



A large eagle (Aves, Accipitridae) from the early Miocene of Panama

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Abstract.—We report the first Tertiary bird fossil from Central America, an ungual phalanx from a large, unknown genus and species of Accipitridae from the early Miocene Centenario Fauna, Panama. This specimen provides another example of a Neogene bird from North and Central America with its possible closest living relatives occurring today in Africa. In contrast, there is no evidence of African affinities among the reptile or mammal fossils from the Centenario Fauna.

Introduction

Pre-Pleistocene fossil vertebrates are poorly known from Central America. In particular, no fossil birds of Tertiary age have been reported from this region (Panama through Guatemala and Belize), including Panama. To the north of Panama, the nearest Tertiary avian fossils are from central Mexico (Steadman and Carranzo-Castañeda, 2006). Thus, it is noteworthy to report the first Miocene bird fossil from Panama. The specimen is a pedal ungual phalanx (claw). Pedal phalanges are surprisingly diagnostic at the generic level in hawks and eagles (Accipitridae; Olson, 1982) as well as in a number of other families of birds such as the Anatidae (Steadman, 1991) and Rallidae (Steadman, 1988). The Panamanian fossil is the ungual of the middle toe (pedal digit III, phalanx 4), which is an integral part of grasping prey. Pedal digit III is the longest of the three front toes, and possesses an ungual that is second in size only to that of the opposing hind toe (pedal digit I). A distinctive feature of pedal digit III, phalanx 4 is that it is markedly bilaterally asymmetrical, and therefore readily distinguished from other unguals.

The purpose of this report is to document the early Miocene eagle fossil from Panama and to discuss its biogeographic affinities and significance.

Geologic setting

The fossil described here, UF 281480, was discovered by Dr. John Turner from outcrops of the Cucaracha Formation along the west side of the Panama Canal on New Year's Day 1962. Dr. Turner, now of Hattiesburg, Mississippi, grew up in the Canal Zone and made fossil collections in this region during the 1950s and early 1960s. He donated a portion of his collection, which included this fossil, to the Florida Museum of Natural History (UF) Vertebrate Paleontology Collection in 2014 (MacFadden et al., 2015). UF 281480 was contained within a box of other fossil vertebrates, all of which are from what is now termed the Centenario Fauna (MacFadden et al., 2010), including the most common taxon, i.e., the protoceratid *Paratoceras*. No other

fossils from other localities were contained in this box, so it is safe to assume that this collection is from the same locality.

With regard to fossil vertebrates from Panama, over the past 50 years various reports have described early Miocene mammals (e.g., Whitmore and Stewart, 1965; MacFadden, 2006; MacFadden et al., 2014), turtles (Cadena et al., 2012), the boid snake *Boa* (Head et al., 2012), and crocodylians (Hastings et al., 2013) from relevant outcrops along the Canal. These occurrences are from the Centenario Fauna, which includes the uppermost part of the Culebra Formation and most of the overlying Cucaracha Formation (MacFadden et al., 2010).

Exposures of the Cucaracha Formation crop out on the east and west sides of the Panama Canal along the Gaillard Cut (Stewart et al., 1980). This formation is moderately fossiliferous in places and the primary collecting localities are well documented (MacFadden, 2006; MacFadden et al., 2014). The distinctive mode of preservation of the bird fossil (jet black within a matrix of off-white indurated silt) is similar to that of other vertebrates collected from these outcrops (contained in both the UF and Smithsonian collections; e.g., Whitmore and Stewart, 1965; MacFadden, 2006). UF 281480 was collected from outcrops of the Cucaracha Formation north of the current location of the Centenario Bridge and south of Contractors Hill (J. Turner, personal communication; Supplementary Document 1) at approximate 9.035°N, 79.641°W (UF VP Locality YPA 002). From what is known about these exposures, UF 281480 was found within the middle third of the stratigraphic extent of the Centenario Fauna. Given the constraints of mode of preservation, the unambiguous documentation provided by the collector, and the lateral and stratigraphic extent of the Centenario Fauna, we are confident of the Cucaracha Formation provenience of UF 281480.

In addition to the spatial and temporal constraints provided here, based on paleomagnetic, geochronological, and biochronological evidence, fossils from the Centenario Fauna are constrained in Chron C5Er between 19.05 and 18.78 Ma during the early Miocene (MacFadden et al., 2014). The fossil mammals, including the diagnostic rhinoceros *Floridaceras*, indicate that the Centenario Fauna is early Hemingfordian (He1)

age, which is the North American Land Mammal Age (NALMA) otherwise known in higher-latitude North America. In many of its faunal characteristics, the Centenario Fauna compares favorably with the slightly younger (ca. 18 to 17 Ma) Thomas Farm Local Fauna of Florida (e.g., Tedford et al., 2004).

Materials and methods

To identify osteological characters, we compared the fossil with the following comparative specimens from the University of Florida (UF) Ornithology Collection. Pandionidae—*Pandion haliaetus*, UF 48491. Accipitridae—*Accipiter gentilis*, UF 41963; *Buteogallus anthracinus*, UF 33744; *Buteogallus urubitinga*, UF 33554; *Buteogallus meridionalis*, UF 38903; *Geranoetus melanoleucus*, UF 38062; *Parabuteo unicinctus*, UF 33745; *Buteo jamaicensis*, UF 42233; *Haliaeetus leucocephalus*, UF 33743; *Aquila chrysaetos*, UF 23962; *Harpia harpyja*, UF 38871; *Circaetus gallicus*, UF 38888; *Hieraaetus spilogaster*, UF 38898; *Polemaetus bellicosus*, UF 38904; *Stephanoetus coronatus*, UF 38905; Falconidae—*Caracara cheriway*, UF 42180. Tytonidae—*Tyto alba*, UF 41181. Strigidae—*Strix varia*, UF 26521; *Bubo virginianus*, UF 44040.

Systematic paleontology

Class Aves Linnaeus, 1758
Order Accipitriformes Vieillot, 1816
Family Accipitridae Vieillot, 1816
Genus indeterminate

Material.—Complete pedal digit III, phalanx 4 (ungual), UF 281480.

Occurrence.—Centenario Fauna, UF VP locality YPA 002, early Miocene, early Hemingfordian (He 1) NALMA, Panama Canal, Panama.

Comparative osteology.—Osteological nomenclature follows that in Boev (2001) and Gala and Lenoble (2015). UF 281480 is referred to the Accipitridae rather than to the other families of birds with “raptorial” unguis phalanges (Pandionidae, Falconidae, Tytonidae, Strigidae) because of these characters (Fig. 1): medial side of corpus phalangis with prominent ridge (see arrows in Figs. 1, 2) originating at the juncture of cotyla articularis (the articulation for phalanx 3) with tuberculum flexorium (the underlying or plantar facet for attachment of flexor tendon III) (except in Strigidae); juncture of lateral and plantar sides of corpus phalangis defined by a sharp ridge (rounded in Pandionidae, Strigidae); in proximal aspect, cotyla articularis higher than wide (wider than high in Strigidae); in plantar aspect, tuberculum flexorium nearly bilaterally symmetrical (medial side much larger than lateral side in Falconidae, Tytonidae); in plantar aspect, tuberculum flexorium longer than wide (wider than long in Falconidae, Tytonidae, and Strigidae); in plantar aspect, the paired foramina for tuberculum flexorium relatively smaller than in Pandionidae, Falconidae, and Strigidae.

Within the Accipitridae, UF 281480 is approximately the size of digit III, phalanx 4 in the largest, most powerful living

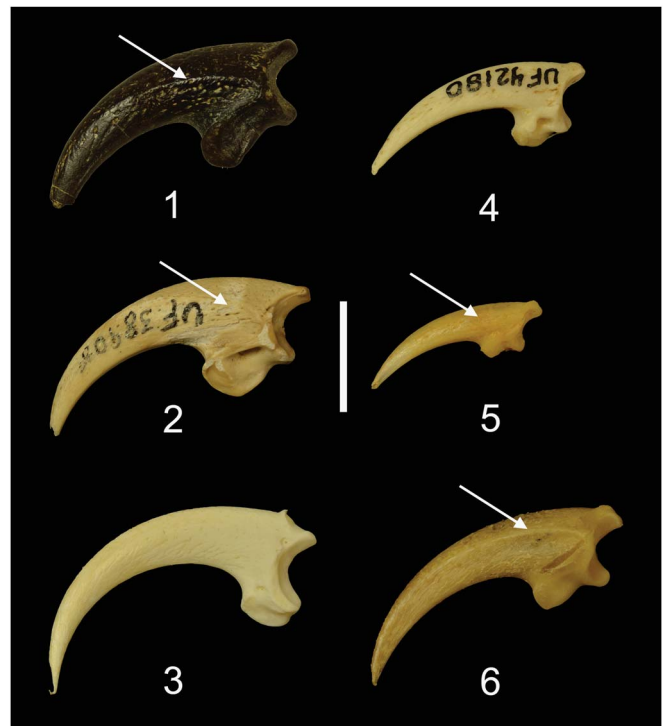


Figure 1. Digit III, phalanx 4 in medial aspect. (1) Accipitridae sp., fossil, UF 281480, Panama. (2) *Stephanoetus coronatus*, UF 38905, Zimbabwe. (3) *Pandion haliaetus*, UF 48491, Florida. (4) *Caracara cheriway*, UF 42180, Florida. (5) *Tyto alba*, UF 41181, Bahamas. (6) *Bubo virginianus*, UF 44040, Florida. White arrows point to the prominent ridge of the medial side of corpus phalangis. Scale bar represents 10 mm.

species of hawks and eagles such as *Harpia harpyja* and *Polemaetus bellicosus* (Table 1, Fig. 2). Compared to any of the living species, UF 281480 has a wider cotyla articularis (ratio of measurements 1 vs. 2 in Table 1), being most closely approached by the Holarctic *Aquila chrysaetos* and African *Stephanoetus coronatus* (see the double-pointed arrows in Fig. 2.6, 2.8, and 2.9.) In its relative length of tuberculum flexorium (ratio of measurements 4 vs. 2 in Table 1), UF 281480 is roughly equivalent to the condition in the North American *Buteo jamaicensis*, and in three African species (*Hieraaetus spilogaster*, *Stephanoetus coronatus*, *Polemaetus bellicosus*).

UF 281480 agrees with the three African genera and disagrees with other accipitrids examined in having a sharp ridge running along the midline of the tuberculum flexorium (Fig. 2.1, 2.5, 2.7, 2.9). This ridge increases the surface area for tendinal attachment, probably resulting in a slight terminal bifurcation of flexor tendon III. This character is especially well developed in the fossil and in *Stephanoetus coronatus*.

Discussion

Biogeographic significance.—Whereas most Neogene North American bird fossils represent taxa of Neotropical and Nearctic affinities, the possible African relationship of the early Miocene accipitrid fossil from Panama is not without precedent. The abundant dove *Arenicolumba prattae* (Columbidae) from the early Miocene Thomas Farm Local Fauna (Florida; Hemingfordian NALMA) represents an extinct genus with closer



Figure 2. Digit III, phalanx 4 of Accipitridae in medial (left column), lateral (middle column), and proximal (right column) aspects. (1) *Hieraaetus spilogaster*, UF 38898 (mirror image), Botswana. (2) *Buteo jamaicensis*, UF 42233, Florida. (3) *Haliaeetus leucocephalus*, UF 33743, Florida. (4) *Geranoetus melanoleucus*, UF 38062, Argentina. (5) *Stephanoetus coronatus*, UF 38905, Zimbabwe. (6) *Aquila chrysaetos*, UF 23962, Texas. (7) *Harpya harpyja*, UF 38871, Costa Rica. (8) Accipitridae sp., fossil, UF 281480, Panama. (9) *Polemaetus bellicosus*, UF 38904, South Africa. White arrows point to the prominent ridge of the medial side of corpus phalangis. White 2-pointed arrows disclose the wide cotyla articularis in three species. Scale bar represents 10 mm.

Table 1. Measurements (in mm) of Digit III, phalanx 4, in selected species of Accipitridae. Based on same specimens as in Figure 2. Cot art = cotyla articularis; Tub flex = tuberculum flexorium; Prox end = entire proximal end (Cot art + Tub flex).

Species	① Cot art: width	② Cot art: depth	③ Tub flex: width	④ Tub flex: length	⑤ Prox end: Oblique depth/length	①/②	④/②
<i>Hieraaetus spilogaster</i>	5.05	5.93	3.77	6.37	9.30	0.85	1.07
<i>Buteo jamaicensis</i>	6.00	6.45	5.75	7.05	10.46	0.93	1.09
<i>Haliaeetus leucocephalus</i>	6.79	8.07	4.59	7.66	11.72	0.84	0.95
<i>Geranoetus melanoleucus</i>	7.05	7.92	5.72	7.57	11.71	0.89	0.96
<i>Stephanoetus coronatus</i>	7.47	7.87	5.89	8.73	12.52	0.95	1.11
<i>Aquila chrysaetos</i>	8.38	8.85	6.92	8.66	12.84	0.95	0.98
<i>Harpya harpyja</i>	8.58	9.61	6.22	9.62	14.52	0.89	1.00
Accipitridae sp., fossil	8.62	8.80	6.64	9.70	14.69	0.98	1.10
<i>Polemaetus bellicosus</i>	8.83	9.98	5.85	10.95	16.36	0.88	1.10

affinities to the living African endemic genera *Oena* and *Turtur* than to any living or extinct New World columbid genus (Steadman, 2008). Moreover, younger Neogene (middle Miocene through Pliocene) North American birds with African affinities include the anatids *Tadorna* s.l. and *Nettapus*, as well as the crane *Balearia* (Olson, 1985, p. 164; Becker, 1987, p. 38, 51, 58, 65; Steadman and Carranza-Castañeda, 2006). To the south of Panama, we note that the middle Miocene avifauna from La Venta, Colombia (7–8 Myr younger than the Centenario Fauna) lacks evidence of accipitrid fossils or of any avian taxa with African affinities (Rasmussen, 1997).

The fossil mammals from the Centenario Fauna represent North American taxa, including considerable overlap at the generic level with those from Thomas Farm (e.g., Whitmore and Stewart, 1965; MacFadden, 2006; MacFadden et al., 2014). The fossil reptiles from the Centenario Fauna are of mixed geographic affinities, although none shows a relationship with African taxa. Among the crocodylians, some have nearest relatives in North America and others in South America (Hastings et al., 2013). The fossil turtles are primarily North American, although a fragmentary pleurodire has South American affinities, as does the fossil *Boa* (Cadena et al., 2012;

Head et al., 2012). The early Miocene pollen flora of Panama is predominantly of “Gondwana Amazonian” affinities (Jaramillo et al., 2014).

Paleoecology.—In its stout, powerful proportions, the Panamanian fossil most closely resembles the unguis phalanx of the large African eagles *Stephanoetus coronatus* and *Polemaetus bellicosus*. The former, known as the Crowned Hawk-eagle, is said to feed on “Mainly mammals, especially monkeys and small antelopes in lowland rain forest, or hyraxes and viverrids in drier forests.” (Thiollay, 1994, p. 205). The Martial Eagle (*P. bellicosus*) feeds on “Mainly vertebrates weighing 1–5 kg, with large birds (e.g., gamebirds and waterfowl), monitor lizards, or mammals (e.g., hares, hyraxes, mongooses, and small antelopes) predominating ...” (Thiollay, 1994, p. 200). Although the estimated body sizes of the mammals from the Centenario Fauna have not yet been reported, there are several possible prey species in the 1–5 kg size range, including rodents, a procyonid carnivoran, and the small moschid artiodactyls.

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Accessibility of Supplemental Data

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.v1r28>.

References

- Becker, J.J., 1987, Neogene Avian Localities of North America: Washington, DC, Smithsonian Institution Press, 171 p.
- Boev, Z.N., 2001, Early Pliocene avifauna of Muselievo (C Northern Bulgaria): *Acta Zoologica Cracovica*, v. 44, p. 37–52.
- Cadena, E., Bourque, J.R., Rincon, A.F., Bloch, J.I., Jaramillo, C.A., and MacFadden, B.J., 2012, New turtles from the Eocene through middle Miocene of the Panama Canal basin: *Journal of Paleontology*, v. 86, p. 539–557.
- Gala, M., and Lenoble, A., 2015, Evidence of the former existence of an endemic macaw in Guadeloupe, Lesser Antilles: *Journal of Ornithology*, v. 156, p. 1061–1066.
- Hastings, A.K., Bloch, J.I., Jaramillo, C.A., Rincón, A.F., and MacFadden, B.J., 2013, Systematics and biogeography of crocodylians from the Miocene of Panama: *Journal of Vertebrate Paleontology*, v. 33, p. 239–263.

- Head, J.J., Rincon, A.F., Suarez, C., Montes, C., and Jaramillo, C., 2012, Fossil evidence for earliest Neogene American Faunal Interchange: *Boa* (Serpentes, Boinae) from the early Miocene of Panama: *Journal of Vertebrate Paleontology*, v. 32, p. 1328–1334.
- Jaramillo, C., Moreno, E., Ramírez, V., da Silva, S., Barrera, Atria, Barrera, Adara, Sánchez, C., Morón, S., Herrera, F., Escobar, J., Koll, R., Manchester, S.R., and Hoyos, N., 2014, Palynological record of the last 20 million years in Panama, in Stevens, W. D., Montiel, O.M., and Raven, P., eds., *Paleobotany and Biogeography: A Festschrift for Alan Graham in His 80th Year*: St. Louis, Missouri Botanical Garden Press, p. 134–251.
- MacFadden, B.J., 2006, North American Miocene land mammals from Panama: *Journal of Vertebrate Paleontology*, v. 26, p. 720–734.
- MacFadden, B.J., Kirby, M.X., Rincon, A., Montes, C., Moran, S., Strong, N., and Jaramillo, C., 2010, Extinct peccary “*Cynorca*” *occidentale* (Tayassuidae, Tayassuinae) from the Miocene of Panama and correlations to North America: *Journal of Paleontology*, v. 84, p. 288–298.
- MacFadden, B.J., Bloch, J.I., Evans, H., Foster, D.A., Morgan, G.S., Rincon, A.F., and Wood, A.R., 2014, Temporal calibration and biochronology of the Centenario Fauna, early Miocene of Panama: *Journal of Geology*, v. 122, p. 113–135.
- MacFadden, B.J., Morgan, G.S., Jones, D.S., and Rincon, A., 2015, Gomphothere proboscidean (*Gomphotherium*) from the late Neogene of Panama: *Journal of Paleontology*, v. 89, p. 360–365.
- Olson, S.L., 1982, The distribution of fused phalanges of the inner toe in the Accipitridae: *Bulletin of the British Ornithologists’ Club*, v. 102, p. 8–12.
- Olson, S.L., 1985, The fossil record of birds: *Avian Biology*, v. 8, p. 79–252.
- Rasmussen, D.T., 1997, Birds, in Kay, R.F., Madden, R.H., Cifelli, R.K., and Flynn, J.J., eds., *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*: Washington, DC, Smithsonian Institution, p. 171–183.
- Steadman, D.W., 1988, A new species of *Porphyrio* (Aves: Rallidae) from archaeological sites in the Marquesas Islands: *Proceedings of the Biological Society of Washington*, v. 101, p. 162–170.
- Steadman, D.W., 1991, Extinct and extirpated birds from Aitutaki and Atiu, Southern Cook Islands: *Pacific Science*, v. 45, p. 325–347.
- Steadman, D.W., 2008, Doves (Columbidae) and cuckoos (Cuculidae) from the early Miocene of Florida: *Bulletin of the Florida Museum of Natural History*, v. 48, p. 1–16.
- Steadman, D.W., and Carranza-Castañeda, O., 2006, Early Pliocene to Early Pleistocene birds from central Mexico, in Carranza-Castañeda, O., and Lindsay, E.H., eds., *Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange*: Universidad Nacional Autónoma de México, Instituto de Geología, & Centro de Geociencias, *Publicación Especial no. 4*, p. 61–71.
- Stewart, R.H., Stewart, J.L., and Woodring, W.P., 1980, Geologic map of the Panama Canal and vicinity, Republic of Panama: United States Geological Survey Miscellaneous Investigations Series Map I-1232, scale 1:100,000, 1 sheet.
- Tedford, R.H., Albright, L.B. III, Barnosky, A.D., Ferrusquía-Villafranca, I., Hunt, R.M. Jr., Storer, J.E., Swisher, C.C. III, Voorhies, M.R., Webb, S.D., and Whistler, D.P., 2004, Mammalian biochronology of the Arikarean through Hemphillian interval (late Oligocene through early Pliocene epochs), in Woodburne, M.O., ed., *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*: New York, Columbia University Press, p. 169–231.
- Thiollay, J.-M., 1994, Family Accipitridae (hawks and eagles), in del Hoyo, J., Elliott, A., and Sargatal, J., eds., *Handbook of the Birds of the World*, vol. 2., *New World Vultures to Guinea-fowl*: Barcelona, Lynx Edicions.
- Whitmore, F.C. Jr., and Stewart, R.H., 1965, Miocene mammals and Central American seaways: *Science*, v. 148, p. 180–185.

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