THE CUBAN FOSSIL EAGLE AQUILA BORRASI ARREDONDO: A SCALED-UP VERSION OF THE GREAT BLACK-HAWK BUTEOGALLUS URUBITINGA (GMELIN)

Authors: Suárez, William, and Olson, Storrs L.

Source: Journal of Raptor Research, 41(4) : 288-298

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/0892-1016(2007)41[288:TCFEAB]2.0.CO;2

J. Raptor Res. 41(4):288–298

THE CUBAN FOSSIL EAGLE *AQUILA BORRASI* ARREDONDO: A SCALED-UP VERSION OF THE GREAT BLACK-HAWK *BUTEOGALLUS URUBITINGA* (GMELIN)

WILLIAM SUÁREZ
Museo Nacional de Historia Natural, Obispo 61, Plaza de Armas, Ciudad de La Habana, CP. 10100 Cuba

STORRS L. OLSON[1]
Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560 U.S.A.

ABSTRACT.—The fossil eagle *Aquila borrasi* Arredondo from the Quaternary of Cuba is redescribed and transferred to the genus *Buteogallus* Lesson, in which it represents a gigantic version (ca. 33% larger) of the morphology present in the living Great Black-Hawk *B. urubitinga* (Gmelin). *Buteogallus borrasi* differs from the other large fossil accipitrids recorded in the West Indies, *Amplibuteo woodwardi*, *Gigantohierax suarezi*, and *Titanohierax gloveralleni*, in being smaller, less robust, and with proportionately slender hindlimb elements, especially the tarsometatarsus. Although now known with certainty only from Cuba, *B. borrasi* may have had a wider distribution in the West Indies and perhaps even mainland North America.

KEY WORDS: Aquila borrasi; Buteogallus borrasi; *Great Black-Hawk*; Buteogallus urubitinga; *Cuba*; *eagle*; *fossil*.

EL ÁGUILA FÓSIL CUBANA *AQUILA BORRASI* ARREDONDO: UNA VERSIÓN AGIGANTADA DE *BUTEOGALLUS URUBITINGA*

RESUMEN.—El águila fósil *Aquila borrasi* Arredondo, del Cuaternario de Cuba, es redescrita y transferida al género *Buteogallus* Lesson. Esta especie representa una versión agigantada (~33% mayor) de la morfología presente en el taxón viviente *B. urubitinga* (Gmelin). *Buteogallus borrasi* difiere de los grandes gavilanes fósiles registrados en Las Antillas (*Amplibuteo woodwardi*, *Gigantohierax suarezi* y *Titanohierax gloveralleni*) por ser una especies de menor tamaño y menos robusta, con los elementos de sus miembros posteriores, especialmente el tarsometatarso, proporcionalmente más alargados. Aunque actualmente se conoce sólo de Cuba, *B. borrasi* quizás presentó una distribución más amplia en Las Antillas, e incluso, pudo estar presente en tierras continentales de Norte América.

[Traducción de los autores editada]

Arredondo (1970) described the extinct eagle *Aquila borrasi* based on an incomplete left tarsometatarsus (the holotype), a fragmentary right femur, and some phalanges from two Quaternary cave deposits in western Cuba. This was a composite type series, with the femur and one of the largest phalanges later being referred to the huge hawk *Gigantohierax suarezi* (Arredondo and Arredondo 2002a). Prior to this, Wetmore (1937) had described another eagle-sized buteonine hawk, *Titanohierax gloveralleni*, supposedly from Great Exuma (later determined to be Little Exuma), Bahama Islands, based on an incomplete tarsometatarsus and a fragment of a carpometacarpus. This material has since been augmented only by pieces of two ulnae from New Providence Island, Bahamas, reported by Olson and Hilgartner (1982), who explored the relationships of *Titanohierax*. They commented that the holotypical tarsometatarsus of *Aquila borrasi* was long and slender, unlike species of *Aquila*, suggested that it be referred to *Titanohierax*, and thought that it might be conspecific with *T. gloveralleni*.

Suárez (2004) made the first direct comparisons between large fossil West Indian accipitrids and related continental taxa, concluding that *Aquila borrasi* is a valid taxon, not referable to the genus *Titanohierax*. Considerable new material of this and other Cuban raptors now makes possible a reassessment and generic reassignment of *Aquila borrasi*. One of the most distinctive osteological characters of buteo-

[1] Email address: Olsons@si.edu

galline hawks is the very short inner calcaneal ridge of the hypotarsus. Upon ascertaining that this condition existed in the tarsometatarsi of *Aquila borrasi*, comparisons quickly revealed that the proportions of this species were almost exactly like those of the Great Black-Hawk (*Buteogallus urubitinga*) and unlike those of other members of the group. This is the second example documenting a hitherto unappreciated radiation of living and fossil New World Accipitridae derived from or referable to the genus *Buteogallus* (see Olson 2007).

MATERIALS AND METHODS

The specimens of *Aquila borrasi* we examined are housed in the following Cuban institutional and private collections, all except the last being in La Habana: Museo Nacional de Historia Natural de Cuba (MNHNCu); Instituto de Ecología y Sistemática (CZACC; formerly Colecciones del Instituto de Zoología, Academia de Ciencias de Cuba); Universidad de La Habana (DPUH; formerly Departamento de Paleontología, Facultad de Biología, of the same institution); Oscar Arredondo collection (OA); Carlos Arredondo collection (CA); William Suárez collection (WS); ArqueoCentro (AC), Villa Clara. Comparisons with skeletons of modern Accipitridae were made with all appropriate taxa in the collections of the National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A. (USNM). In addition, we examined one skeleton of *Harpyhaliaetus solitarius* Tschudi (Natural History Museum of Los Angeles County, LACM 110091), and another of *H. coronatus* Vieillot (Nationaal Natuurhistorich Museum, Leiden, the Netherlands). Comparisons with fossils of *Buteogallus fragilis* (L. Miller), *Buteogallus daggetti* (L. Miller), and *Amplibuteo woodwardi* (L. Miller), from Rancho La Brea, California, were made with the extensive collections of the George C. Page Museum, La Brea Discoveries, Los Angeles. A partial skeleton (WS 365) of *Amplibuteo woodwardi* from Cuba was examined as well. We also borrowed type material of *Titanohierax gloveralleni* from the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts (holotypical tarsometatarsus MCZ 2257; paratypical proximal carpometacarpus MCZ 2258) along with a femur (P-26) of *Gigantohierax suarezi* Arredondo and Arredondo. Of this last taxon, the holotypical complete femur (MNHNCu 75.574), the paratypical fragmentary tarsometatarsus (WS 80120.E), and a referred shaft of right tarsometatarsus (WS 8012) were used for comparisons as well. Osteological terminology follows Howard (1929), with some necessary modifications. Measurements were taken with digital calipers to the nearest 0.1 mm.

RESULTS

Systematics

Class Aves
Family Accipitridae
Genus *Buteogallus* Lesson, 1830

Differs from *Aquila* and agrees with *Buteogallus* in having the tarsometatarsus much more slender and elongate, with the inner calcaneal ridge shorter, the tubercle for tibialis anticus situated much more proximad, and wing of outer trochlea smaller and more posteriorly directed. The tibiotarsus is likewise more slender and elongate, the inner cnemial crest is smaller and does not extend as far anteriorly, and the openings of the distal tendinal canal are proportionately smaller. The femur is relatively shorter and more robust, with the head less distinctly set off from the shaft.

Buteogallus borrasi (Arredondo 1970), new combination
(Figs. 1, 2, 3)

Aquila borrasi Arredondo 1970: 3 (part), Arredondo 1971, Brodkorb 1971, Arredondo 1972, Arredondo and Varona 1974, Acevedo-González et al. 1975, Arredondo 1975, 1976, Olson 1978, Campbell 1979, Varona and Arredondo 1979, Morgan et al. 1980, Acevedo-González and Arredondo 1982, Arredondo 1982, 1984, Vergara 1988, Morgan and Ottenwalder 1993, Emslie and Czaplewski 1999, Feduccia 1999.

Aquila sp.: Fischer 1977, Acevedo-González and Arredondo 1982, Arredondo 1984, Cuello 1988.

Titanohierax borrasi: Olson and Hilgartner 1982, Cuello 1988, Alcover and McMinn 1994, Jiménez and Valdés 1995, Chirino 1996, Garrido and Kirkconnell 2000, Iturralde-Vinent et al. 2000, Suárez 2000a, 2000b, 2001, Arredondo and Arredondo 2002a, 2002b, Vergara 2003.

Sarcoramphus sp.?: Acevedo-González and Arredondo 1982, Arredondo 1984, Cuello 1988, Arredondo and Arredondo 2002a, 2002b.

Sarcoramphus? sp. Suárez 2000a.

''*Aquila*'' *borrasi*: Suárez 2004.

Holotype. Left tarsometatarsus lacking distal end (DPUH 1250).

Type locality. Cueva del Túnel, La Salud, Municipality of Quivicán, La Habana Province, Cuba.

Chronology. Quaternary, probably late Pleistocene, but not dated.

Figure 1. Tarsometatarsi in anterior view of large fossil West Indian Accipitridae compared with that (B) of the Great Black-Hawk *Buteogallus urubitinga* (USNM 345775). A, *Buteogallus borrasi* (CZACC 400-659); C, *Amplibuteo woodwardi* (WS 365); D, *Titanohierax gloveralleni*, holotype (MCZ 2257). The bone of *B. urubitinga* has been photographically enlarged to the same size as that of *B. borrasi* and the scale bar does not apply to image B.

Status and distribution. Extinct species, known only from Cuba.

Referred material. *Cueva de Paredones, Ceiba del Agua, Municipality of Caimito, La Habana Province, Cuba*: Left (CZACC 400-662) and right (CZACC 400-690) scapulae without posterior terminus; shaft of right coracoid (OA 3926); left humerus (CZACC 400-732); distal end of left humerus without ectepicondyle (CZACC 400-681); shaft of right humerus (CZACC 400-673); shaft of left ulna (WS 921E);

Figure 2. Wing elements of *Buteogallus borrasi* (A, C) compared with *B. urubitinga* (USNM 345775;B, D). A, left humerus in anconal view (CZACC 400-732); C, right ulna in palmar view (CZACC 400-671).

right ulna without olecranon (CZACC 400-671); distal half of right ulna (WS 920E); proximal and distal ends of a left carpometacarpus (WS 78); right carpometacarpus without metacarpal III and distal metacarpal symphysis (CZACC 400-687); left femur (WS 919E); right femur without head and external condyle (WS 919B); right femur without distal end (CZACC 400-672); proximal end of right femur (OA X-2972); distal end of right femur (OA 2967); proximal end of left fibula (CZACC 400-688); fragmentary left tibiotarsus without distal end (CZACC 400-670); distal ends of left tibiotarsi without external condyles (CZACC 400-683, WS 64); right tibiotarsus without proximal end (CZACC 400-650); shaft of right tibiotarsus (CZACC 400-656); proximal segment of shaft of right tibiotarsi (WS 1001,1002); proximal half of left tarsometatarsus lacking inner calcaneal ridge (WS 933); fragmentary distal ends of left tarsometatarsi (OA 3206, WS105); right tarsometatarsus (CZACC 400-659); proximal halves of right tarsometatarsi (CZACC 400-94, 400-665); ungual phalanx of right digit I (WS 63).

Cueva de Sandoval, Vereda Nueva, Municipality of Caimito, La Habana Province, Cuba: Shaft of left ulna (WS 967E); fragmentary left femur (WS 1115); proximal end of left femur (WS 968); fragmentary proximal end of left tibiotarsus (WS 995E); distal end of left tibiotarsus (WS 994E); right tibiotarsus without distal end (WS 966E); proximal segment of left tarsometatarsus (WS 1122); shaft of right tarsometatarsus (WS 993E); distal portion of shaft of right tarsometatarsus (WS 1116); left metatarsals I (WS 1013, 1121); right metatarsal I (WS 1120); phalanx 1 of left digit I (WS 955); ungual phalanx of right digit I (WS 982); phalanx 2 of right digit II (WS 0223); ungual phalanx of left digit III (WS 65).

Cueva Lamas, Santa Fé, Municipality of Playa, Ciudad de La Habana Province, Cuba: Shafts of left (OA P-2979) and right (OA P-2980) tarsometatarsi.

Cueva del Indio, Calabazar, Municipality of Boyeros, Ciudad de La Habana Province, Cuba: Distal end of left ulna (OA 2973).

Cueva del Túnel, La Salud, Municipality of Quivicán, La Habana Province, Cuba: Holotype; shaft of left humerus (WS 202); proximal half of left ulna (CA 80); proximal end of left ulna without articular portion (OA 2977); distal end of left ulna (CA 79); distal half of left tibiotarsus without internal condyle (OA 798.B).

Cueva de Insunza, La Salud, Municipality of Quivicán, La Habana Province, Cuba: Shaft of right tarsometatarsus (WS 123).

Cuevas Blancas, Aguacate, Municipality of Quivicán, La Habana Province, Cuba: Right radius without proximal end (WS 594); right femur without condyles (WS 970); left tibiotarsus without distal end (WS 969); distal half of right tibiotarsus (WS 971).

Cueva del Indio, Tapaste, Municipality of San José de Las Lajas, La Habana Province, Cuba: Distal half of right humerus (CZACC 27.03); distal end of left femur (CZACC 27.01).

Las Breas de San Felipe, Martí, Municipality of Martí, Matanzas Province, Cuba: Distal ends of left tibiotarsi (MNHNCu 75.4665, 75.4693); distal right tibiotarsus (MNHNCu 75.4678); left tarsometatarsus without distal end (MNHNCu 75.4666); left tarsometatarsus without articular region and trochleae for digits II and III (MNHNCu 75.4667); proximal half of left tarsometatarsus lacking inner calcaneal ridge (MNHNCu 75.4686); proximal end of left tarsometatarsus lacking calcaneal ridges (MNHNCu 75.4692); distal halves of left tarsometatarsi

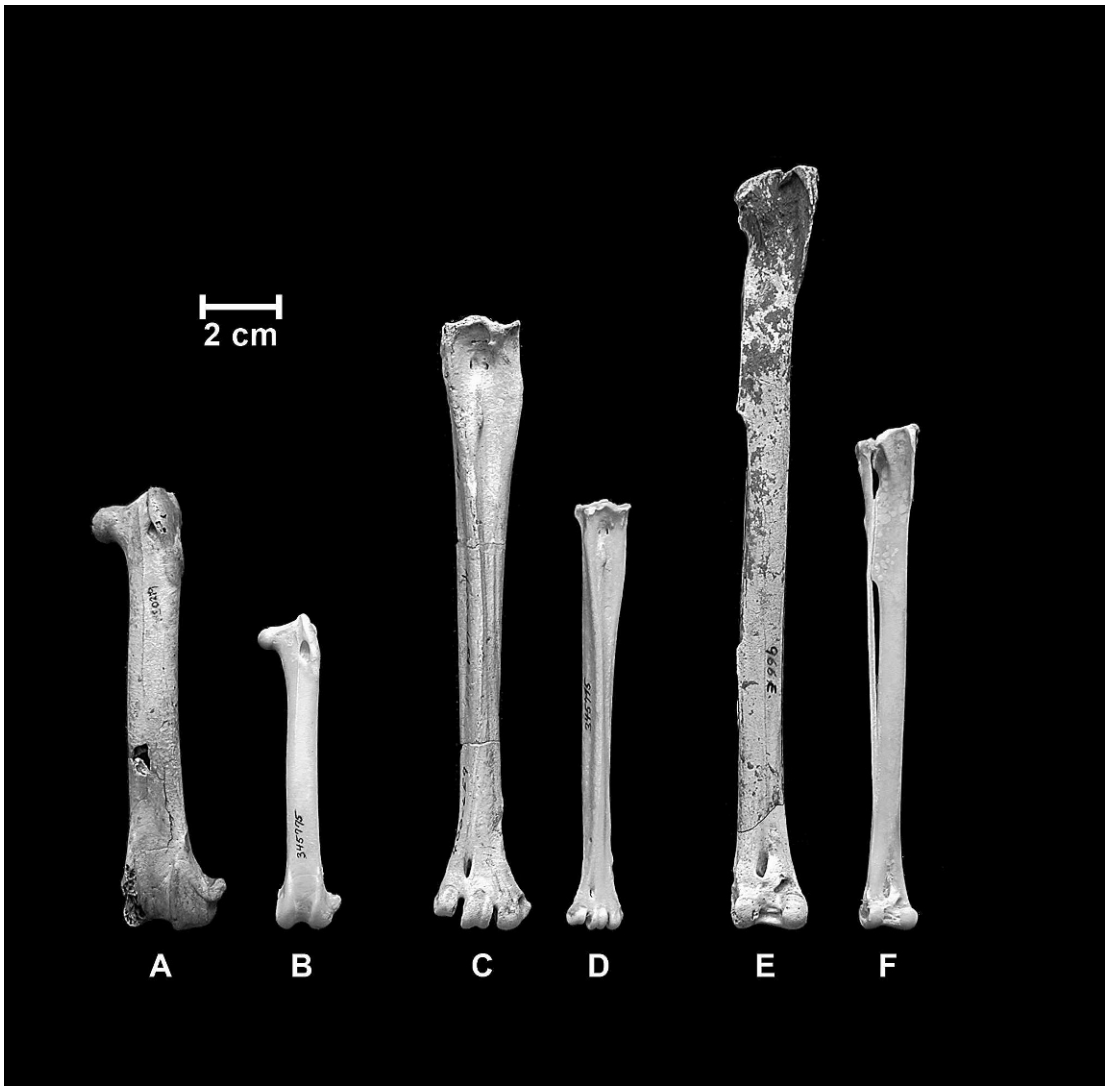

Figure 3. Hindlimb elements in anterior view of *Buteogallus borrasi* (A, C, E) compared with *B. urubitinga* (USNM 345775; B, D, F). A, left femur (WS 1115); C, right tarsometatarsus (CZACC 400-659); composite right tibiotarsus (proximal WS 966E, distal WS 971).

(MNHNCu 75.4687-88); fragmentary distal end of left tarsometatarsus (MNHNCu 75.4691); proximal end of right tarsometatarsus lacking inner calcaneal ridge (MNHNCu 75.4677); proximal segment of shaft of right tarsometatarsus (MNHNCu 75.4669); distal end of right tarsometatarsus (MNHNCu 75.4670); distal ends of right tarsometatarsi lacking trochlea for digit IV (MNHNCu 75.4689-90); distal segment of shaft of right tarsometatarsus (MNHNCu 75.4668); left metatarsal I (MNHNCu 75.4694); right metatarsal I (MNHNCu 75.4682); phalanx 1 of left digit I (MNHNCu 75.4697); phalanx 1 of left digit I lacking distal end (MNHNCu 75.4671); phalanges 1 of right digit I (MNHNCu 75.4695-96); ungual phalanges of left digit I (MNHNCu 75.4672, 75.4684-85); ungual phalanx of right digit I (MNHNCu 75.4683); ungual phalanges of left digit II (MNHNCu 75.4679-80); ungual

Table 1. Selected measurements of *Buteogallus borrasi* compared with *B. urubitinga*; range, (mean), *N*. For *B. urubitinga* $N = 9$.

MEASUREMENT	*B. BORRASI*	*B. URUBITINGA*	DIFFERENCE (%)[1]
Humerus			
Total length	(178.4) 1	114.6–130.3 (123.4)	30.8
Distal width	28.3–30.3 (29.2) 3	19.8–22.5 (21.1)	27.7
Ulna			
Length from external cotyla to external condyle	(183.4) 1	123.5–143.1 (134.8)	26.5
Femur			
Total length	117.7–120.2 (118.9) 2	81.3–89.9 (86.8)	30.0
Distal width from internal to fibular condyle	27.1–29.5 (28.1) 3	17.4–20.4 (18.7)	33.4
Tibiotarsus			
Least width of shaft at midpoint	11.4–12.1 (11.8) 6	6.9–8.0 (7.6)	35.6
Distal width	19.5–20.9 (20.2) 3	13.7–16.3 (15.1)	25.2
Tarsometatarsus			
Total length	162.1–165.2 (163.6) 2	109.0–124.2 (117.4)	28.2
Proximal width	20.5–22.4 (21.4) 8	14.4–16.4 (15.3)	28.5
Least width of shaft	9.2–11.3 (11.0) 7	6.4–8.3 (7.1)	35.4
Distal width	24.0–26.3 (25.3) 3	15.4–18.3 (16.8)	33.6

[1] Difference (%) = how much larger the means of *B. borrasi* are than those of *B. urubitinga*.

phalanges of right digit II (MNHNCu 75.4673-76); ungual phalanx of left (MNHNCu 75.4681) and right (MNHNCu 75.4707) digit III.

Solapa del Megalocnus, El Charcón, Municipality of Corralillo, Villa Clara Province, Cuba: Right femur (CA 77); ungual phalanx of right digit III (CA 78).

Casimba Hueco Chico, Malpaez, Municipality of Sagua La Grande, Villa Clara Province, Cuba: Left (AC 1) and right tarsometatarsi (AC 2) from the same individual.

Cueva Funeraria de Los Niños, Cayo Salinas, Municipality of Yaguajay, Sancti Spíritus Province, Cuba: Distal end of right tibiotarsus (OA X-2970).

Measurements. *Buteogallus borrasi* is compared with *B. urubitinga* in Table 1 and with five fossil species in Table 4. Additional measurements of the species are found in Tables 2 and 3.

Amended Diagnosis. A scaled-up version, about 33% larger, of the morphology of *B. urubitinga*, differing from that species by having the humerus with the capital groove thin, pneumatic foramen larger, and brachial depression deeper; ulna more curved with brachial depression shallow, and carpal tuberosity shorter; shaft of femur more compressed anteroposteriorly, trochanteric ridge better developed and condyles shorter; proximal articular surface of the tibiotarsus constricted latero-medially, outer cnemial crest short, inner cnemial crest more compressed medially and externally, thus having a more pronounced depression on either side, internal condyle less projected medially, and shaft more compressed in its distal-internal border; tarsometatarsus with shorter inner calcaneal ridge, and flared distal end, especially the trochlea for digit II. Many of these differences are likely to be size-related.

All the other living species of *Buteogallus* (which includes *Heterospizias*; see Olson 2007) are much smaller than *B. borrasi*. In the Savanna Hawk (*B. meridionalis*), the tarsometatarsus is even more slender and gracile than in *B. borrasi*, whereas in the other species and in both species of *Harpyhaliaetus* the tarsometatarsus is proportionately shorter and more robust than in *B. borrasi* or *B. urubitinga*.

Comparison with Other Fossil Accipitridae. The supposedly congeneric fossil species *B. fragilis* is easily segregated from *B. borrasi*, as it is a much smaller, stouter bird, and as noted by Howard (1932) is similar in proportions to the Common Black-Hawk (*B. anthracinus*), rather than the Great Black-Hawk (*B. urubitinga*). *Gigantohierax suarezi* is instantly separated from *B. borrasi* by its huge size. *Amplibuteo woodwardi*, *Gigantohierax suarezi*, and *Titanohierax gloveralleni* are in general larger, more robust species than *B. borrasi*, with proportionately shorter, stouter hindlimb elements, especially the tarsometatarsus.

Compared with the known elements in the skeleton of *Wetmoregyps* (= *Buteogallus*) *daggetti*, *B. borrasi* differs by having the ulna larger with carpal tuberosity less projected; femur also larger with shorter and deeper condyles, posterior-external side flat,

Table 2. Additional measurements (mm) of pectoral elements of *Buteogallus borrasi*.

MEASUREMENT	MEAN (*N*)	RANGE
Scapula		
Proximal width	14.4 (2)	13.7–15.1
Width from tip of acromion to external tip of glenoid facet	18.0 (2)	17.4–18.6
Least width of neck	8.0 (2)	7.6–8.4
Depth of glenoid facet	7.6 (2)	6.9–8.3
Coracoid		
Least width of shaft	10.7 (1)	—
Humerus		
Proximal width	31.8 (1)	—
Proximal depth	14.1 (1)	—
Depth of head	10.1 (1)	—
Least width of shaft at midpoint	13.4 (2)	13.3–13.5
Least depth of shaft at midpoint	12.1 (2)	12.0–12.2
Distal depth	14.9 (3)	14.5–15.4
Ulna		
Proximal width	19.5 (1)	—
Proximal depth	13.8 (3)	13.4–14.0
Least width of shaft at midpoint	9.2 (4)	8.9–9.5
Least depth of shaft at midpoint	8.7 (5)	8.0–9.1
Distal width	11.6 (1)	—
Distal depth	14.2 (3)	13.8–14.8
Radius		
Least width of shaft at midpoint	5.8 (1)	—
Least depth of shaft at midpoint	4.4 (1)	—
Distal width	12.9 (1)	—
Carpometacarpus		
Proximal width	8.3 (2)	8.3–8.4
Proximal depth	21.6 (2)	21.1–22.1
Width of metacarpal II at midpoint	7.5 (1)	—
Depth of metacarpal II at midpoint	5.7 (1)	—

Table 3. Additional measurements (mm) of pelvic elements of *Buteogallus borrasi*.

MEASUREMENT	MEAN (*N*)	RANGE
Femur		
Length from head to internal condyle	113.6 (3)	113.0–115.8
Proximal width	26.0 (5)	24.8–26.8
Least width of shaft at midpoint	13.2 (6)	12.0–13.8
Least depth of shaft at midpoint	11.7 (6)	11.3–12.0
Internal condyle depth	18.1 (5)	17.4–19.2
External condyle depth	22.3 (4)	20.8–23.6
Fibula		
Proximal depth	15.5 (1)	—
Tibiotarsus		
Proximal width through articular surface	22.5 (2)	22.3–22.7
Length of fibular crest	42.1 (3)	40.0–43.3
Least width of shaft at midpoint	11.8 (6)	11.4–12.1
Least depth of shaft at midpoint	9.6 (6)	8.9–10.2
Internal condyle depth	14.2 (4)	13.0–14.9
External condyle depth	14.1 (2)	14.1–14.2
Metatarsal I		
Total length	26.6 (5)	25.8–27.7
Width through digital condyle	13.9 (5)	13.5–14.7
Phalanx 1 digit I		
Total length	37.6 (4)	36.6–38.9
Proximal width	16.8 (5)	16.1–18.0
Least width at midpoint	8.0 (5)	7.6–8.6
Depth at midpoint	5.6 (5)	5.3–5.7
Distal width	9.2 (4)	8.9–10.0
Phalanx 2 digit II		
Total length	35.0 (1)	—
Proximal width	10.9 (1)	—
Proximal depth	9.6 (1)	—
Width at midpoint	7.5 (1)	—
Depth at midpoint	6.6 (1)	—
Distal width	8.7 (1)	—
Distal depth	8.4 (1)	—
Ungual phalanx digit I		
Articulation width	10.2 (5)	9.7–10.5
Articulation depth	11.1 (5)	10.8–11.5
Ungual phalanx digit II		
Articulation width	8.6 (6)	8.3–8.9
Articulation depth	10.7 (6)	10.5–11.2
Ungual phalanx digit III		
Articulation width	7.6 (4)	7.4–8.1
Articulation depth	7.5 (2)	7.5–7.6

and intercondylar sulcus wider; tibiotarsus shorter, with fibular crest high on shaft (or proximal) and less projected, supratendinal bridge wider, tendinal groove deeper and thin, external-distal border of shaft greatly compressed antero-posteriorly, forming a distinct depression in the posterior surface; tarsometatarsus shorter and more robust, more curved posteriorly in lateral view, with the tubercle for M. tibialis anticus larger and laterally located (in the center of shaft in *B. daggetti*), trochlea for digit II much more distally projected. *B. daggetti* is a scaled-up version of *B. meridionalis* (Olson 2007) and thus differs from *B. borrasi* in the same way that *B. meridionalis* differs from *B. urubitinga*.

Buteogallus borrasi differs from the type material of *Titanohierax gloveralleni* in having a much smaller carpometacarpus (the fragmentary nature of the single carpometacarpus referred to the latter species prevents further comparison), and a more slender and elongated tarsometatarsus, with the outer side deeply excavated; shaft not compressed distally in an antero-posterior direction, resulting in a more triangular shaft in cross section, and much less ex-

Table 4. Measurements (mm) of the tarsometatarsus in fossil hawks from North America (Rancho La Brea) and the West Indies. Range, (mean), *N*.

CHARACTER	*BUTEOGALLUS BORRASI*	*BUTEOGALLUS FRAGILIS*	*BUTEOGALLUS DAGGETTI*	*TITANOHIERAX GLOVERALLENI*	*AMPLIBUTEO WOODWARDI*	*GIGANTOHIERAX SUAREZI*
Total length	162.1–165.2 (163.6) 2	98.5–112.9 (102.8) 33	167.9–174.8 (171.3) 2	—	125.6–140.2 (131.6) 20	—
Proximal width	20.5–22.4 (21.4) 8	15.0–18.1 (16.5) 33	20.7–21.1 (20.9) 3	—	21.4–25.5 (23.0) 20	—
Least width of shaft	9.2–11.3 (11.0) 7	6.4–8.4 (7.3) 33	8.2–9.0 (8.7) 6	13.3	8.9–11.9 (10.1) 28	17.3–19.6 (18.4) 2
Least depth of shaft at proximal end of metatarsal facet	7.7–9.0 (8.5) 7	5.7–7.4 (6.3) 33	7.2–7.8 (7.5) 5	9.5	7.7–10.0 (8.7) 28	13.7
Distal width	24.0–26.3 (25.3) 3	17.4–20.4 (18.9) 32	21.9–23.9 (22.8) 7	—	23.1–28.8 (26.1) 25	—
Depth of trochlea for digit II	12.5–13.4 (12.9) 4	8.3–10.7 (9.7) 33	11.0–12.3 (11.5) 5	—	12.5–15.5 (14.0) 27	—
Width of trochlea for digit III	6.4–7.4 (6.9) 5	4.9–5.9 (5.4) 33	6.0–7.1 (6.6) 7	7.6	6.8–8.4 (7.4) 28	—
Depth of trochlea for digit III	8.8–10.0 (9.3) 4	6.8–8.1 (7.6) 33	7.7–8.6 (8.2) 5	11.0	9.8–12.1 (10.2) 27	—
Depth of trochlea for digit IV	10.2–12.4 (11.8) 6	8.1–10.3 (8.9) 31	10.5–11.6 (10.8) 4	14.2	11.3–13.7 (11.7) 24	—

pansion at the distal end; trochleae flaring more gradually, not abruptly from shaft.

Buteogallus borrasi differs from *Amplibuteo woodwardi* by having the humerus smaller and relatively more gracile, with proportionally longer shaft, reduced ligamental furrow, bicipital surface more projected and rounded, deltoid crest turning internally (or more centrally orientated), forming a more open angle in relation with shaft; distal end less flared (narrower), brachial depression larger and deeper; in posterior view the pneumatic foramen is larger, and the capital groove thin and shallow; ulna much smaller and gracile, with anconal and inner papillae of the secondaries less defined; carpometacarpus also much smaller, although similar in general configuration; femur slightly smaller, weakly pneumatic with one or two small, more rounded pneumatic foramina; fovea capitis extended and shallow, vertically oriented; shaft compressed antero-posteriorly (flatter), especially at the ends; anterior intermuscular line more laterally located, not developed and restricted to the proximal half of shaft (more centrally placed, extending farther down on shaft in *Amplibuteo woodwardi*), condyles short; tibiotarsus with gracile shaft, fibular crest larger and much less projected, tendinal groove deep and thin, distal point of fusion of fibula higher, internal condyle small and less projected internally, posterior-internal side acute at distal end; tarsometatarsus very slender with a gracile shaft, trochleae flaring greatly, trochlea for digit II projecting farther distally, deep anterior and posterior metatarsal grooves; phalanx 1 of digit I slender, less robust and even more curved downward; ungual phalanges more curved (see Suárez 2004, for additional comparisons with material of *A. woodwardi* from Cuba).

Buteogallus borrasi differs from *Gigantohierax suarezi* in the following qualitative characters: femur stout, not flaring greatly at ends (greatly flared and expanded at proximal and distal ends in *G. suarezi*), shaft slightly compressed antero-posteriorly (greatly compressed in *G. suarezi*), shaft not twisted, one or two small, rounded pneumatic foramina (twisted at proximal end, greater pneumaticity with presence of a very large, shallow, proximal pneumatic foramen, and a very deep, semi-triangular distal pneumatic foramen in *G. suarezi*); tarsometatarsus much smaller, gracile, and slender, with shaft very long, not compressed antero-posteriorly, metatarsal grooves greatly excavated (greatly compressed antero-posteriorly, wide and stout, metatarsal grooves poorly excavated in *G. suarezi*).

DISCUSSION

Wetmore (1937) described *Titanohierax gloveralleni* as supposedly similar to the living Great Black-Hawk (*Hypomorphnus* [= *Buteogallus*] *urubitinga*), but larger. Olson and Hilgartner (1982:27) considered that *Titanohierax* Wetmore is even more similar to *Geranoaetus* Kaup than to *Buteogallus* Lesson. Apart from size, characters described by Wetmore (1937) as distinctive of the tarsometatarsus of *T. gloveralleni*, in comparison with *Hypomorphnus* (= *Buteogallus*) *urubitinga*, also serve to distinguish the Bahaman fossils from *B. borrasi*, which is a more gracile bird than the other three large fossil raptors recorded in the West Indies (*Titanohierax gloveralleni*, *Gigantohierax suarezi*, and *Amplibuteo woodwardi*).

The so-called ''walking eagle'' (*Wetmoregyps daggetti*) from fossil deposits in California and Mexico proved to be a scaled-up version of the Savanna Hawk (*B. meridionalis*) and was transferred to the genus *Buteogallus* (Olson 2007). It was postulated that *B. daggetti* may have occupied the niche of a Secretary Bird (*Sagittarius serpentarius*) and may have been as large or larger than that species, averaging some 40% larger than *B. meridionalis* (Olson 2007).

Buteogallus borrasi averaged about 33% larger than *B. urubitinga* (Table 1), but because the latter species is considerably larger than *B. meridionalis*, the two fossil species (*B. borrasi* and *B. daggetti*) may have been of roughly equivalent bulk. The Great Black-Hawk (*B. urubitinga*) is widely distributed from Mexico to Argentina. Although it is generally a forest bird, its choice of habitats are extremely diverse and it may occur in wooded savanna or even dry scrub or cultivated areas with scattered trees (Ferguson-Lees and Christie 2001). *Buteogallus borrasi* is the most common accipitrid in Quaternary deposits of Cuba, especially in those located at Llanura Meridional de La Habana, where most of the avian taxa recorded indicate the presence of savannas around the caves during deposition (see Suárez 2000b). The morphology of the tarsus suggests that it was probably not as terrestrial in habits as *B. daggetti*, however.

Considering that the morphology of *B. borrasi* is so similar to that of the Great Black-Hawk (*B. urubitinga*), it could be postulated that the former was derived from the latter. Emslie (1998) recorded *B. urubitinga* from late Pliocene deposits in Florida and the species might thus have reached Cuba from there. During the Pleistocene, Cuba supported a variety of small to medium-sized land mammals such as rodents and insectivores that may have been prey for *B. borrasi*. It is also highly probable that there was a greater diversity of reptiles in dry open areas (a large sample of unidentified reptiles from Quaternary cave deposits exists in Cuban collections; W. Suárez unpubl. data).

On the other hand, *B. borrasi* may have evolved on the mainland, where it has gone undetected or unrecognized in the fossil record, colonized Cuba, became extinct on the mainland, and by the late Pleistocene survived only as a relict in Cuba. In this connection, we call attention to the species *Urubitinga* (=*Buteogallus*) *milleri* Howard (1932:25), which was described as slightly larger than *B. fragilis*. It is known only from two incomplete specimens, a fragmentary coracoid (holotype) and the distal half of a humerus from Quaternary deposits at Hawver Cave, El Dorado County, California. Although these elements are apparently close in size to *B. borrasi*, the generic allocation of *B. milleri* is unclear because of the paucity and nondiagnostic nature of the specimens. Comparison is hampered further because the single known coracoid of *B. borrasi* is fragmentary. Adequate taxonomic assessment of the possible similarities between these two taxa would require the recovery of additional material, especially of the continental species.

It is not unlikely that *B. borrasi* had a wider distribution in the West Indies, as was the case for other species of Accipitridae. Morgan (1994) recorded from Crab Cave in Grand Cayman, Cayman Islands, two partial mandibles of a large accipitrid he identified as *Titanohierax gloveralleni*, noting its resemblance to *Buteogallus*. For the present, this record should be listed only as Accipitridae gen. et sp. indet., because two of the large hawks recorded in Cuba, *B. borrasi* and *Amplibuteo woodwardi*, are more or less similar in size to *Titanohierax gloveralleni*, and both are more closely related to *Buteogallus* than is the Bahaman bird. Additional fossils of the Cayman Island hawk will probably be needed to resolve its identity.

As we will continue to document, the living medium-sized hawks of the genus *Buteogallus* are very closely related to several eagle-sized species both living and fossil. This may be a common pattern in the Accipitridae, so that the closest affinities of various lineages of large ''eagles,'' living and fossil, may eventually be shown to lie with smaller species, rather than with each other.

ACKNOWLEDGMENTS

W. Suárez' visits to the National Museum of Natural History, Smithsonian Institution, and to the George C.

Page Museum of La Brea Discoveries, Los Angeles, California, were made possible by the Alexander Wetmore Endowment Fund of the Division of Birds, Smithsonian Institution. We express our gratitude to Kenneth E. Campbell, Jr., Natural History Museum of Los Angeles County, for his assistance to W. Suárez during revision of collections from Rancho La Brea. We are grateful to René Dekker (Leiden) and Douglas Causey (MCZ) for the loan of critical specimens. Thanks are extended to many Cuban colleagues who helped during study of collections in Cuba. W. Suárez especially thanks Fritz Hertel, California State University, Northridge, and Steven J. Parry, Bird Group, The Natural History Museum, Tring, U.K., for their help and kindness during his visit to Los Angeles. The figures were composed by Brian Schmidt, Smithsonian Institution. We are grateful to David Steadman, Florida State Museum, Fritz Hertel, and an anonymous reviewer for their comments on the manuscript.

LITERATURE CITED

ACEVEDO-GONZÁLEZ, M. AND O. ARREDONDO. 1982. Paleogeografía y geología del Cuaternario de Cuba: Características y distribución geográfica de los depósitos con restos de vertebrados. *Actas IX Jornada Científica del Instituto de Geología y Paleontología*: 59–70.

———, ———, AND N. GONZÁLEZ GOTERA. 1975. La Cueva del Túnel. Editorial Pueblo y Educación, Instituto Cubano del Libro, La Habana, Cuba.

ALCOVER, J.A. AND M. MCMINN. 1994. Predators of vertebrates on islands. *BioScience* 44:12–18.

ARREDONDO, O. 1970. Nueva especie de ave pleistocénica del orden Accipitriformes (Accipitridae) y nuevo género para las Antillas. *Cienc. Biol.* Univ. La Habana, ser. 4, 8:1–19.

———. 1971. Nuevo género y especie de ave fósil (Accipitriformes: Vulturidae) del Pleistoceno de Cuba. *Mem. Soc. Cienc. Nat. La Salle* 31:309–323.

———. 1972. Nueva especie de ave fósil (Strigiformes: Tytonidae) del Pleistoceno superior de Cuba. *Bol. Soc. Venez. Cienc. Nat.* 29:415–431.

———. 1975. Distribución geográfica y descripción de algunos huesos de *Ornimegalonyx oteroi* Arredondo, 1958 (Strigiformes: Strigidae) del Pleistoceno superior de Cuba. *Mem. Soc. Cienc. Nat. La Salle* 35:133–190.

———. 1976. The great predatory birds of the Pleistocene of Cuba [translated and amended by S.L. Olson]. Pages 169–187 *in* S.L. Olson [ED.], Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. *Smithson. Contrib. Paleobiol.* 27.

———. 1982. Los Strigiformes fósiles del Pleistoceno cubano. *Bol. Soc. Venez. Cienc. Nat.* 140:33–55.

———. 1984. Sinopsis de las aves halladas en depósitos fosilíferos pleisto-holocénicos de Cuba. *Reporte de Investigación del Instituto de Zoología* 17:1–35.

——— AND C. ARREDONDO. 2002a. Nuevos género y especie de ave fósil (Falconiformes: Accipitridae) del Cuaternario de Cuba. *Poeyana* 470–475 (for 1999):9–14.

——— AND ———. 2002b. Nueva especie de ave (Falconiformes: Teratornithidae) del Pleistoceno de Cuba. *Poeyana*, 470–475 (for 1999):15–21.

——— AND L.S. VARONA. 1974. Nuevos género y especie de mamífero (Carnivora: Canidae) del Cuaternario de Cuba. *Poeyana* 131:1–12.

BRODKORB, P. 1971. Catalogue of fossil birds. Part 4 (Columbiformes through Piciformes). *Bull. Fla. State Mus. Biol. Sci.* 15:163–266.

CAMPBELL, K.E., JR. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *Contrib. Life Sci. Div. R. Ont. Mus.* 118:1–203.

CHIRINO, N. 1996. Subphylum Vertebrata. Clase Aves. Pages 104–178 *in* C. Arredondo Antúnez, R. Armiñana García, N. Chirino Flores, and R. Agüero Cobiellas [EDS.]. Zoología de los Cordados. Pueblo y Educación, La Habana, Cuba.

CUELLO, J.P. 1988. Lista de las aves fósiles de la región neotropical y las islas antillanas. *Paula-Coutiana* 2:3–79.

EMSLIE, S.D. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida peninsula. *Ornithol. Monogr.* 50:1–113.

——— AND N.J. CZAPLEWSKI. 1999. Two new fossil eagles from the late Pliocene (late Blancan) of Florida and Arizona and their biogeographic implications. Pages 185–198 *in* S.L. Olson [ED.], Avian paleontology at the close of the 20th century: proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, DC, 4–7 June 1996. *Smithson. Contrib. Paleobiol.* 89. Washington, DC U.S.A.

FEDUCCIA, A. 1999. The origin and evolution of birds. Second Ed. Yale Univ. Press, New Haven, CT U.S.A.

FERGUSON-LEES, J. AND D.A. CHRISTIE. 2001. Raptors of the world. Christopher Helm, London U.K.

FISCHER, K. 1977. Quartäre mikromammalia Cubas, vorwiegend aus der höhle San José de la Lamas, Santa Fé, Provinz Habana. *Z. Geologische Wiss.* 5:213–255.

GARRIDO, O.H. AND A. KIRKCONNELL. 2000. Field guide to the birds of Cuba. Cornell Univ. Press, Ithaca, NY U.S.A.

HOWARD, H. 1929. The avifauna of Emeryville shellmound. *Univ. Calif. Publ. Zool.* 32:301–394.

———. 1932. Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea. *Carnegie Inst. Washington Publ.* 429:1–82.

ITURRALDE-VINENT, M., R.D.E. MACPHEE, S. DÍAZ-FRANCO, R. ROJAS-CONSUEGRA, W. SUÁREZ, AND A. LOMBA. 2000. Las Breas de San Felipe, a Quaternary asphalt seep near Martí (Matanzas Province, Cuba). *Caribb. J. Sci.* 36:300–313.

JIMÉNEZ, V.O. AND P.R. VALDÉS. 1995. Los vertebrados fósiles de la Cueva del Indio, San José de las Lajas, Habana, Cuba. Pages 62–63 *in* Congreso Internacional LV Aniversario de la Sociedad Espeleológica de Cuba, Resúmenes, La Habana, Cuba.

MORGAN, G.S. 1994. Late Quaternary fossil vertebrates from the Cayman Islands. Pages 465–508 *in* M.A. Brunt and J.E. Davies [EDS.], The Cayman Islands: natural history and biogeography. Kluwer Academic Publishers, Dordrecht, Netherlands.

——— AND J.A. OTTENWALDER. 1993. A new extinct species of *Solenodon* (Mammalia: Insectivora: Solenodontidae) from the late Quaternary of Cuba. *Ann. Carnegie Mus.* 62:151–164.

———, C.E. RAY, AND O. ARREDONDO. 1980. A giant extinct insectivore from Cuba (Mammalia: Insectivora: Solenodontidae). *Proc. Biol. Soc. Wash.* 93:597–608.

OLSON, S.L. 1978. A paleontological perspective of West Indian birds and mammals. *Spec. Publ. Acad. Nat. Sci. Phila.* 13:99–117.

———. 2007. The ''walking eagle'' *Wetmoregyps daggetti* Miller—a scaled-up version of the Savanna Hawk *Buteogallus meridionalis*. *Ornithol. Monogr.* 63:110–113.

——— AND W.B. HILGARTNER. 1982. Fossil and subfossil birds from the Bahamas. Pages 22–56 *in* S.L. Olson [ED.], Fossil vertebrates from the Bahamas. *Smithson. Contrib. Paleobiol.* 48.

SUÁREZ, W. 2000a. Contribución al conocimiento del estatus genérico del cóndor extinto (Ciconiiformes: Vulturidae) del Cuaternario cubano. *Ornitol. Neotrop.* 11: 109–122.

———. 2000b. Fossil evidence for the occurrence of Cuban Poorwill *Siphonorhis daiquiri* in western Cuba. *Cotinga* 14:66–68.

———. 2001. A reevaluation of some fossils identified as vultures (Aves: Vulturidae) from Quaternary cave deposits of Cuba. *Caribb. J. Sci* 37:110–111.

———. 2004. The identity of the fossil raptor of the genus *Amplibuteo* (Aves: Accipitridae) from the Quaternary of Cuba. *Caribb. J. Sci* 40:120–125.

VARONA, L.S. AND O. ARREDONDO. 1979. Nuevos taxones fósiles de Capromyidae (Rodentia: Caviomorpha). *Poeyana* 195:1–15.

VERGARA, R.R. 1988. Relaciones biogeográficas de la avifauna cubana. I. Biogeografía histórica. *Cienc. Biol.* 19–20:51–61.

———. 2003. Relaciones biogeográficas de la avifauna cubana. II.Biogeografía descriptiva. *Ornitol. Neotrop.* 14:441–467.

WETMORE, A. 1937. Bird remains from cave deposits on Great Exuma Island in the Bahamas. *Bull. Mus. Comp. Zool.* 80:427–441.

Received 10 January 2007; accepted 20 April 2007