985) that *Neococcyx* probably is a cuckoo, although the limited material precludes any precise hypothesis of relationship.

Moving to the Neogene, roughly contemporaneous with *Thomasococcyx* is *Cursoriococcyx geraldinae*, based on a humeral end of coracoid, a nearly complete carpometacarpus, and a proximal end of tarsometatarsus from the early Miocene (Hemingfordian LMA) Martin Canyon local fauna of Colorado (Martin & Mengel 1984). While I agree with Martin and Mengel (1984) that it belongs in the Neomorphinae, *C. geraldinae* is much larger than *T. philohippus* (Table 2) and differs further in four characters of the tarsometatarsus (the only directly comparable element in the two species).

Finally, Olson (1985:111) mentioned the distal end of a tibiotarsus from “a large cuckoo of uncertain affinities” from the early Pliocene (late Hemphillian LMA) Lee Creek local fauna, North Carolina. This specimen (USNM 256228) was tentatively referred to the Galliformes (family, genus, and species indeterminate) by Olson & Rasmussen (2001), who also noted that this fossil may derive from the early to middle Miocene Pungo River Formation (Barstovian LMA) rather than the Hemphillian Yorktown Formation.

The interpretation of *Thomasococcyx philohippus* as a ground-dwelling species is compatible with the osteological characters that ally it more closely to living New World genera of ground-dwelling cuckoos (Neomorphinae, which I regard as monophyletic and more closely allied to the Crotophaginae than to the Cuculinae) than to any of the living Old World genera of Cuculidae. Following the classification of Payne (2005), which is based on morphology, DNA, and breeding ecology, my assignment of *Thomasococcyx* to the Neomorphinae suggests that the split between the New World ground-dwelling cuckoos and other cuculid subfamilies already had occurred by the early Miocene. At this time at least two genera of Neomorphinae (*Cursoriococcyx*, *Thomasococcyx*) existed in North America. Today, *Geococcyx* is the only neomorphine cuckoo north of ca. 24°N, the remaining four genera

(*Tapera*, *Dromococcyx*, *Morococcyx*, *Neomorphus*) being strictly neotropical. I note here that Hughes (2000) placed *Morococcyx*, *Geococcyx*, and *Neomorphus* in the Neomorphinae, but *Tapera* and *Dromococcyx* in the Cuculinae. I disagree, as does Payne (2005).

It is beyond the scope of this paper to assess the novel hypothesis of Mayr & Ericson (2004) that the Mesitornithidae (endemic to Madagascar; traditionally placed in the Gruiformes) has a sister group relationship to the Cuculidae. Of the 80 osteological characters used by Mayr & Ericson (2004) to propose a close relationship between the Cuculidae and Mesitornithidae, only nine (their characters numbered 40, 54, 55, 73-78) can be evaluated in the available material of *Thomasococcyx philohippus*. In each case, the character state of *T. philohippus* agrees with that given for modern skeletons of both Cuculidae and Mesitornithidae by Mayr & Ericson (2004), except that *Thomasococcyx* agrees with Cuculidae to the exclusion of Mesitornithidae in character 78.

Of the seven osteological characters that Livezey & Zusi (2006) found to be diagnostic or supportive for the Cuculidae (their characters number 1007, 1336, 1572, 1614, 1651, 1658, 1866), none can be evaluated in *Thomasococcyx*. Nevertheless, I found six of these seven characters to be generalized (applicable to numerous families of birds; unlikely to represent homologies) and the other one (1651) impossible to interpret.

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