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# A new fossil raptor (Accipitridae: *Buteogallus*) from Quaternary cave deposits in Cuba and Hispaniola, West Indies

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**SUMMARY.**—A large, extinct species of *Buteogallus* Lesson is described from post-cranial elements in Quaternary cave deposits in western Cuba and south-central Hispaniola. The new taxon was approximately the same size as females of the extinct continental *B. woodwardi*, but more robust. Some fossils, recently documented from Hispaniola as Accipitridae genus and species indeterminate, are probably referable to taxa previously known from Cuba, including the new species described herein. Osteological comparisons of both living and extinct species indicate that the extinct genus *Amplibuteo* Campbell is synonymous with *Buteogallus*.

A partial skeleton of a large accipitrid from a Quaternary deposit at Cueva de Sandoval, western Cuba, was recorded as *Amplibuteo* sp. by Suárez & Arredondo (1997). This report extended the distribution of the genus to the West Indies; it was previously restricted to fossil localities in the continental Americas (Campbell 1979, Emslie & Czaplewski 1999). The material was subsequently identified (Suárez 2004) as *A. (Morphnus* auct.) *woodwardi* (L. Miller, 1911), a palaeospecies well known from the late Pleistocene of Rancho La Brea (RLB), California, south-west USA (Miller 1911, 1925, Howard 1932, Campbell 1979), but also recorded from the middle and late Pleistocene of Florida (Emslie 1995, 1998). Suárez (2004: 122) noted that Cuban material differed from continental *A. woodwardi* and that ‘the middle trochlea of the tarsometatarsus is proportionally slightly smaller. Although the series of tarsometatarsi from RLB ( $n=31$ ) show a high degree of individual variation, especially in proportions and shape of the shaft and trochleae, no specimen agrees with the Cuban one in this small detail’.

More recently, we examined fossil raptors from the late Pleistocene Talara Tar Seeps, north-west Peru (Suárez & Olson 2009b, 2014; see Seymour 2015) at the Royal Ontario Museum, Toronto, Canada, especially specimens of *Amplibuteo hibbardi* Campbell, 1979, to compare the type species of the genus (Campbell 1979: 83). An incomplete fossil tarsometatarsus from the Dominican Republic (Hispaniola), collected by C. Woods and identified as *Titanohierax* sp. by Olson & Hilgartner (1982: 28) was included in these comparisons and found to represent an undescribed species of *Amplibuteo* together with the previously known Cuban material (see Suárez & Olson 2008: Fig. 1C). Moreover, this specimen from Hispaniola, with better preserved trochleae, matches all characters of the single tarsometatarsus previously interpreted as individual variation within *A. woodwardi* (Suárez 2004).

The extinct genus *Amplibuteo* Campbell was described as closely related to living *Buteo* Lacépède and *Geranoaetus* Kaup (Campbell 1979: 83), but Emslie & Czaplewski (1999: 189) considered it more similar to, and a possible synonym of, *Harpyhaliaetus* Lafresnaye. Following comparison of the two large *Amplibuteo* species—from the Pleistocene of South and North America—and the two living *Harpyhaliaetus*—Black Solitary Eagle *H. solitarius* (von Tschudi, 1844) and Crowned Solitary Eagle *H. coronatus* (Vieillot, 1817)—we observed

a strong resemblance between the palaeospecies and the skeletal morphology of *H. solitarius*, and could not find any generic distinction between *Harpyhaliaetus* and *Amplibuteo*. The tarsometatarsi exhibit only characters of specific value, related to (or derived from) differences in raptorial habits between living (see Seminario *et al.* 2011, Phillips 2012) and fossil species, due to specialisation on particular prey. Some of these osteological characters (see Results), frequently present in other accipitrids, perhaps misled Campbell (1979: 83) who thought *Amplibuteo* more closely related to *Buteo* and *Geranoaetus* than to *Harpyhaliaetus*. But contrarily, Campbell (1979: 83) correctly stated that *Amplibuteo* 'is quite distinct from... *Titanohierax*', a large extinct buteonine hawk from the Bahamas, similar to *Geranoaetus* (Olson & Hilgartner 1982: 27).

Black Solitary Eagle (see Amadon 1949) was considered congeneric with Crowned Solitary Eagle in the genus *Harpyhaliaetus* since Sharpe (1874), but has also been placed in *Urubitornis* J. Verreaux, 1856, and other genera (Peters 1931, van Rossem 1948, Friedmann 1950, Wetmore 1965). This species, which is darker overall than *H. coronatus*, has a plumage pattern (in different ontogenic stages) similar to Common Black Hawk *Buteogallus anthracinus* (Deppe, 1830) and Great Black Hawk *B. urubitinga* (J. F. Gmelin, 1788), being larger and more robust, with a heavier tarsus, shorter tail and general morphology indicative of more rapacious habits (Amadon 1949: 54, Brown & Amadon 1968: 559–560). As we previously indicated (Olson 2007: 111, Suárez & Olson 2008: 296, 2009b: 249, Suárez 2020: 27), strong osteological similarities exist between *Amplibuteo* (or *Harpyhaliaetus*) and other living and extinct species of *Buteogallus* Lesson. *Harpyhaliaetus* is nowadays considered a junior synonym of *Buteogallus* based on morphological and mtDNA sequence data (Amaral *et al.* 2006, 2009, Lerner *et al.* 2008; see Chesser *et al.* 2012), and we concur.

Herein we relocate under *Buteogallus* the fossil material identified as *Titanohierax* sp. from Hispaniola (Olson & Hilgartner 1982), and *Amplibuteo woodwardi* from Cuba (Suárez 2004), and describe it as a new species shared by the two largest islands of the Greater Antilles.

## Material and Methods

Comparison was made with all modern Accipitridae in the skeletal collection of the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM; fossils at the Dept. of Paleobiology are registered under the acronym USNM PAL), the American Museum of Natural History, New York (AMNH), and University of Michigan Museum of Zoology, Ann Arbor (UMMZ), including *Buteogallus anthracinus*, Cuban Black Hawk *B. gundlachi* (Cabanis, 1855), Rufous Crab Hawk *B. aequinoctialis* (J. F. Gmelin, 1788), Savanna Hawk *B. meridionalis* (Latham, 1790) and *B. urubitinga*. One skeleton of *Buteogallus* ('*Harpyhaliaetus*') *solitarius* from the Los Angeles County Natural History Museum (LACM 110091) and another of *B.* ('*H.*') *coronatus* from Naturalis, Leiden (uncatalogued) were available for comparison and measurements (see Table 1). Fossil material of Accipitridae examined in the extensive collections of the George C. Page Museum, La Brea Discoveries, Los Angeles, include *B. fragilis* (L. Miller, 1911), *B. daggetti* (L. Miller, 1915), '*Amplibuteo*' *woodwardi*, *Spizaetus grinnelli* (L. Miller, 1911), Golden Eagle *Aquila chrysaetos* (Linnaeus, 1758) and Bald Eagle *Haliaeetus leucocephalus* (Linnaeus, 1766). The type material of '*Amplibuteo*' *hibbardi* and *Buteogallus terrestris* (Campbell, 1979) from Peru (Campbell 1979; see Suárez & Olson 2009b) was examined at the Royal Ontario Museum, Toronto (ROM). Fossils of *B. borraasi* (Arredondo, 1970) from Cuba used in this study are the specimens and deposits listed by Suárez & Olson (2008: 289–293) including the holotype left tarsometatarsus (Dpto. de Paleontología Universidad de la Habana, DPUH 1250). From the Museo Nacional de Historia Natural de Cuba (MNHNCu), La Habana, and William Suárez collection (WS), La

TABLE 1

Measurements (mm) of tarsometatarsi of *Buteogallus irpus* sp. nov., compared to those of other extinct and living congeneric species of approximately similar size, in the format: range (mean, sample size).

Character	<i>B. irpus</i> sp. nov.	<i>B. woodwardi</i>	<i>B. hibbaridi</i>	<i>B. borraisi</i>	<i>B. coronatus</i>	<i>B. solitarius</i>
Total length	132.7	125.6–140.2 (131.6, 20)	132.3–136.5 (134.3, 3 <sup>A</sup> )	162.1–165.2 (163.6, 2 <sup>B</sup> )	118.9	126.0
Proximal width	25.5	21.4–25.5 (23.0, 20)	22.2–25.0 (23.7, 3 <sup>A</sup> )	20.5–22.4 (21.4, 8 <sup>B</sup> )	21.9	20.6
Minimum shaft width	11.3–11.8 (11.6) 2	8.9–11.9 (10.1, 28)	10.1–11.7 (10.9, 2 <sup>A</sup> )	9.2–11.3 (11.0, 7 <sup>B</sup> )	10.2	9.9
Shaft width above metatarsal facet	13.0	10.1–12.4 (11.0, 20)	11.9–12.1 (11.0, 2)	10.4–11.4 (10.8, 7)	11.2	10.0
Distal width	26.3+, 27+	23.1–28.8 (26.1, 25)	25.2–29.3 (27.1, 6 <sup>A</sup> )	24.0–26.3 (25.3, 3 <sup>B</sup> )	25.2	23.4
Width of trochlea III	8.1–8.3 (8.2) 2	6.8–8.4 (7.4, 28)	6.9–8.1 (7.4, 8 <sup>A</sup> )	6.4–7.4 (6.9, 5 <sup>B</sup> )	7.0	6.2

<sup>A</sup> Campbell (1979: Table 6).

<sup>B</sup> Suárez & Olson (2008: Table 4).

Habana, we examined the holotype left tarsometatarsus of *B. royi* Suárez, 2020 (MNHNCu 75.4909), the holotype distal right tarsometatarsus of *Gigantohierax itchei* Suárez, 2020 (MNHNCu 75.4869), and selected material of *G. suarezi* Arredondo & Arredondo, 2002, including a right tarsometatarsus lacking proximal end and part of the medial border (MNHNCu 75.4728), distal half of left tarsometatarsus (MNHNCu 75.4729), distal end of left tarsometatarsus without trochlea IV (MNHNCu 75.4730), paratype fragmentary tarsometatarsus (WS 80120.E) and paratype shaft of right tarsometatarsus (WS 8012). The holotype tarsometatarsus (MCZ 2257) of *Titanohierax gloveralleni* Wetmore, 1937, on loan from the Museum of Comparative Zoology, Harvard Univ., MA, was also examined. Photographs, measurements and descriptions published by Emslie & Czaplewski (1999) and Steadman *et al.* (2019) were used for comparisons with '*Amplibuteo*' *concordatus* Emslie & Czaplewski, 1999, and to evaluate fossil specimens of accipitrids recorded from Hispaniola, respectively. Osteological terminology is modified from Howard (1929) and Baumel & Witmer (1993). Measurements were taken to the nearest 0.1 mm using digital callipers. The annotation (+) indicates fracture or abrasion to the specimen, and that the given measurement will be less than the original value. A vernacular name for the newly described species is proposed, along with its Spanish equivalent.

## Results

### *Systematic paleontology*

Order ACCIPITRIFORMES Vieillot

Family ACCIPITRIDAE Vieillot

Genus *Buteogallus* Lesson, 1830, *Traité d'Orn.*, livr. 2, p. 83. Type, by monotypy, *Buteogallus cathartoides* Lesson, 1830 = *Falco aequinoctialis* J. F. Gmelin, 1788.

**Synonym.** *Amplibuteo* Campbell, 1979: 77; type species by original designation *Amplibuteo hibbaridi* Campbell, new synonymy.

Characters of the tarsometatarsus described by Campbell (1979: 77) as diagnostic of '*Amplibuteo*', but recorded by him as present in *Buteogallus* (= '*Haryphalictus*' and

'*Heterospizias Sharpe*', see diagnosis of '*Miraquila*' Campbell 1979: 74), include: '(1) inner calcaneal ridge of hypotarsus projecting posteriad at approximately 60–70° to vertical axis of shaft [= '*Harpyhaliaetus*']; (2) intercotylar area elevated slightly [= '*Heterospizias*' and '*Buteogallus*']; (3) edge of shaft external to outer calcaneal ridge of hypotarsus without ridge [more similar to '*Harpyhaliaetus*', character of specific value, variable in '*Buteogallus*', see Suárez & Olson 2009b: 250]; (4) anterior metatarsal groove moderately deep [= '*Heterospizias*' and '*Buteogallus*']; (5) internal anterior metatarsal ridge only slightly developed [= '*Buteogallus*']; (6) attachment of tibialis anticus not separated from external anterior metatarsal ridge by groove [= '*Harpyhaliaetus*' and '*Heterospizias*']; (7) middle trochlea short, turned significantly externally in anterior view [= '*Harpyhaliaetus*']; (8) internal trochlea rotated posteriad such that posteromedial edge is at same level as posterolateral edge of middle trochlea [= '*Heterospizias*' and '*Buteogallus*']; (9) internal trochlea projecting distad beyond middle trochlea and rotated significantly externally in anterior view [= '*Harpyhaliaetus*']; (10) internal trochlea with distinct angular proximolateral projection [= '*Harpyhaliaetus*' and '*Heterospizias*']. Therefore, the extinct taxa currently placed in '*Amplibuteo*' are treated herein under '*Buteogallus*', as *B. woodwardi* (L. Miller, 1911) new comb., *B. hibbardi* (Campbell, 1979) new comb., and *B. concordatus* (Emslie & Czaplewski, 1999) new comb., which are all members of the Buteogalline radiation among extinct Accipitridae from America (cf. Olson 2007, Suárez & Olson 2008, 2009b). Specimens of the new species also replicate the general skeletal morphology present in the living *B. solitarius* (or vice versa), being part of a small (apparently monophyletic) assemblage of allopatric-allochronic fossil species that includes *B. concordatus* and *B. woodwardi*, from North America, and *B. hibbardi* from South America.

***Buteogallus irpus* sp. nov.**

Wolf Hawk / Gavilán Lobo

(Figs. 1A–E, 2A–B, 3; Table 1)

References:

*Titanohierax gloveralleni*: Woods 1980: 8 (part).

*Titanohierax* sp.: Olson & Hilgartner 1982: 28.

*Amplibuteo* sp.: Suárez & Arredondo 1997: 100.

*Amplibuteo woodwardi*: Suárez 2004: 121.

**Holotype.**—Left tarsometatarsus lacking proximal end, USNM PAL 299573 (Figs. 1A–E, 2A; not 'USNM 244573' [*lapsus calami*], as reported by Olson & Hilgartner 1982: 28). Collected by Charles Woods under 60 cm of red earth, at the type locality, on 24 April 1978. This specimen was incorrectly cited as 'a tarsometatarsus lacking its distal end (USNM 244573, from Cueva de las Abejas)' by Steadman *et al.* (2019: 328).

**Paratype.**—Cueva de Sandoval (Sandoval III low deposit), c.4 km south of Vereda Nueva, Caimito municipality, Artemisa (formerly La Habana) province, Cuba: partial skeleton WS 365, with one cervical (axis) and three thoracic vertebrae, seven fragments of ribs, fragmentary pelvis, proximal fragmentary right humerus, distal fragments of left humerus, segment of shaft of left ulna, left fragmentary femur without distal end, proximal and distal fragmentary ends of right femur, shaft of left tibiotarsus, proximal right fibula, left tarsometatarsus (lacking inner calcaneal ridge, part of the proximal end of the metatarsal facet, wing of trochlea II and posterior surface of trochlea III) (Fig. 2B), left digit I-phalanx 1 and 2, left digit III-phalanx 2 and 3, right digit III-phalanx 4, right digit IV-phalanx 4. Collected by WS on 2 March 1995. Quaternary, probably late Pleistocene, but not directly dated (see Suárez 2000). For illustrations and description see Suárez (2004: 121–123, Figs. 1–2).



Figure 1. Holotype left tarsometatarsus (USNM PAL 299573) of *Buteogallus irpus* sp. nov., in anterior (A), medial (B), distal (C), posterior (D) and lateral (E) views. Scale = 2 cm.

**Measurements of holotype.**—Total length as preserved: 124.9 mm; proximal width at distal level of tubercle for tibialis anticus: 17.0 mm; width of shaft at midpoint: 13.2 mm; minimum width of shaft: 11.8 mm; minimum width of shaft at proximal end of metatarsal facet: 13.0 mm; depth of lateral side at proximal end of metatarsal facet: 9.8 mm; distance from proximal edge of metatarsal facet to inner inter-trochlear notch: 30.3 mm; distal width: 27+ mm; width of trochlea III: 8.3 mm; depth of trochlea IV: 12.2 mm (Table 1).

**Diagnosis.**—Resembles *B. woodwardi* and *B. hibbardi* in size and general morphology, but tarsometatarsus more robust, with shaft expanded at distal end, and trochleae relatively shorter in *B. irpus*.

**Measurements of paratype.**—See Suárez (2004: 123–124, Table 1, Fig. 3), Table 1.

**Type locality and age.**—Cueva de las Abejas (18°01'N, 71°40'W; c.20 m), near Cabo Rojo, 8 km south-east of Pedernales, 1.5 km north of Highway 44, Pedernales province, Dominican Republic. Quaternary, probably late Pleistocene, but not directly dated (see Olson & Hilgartner 1982: 28, Steadman *et al.* 2019: 321).

**Etymology.**—From Latin *irpus*, = wolf, in reference to the ecological role played by this large raptor in controlling the regional 'megafauna' on the two largest islands of the Greater Antilles, occupying the ecological niche of a carnivorous mammal (*cf.* Arredondo 1976, Morgan *et al.* 1980).

**Status.**—Extinct, known only from fossil material.

**Description.**—The skeleton of *B. irpus* sp. nov. (Figs. 1–2; see Suárez 2004: Figs. 1–2, Suárez & Olson 2008: Fig. 1) is partially represented by fragmentary material, with the tarsometatarsus best preserved and more diagnostic of the known elements (see Olson



Figure 2. Tarsometatarsi of large extinct West Indian and North American Accipitridae in anterior view (A–F). *Buteogallus irpus* sp. nov.: (A) left without proximal end (holotype, USNM PAL 299573), (B) left (paratype, WS 365 [part of the proximal end of the metatarsal facet is lacking due to fracture, so the complete specimen would be wider at this point]). *B. woodwardi* new comb.: (C) left (RLB D1970). *Gigantohierax itchei*: (D) distal third of right without trochlea IV (holotype, MNHNCu 75.4869). *Titanohierax gloveralleni*: (E) right without proximal end and trochlea II (holotype, MCZ 2257). *Buteogallus borrasii*: (F) right (CZACC 400-659). Images D–F are reversed to facilitate comparisons. Scale = 2 cm.

& Hilgartner 1982: 28, Suárez 2004: 121). Both tarsometatarsi under study (holotype and paratype, see above) represent adults, probably of different sexes. These fossils are similar in general morphology to the equivalent elements in the extant *B. solitarius* and the Quaternary extinct *B. woodwardi* and *B. hibbardi*, but *B. irpus* is much larger and robust than material available of the living species (Table 1). All other modern *Buteogallus* examined, including *B. anthracinus*, *B. gundlachii*, *B. aequinoctialis* (see Olson 2006, for discussion of some skeletal elements of this species), *B. meridionalis* and *B. urubitinga*, are much smaller than *B. irpus* sp. nov., and therefore do not require further comparison. *B. irpus* differs from the extinct *B. woodwardi* (Fig. 2C) and *B. hibbardi* (see Campbell 1979: Fig. 28 A(i)–(iii) = holotype ROM 16905) in having tarsometatarsus with stouter shaft (relatively thinner, more gracile in *B. woodwardi* and *B. hibbardi*), distal end flattened and more expanded bilaterally, especially above the trochleae (distal end thinner, less expanded in *B. woodwardi* and *B. hibbardi*), trochlea II short, poorly projected distad (longer, projected more distad in *B. woodwardi* and *B. hibbardi*), trochlea III small, nearly squared, with thin groove and more laterally angled (larger, less squared, with wide groove and less bent laterad in *B. woodwardi* and *B. hibbardi*). Trochleae deep and massive in distal view (trochleae shallower and less massive in *B. woodwardi* and *B. hibbardi*). The new species is larger than *B. concordatus* (see



Figure 3. Hypothetical reconstruction of Wolf Hawk *Buteogallus irpus* (William Suárez)

Suárez 2004: 122) from the late Pliocene (late Blancan) of Florida and Arizona which is the smallest of the former 'Amplibuteo' species (see Emslie & Czaplewski 1999).

Compared with tarsometatarsi of the continental extinct species *B. daggetti* and *B. terrestris* (the latter known from incomplete specimens), both represent more gracile species, with the former (c.40% larger than the average size of *B. meridionalis*, see Olson 2007) being the longest and more gracile of the extinct *Buteogallus* compared. The tarsometatarsus of *B. daggetti* differs from the same elements in *B. irpus* in being extremely elongated, gracile and straight, with a deep anterior metatarsal groove, tubercle for tibialis anticus well centred on the mid-line of the shaft and well separated from the anterior external metatarsal ridge by a wide groove (see Olson 2007: Figs. 1C, 2C, Suárez & Olson 2009b: Fig 1D). *B. daggetti* and *B. terrestris* do not exhibit the characteristic expanded distal end, or the reduction of the trochlea III (see Campbell 1979: Figs. E (i)–(ii), Olson 2007: Figs. 1C, 2C), diagnostic of *B. irpus* sp. nov. The extinct *B. fragilis* and *B. royi* are distinct, apart from their much smaller size when compared to *B. irpus* sp. nov., in having more slender or gracile tarsometatarsi, anterior and posterior metatarsal grooves deeper, and the tubercle for tibialis anticus more proximad (see Suárez 2020: Figs. 9–10).

*B. irpus* differs from comparable elements in extinct *B. borraisi* from Cuba, in having: humerus (see Suárez 2004, Figs. 2A–C, Suárez & Olson 2008, Fig. 2A) larger and robust, proximal head less projected, capital groove wider and deeper, and ligamental furrow larger (smaller and gracile, head more projected, capital groove thin and shallow, and ligamental



furrow smaller in *B. borrasii*). Ulna (in *B. irpus* sp. nov. known only by a segment of middle shaft, see Suárez 2004: Fig. 2D) robust, with better-developed inner and outer papillae of secondaries (more gracile, both papillae smaller or less developed in *B. borrasii*). Femur (see Suárez 2004: Fig. 2F–G) also more robust, with attachment of round ligament smaller and deeper (expanded, shallow and vertically oriented in *B. borrasii*), shaft cylindrical in cross section, less compressed anteroposteriorly at ends (more ovoid and compressed in *B. borrasii*), prominent anterior intermuscular line, more distally extended along the mid-line of the shaft (less developed, more laterally located and restricted to the proximal half of shaft in *B. borrasii*, see Suárez & Olson 2008: Fig. 3A), pneumatic foramen large and oval-shaped (consistently smaller and rounded in *B. borrasii*), and large condyles (smaller in *B. borrasii*). Tibiotarsus (in *B. irpus* sp. nov. known only by a proximal segment of shaft, see Suárez 2004: Fig. 2I) robust with fibular crest short and greatly projected (gracile, fibular crest larger but less projected in *B. borrasii*, see Suárez & Olson 2008: Fig. 3E). Tarsometatarsus (Figs. 1–2; see Suárez 2004: Fig. 2J–L, Suárez & Olson 2008: Fig. 1) shorter, wider, with robust shaft well expanded above the trochleae, and shallow anterior and posterior metatarsal grooves (gracile and slender, not expanded above the trochlea with deeper grooves in *B. borrasii*). Trochleae distally placed on shaft, trochlea III short, with marked lateral orientation. Phalanx I-digit 1 (see Suárez 2004: Fig. 2M) shorter, robust and not too curved downward (longer, less robust and more curved in *B. borrasii*). Ungual phalanges less curved than in *B. borrasii* (see Suárez 2004: Fig. 2N–O, Suárez 2020: Fig. 8H).

Compared with the holotype tarsometatarsus of *Titanohierax gloveralleni* (MCZ 2257) from the Bahamas (Fig. 2E), the same element in *B. irpus* is slightly smaller, shorter and robust, and less flattened, as it is less compressed anteroposteriorly at the distal end, the trochleae are shorter (trochlea II unknown in *T. gloveralleni*), especially trochlea IV, in which the lateral rim (distal view) is also less pronounced (longer, more projected distally, with lateral rim pronounced in *T. gloveralleni*), posterior metatarsal groove shallow (much deeper in *T. gloveralleni*) and metatarsal facet not as highly placed, or proximal (see Wetmore 1937: 430, Olson & Hilgartner 1982: 28).

*B. irpus* is considerably smaller compared to the huge Cuban species *Gigantohierax suarezi*, with the following characters (cf. Suárez 2004: 122–123): femur shaft straight, nearly circular in cross-section (curved anteroposteriorly, greatly compressed in *G. suarezi*), anterior intermuscular line centred on shaft (lateral in *G. suarezi*), proximal and distal end not expanded (greatly expanded in *G. suarezi*), poor pneumaticity proximad (great pneumaticity in *G. suarezi*), head thinner and rounder with long neck, attachment of round ligament smaller (head broad or expanded, with short neck and attachment of round ligament large, vertically oriented, in *G. suarezi*), iliac facet wide (thin in *G. suarezi*), distally the rotular groove is shallow (deep in *G. suarezi*), and reduced but deeper popliteal area (large and shallow in *G. suarezi*). The tarsometatarsus is less compressed anteroposteriorly, being more triangular in cross-section (more compressed, flatter or less triangular in *G. suarezi*), and external proximal half of shaft nearly flat (convex in *G. suarezi*). Differs from *G. itchei* (Fig. 2D) also from Cuba, in having femur smaller, not flared or flattened (compressed anteroposteriorly) at proximal end, with less pneumaticity proximad (wider, flaring greatly proximad, with a distinctive concavity formed by the most proximal pneumatic foramen in *G. itchei*). The tarsometatarsus also lacks the diagnostic thinner and deep anterior metatarsal groove on a flattened shaft, with less anteroposterior compression at the distal end, resulting in a narrower distal end compared to *G. itchei* (see Suárez 2020: 26–27). For additional comparisons, descriptions, measurements and illustrations of fragmentary elements of the paratype skeleton WS 365 with other taxa, including *B. fragilis* and extinct West Indies accipitrids such as *B. borrasii*, *Titanohierax gloveralleni* and

*Gigantohierax suarezi*, see Suárez (2004: 121–124, Figs. 1–3, Table 1) and Suárez & Olson (2008: Fig. 1).

## Discussion

The systematic position of several extinct American *Buteogallus* species has been obscured by the presence of eagle-like large sizes, with erroneous placements in the genera *Aquila* Linnaeus, '*Wetmoregyps*' L. Miller, '*Amplibuteo*' and '*Miraquila*' (Miller 1928, Arredondo 1970, Campbell 1979). No complete tarsometatarsi of *B. terrestris* are known from the Talara Tar Seeps, Peru, and this fossil species' relationships with living Buteogallines are more difficult to establish, although a strong resemblance to the skeleton of *B. meridionalis* exists (Suárez & Olson 2009b: 250). We report here that a variation previously considered a diagnostic character of *B. terrestris* by Campbell (1979: 74), i.e. the inner calcaneal ridge of hypotarsus projecting posteriad at 90° to vertical axis of shaft (see Suárez & Olson 2009b: 250) occurs in some tarsometatarsi of *B. meridionalis* (e.g., USNM 319439). So, this character is invalid in the diagnosis of *B. terrestris*.

The presence of *B. irpus* in Cuba and on Hispaniola is probably due to a similar Quaternary fauna present at one time on both islands (see mammals of the Greater Antilles in Silva Taboada *et al.* 2007: Table 4.1). This distribution suggests that some large raptors formerly known only from Cuba may also be found on Hispaniola. Recently, Steadman *et al.* (2019) reported 24 fossil bones (tibiotarsus, tarsometatarsus, hallux, pedal phalanges) as Accipitridae genus and species indeterminate, which they considered close to genus *Geranoaetus*, from Quaternary cave deposits on Hispaniola (= Haiti and the Dominican Republic), and representing, according to these authors, a single taxon. Illustrations, descriptions and measurements therein indicate instead that the material corresponds to two different-sized accipitrids. The largest of the two incomplete tibiotarsi reported (huge size and supratendinal bridge more horizontal, see Steadman *et al.* 2019: Fig. 1B), agrees with, and was tentatively identified as *Gigantohierax* sp. by Suárez (2020: 25). The smaller and more fragmentary tibiotarsus (Vertebrate Paleontology Collection of the Florida Museum of Natural History, Univ. of Florida, Gainesville, UF 241755) is from Cueva de las Abejas, as is true for the holotype of *B. irpus* sp. nov., and also was collected by C. Woods. It is probable that this fragment of tibiotarsus represents the new species described here. This bone, according to published illustrations, possesses a supratendinal bridge more vertically oriented than in *G. suarezi*, but more horizontal than in *B. woodwardi* or *B. hibbaridi*, probably in accordance with the reduction and configuration of the trochleae in the tarsometatarsus of *B. irpus* sp. nov. *Gigantohierax* is the most distinctive and probably oldest genus of Accipitridae in the West Indies, resembling Old World vultures in some characters, and its osteology and relationships will be described elsewhere (Suárez *et al.* unpubl.). In conclusion, Hispaniola and Cuba appear to have shared two large eagle-sized hawks, both endemic to the West Indies, and not related to the extinct Bahamian genus *Titanohierax* Wetmore, which is so far confined to the Lucayan archipelago (Wetmore 1937, Olson & Hilgartner 1982, Suárez 2020).

The abundance of reptiles and mammals derived from the endemic regional 'megafauna' in the West Indies provided a series of prey (see Steadman *et al.* 2019), potentially partitioned by raptors based on their respective sizes (for a comparable pattern in large Tytonidae from the West Indies, see Suárez & Olson 2015). The evolution in the Antillean subregion of probably pre-Quaternary, highly specialised raptorial lineages (see Suárez & Olson 2009a), which became extinct in the Holocene apparently linked to the extinction of the 'megafauna', corresponds with other non-raptorial, ancient bird lineages also identified on these islands (*cf.* Olson 1978, 1985, Olson & Wiley 2016, among others).

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### References:

- Amadon, D. 1949. Notes on *Harpyhaliaetus*. *Auk* 66: 53–66.
- Amaral, F. S. R., Miller, M. J., Silveira, L. F., Bermingham, E. & Wajntal, A. 2006. Polyphyly of the hawk genera *Leucopternis* and *Buteogallus* (Aves, Accipitridae): multiple habitat shifts during the Neotropical buteonine diversification. *BMC Evol. Biol.* 6: 10.
- Amaral, F. R., Sheldon, F. H., Gamauf, A., Haring, E., Riesing, M., Silveira, L. F. & Wajntal, A. 2009. Patterns and processes of diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). *Mol. Phylo. & Evol.* 53: 703–715.
- Arredondo, O. 1970. Nueva especie de ave pleistocénica del orden Accipitriformes (Accipitridae) y nuevo género para las Antillas. *Cienc. Biol. Univ. Habana* 4(8): 1–19.
- Arredondo, O. 1976. The great predatory birds of the Pleistocene of Cuba. *Smiths. Contrib. Paleobiol.* 27: 169–187.
- Arredondo, O. & Arredondo, C. 2002 [1999]. Nuevos género y especie de ave fósil (Falconiformes: Accipitridae) del Cuaternario de Cuba. *Poeyana* 470–475: 9–14.
- Baumel, J. J. & Witmer, L. M. 1993. Osteologia. Pp. 45–132 in Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E. & Vanden Berge, J. C. (eds.) *Handbook of avian anatomy: Nomina anatomica avium*. Publ. Nuttall Orn. Cl. 23. Nuttall Orn. Cl., Cambridge, MA.
- Brown, L. & Amadon, D. 1968. *Eagles, hawks and falcons of the world*, 2 vols. McGraw-Hill, New York.
- Campbell, K. E. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *Contrib. Life Sci. Div. Royal Ontario Mus.* 118: 1–203.
- Chesser, R. T., Banks, R. C., Barker, F. K., Cicero, C., Dunn, J. L., Kratter, A. W., Lovette, I. J., Rasmussen, P. C., Remsen, J. V., Rising, J. D., Stotz, D. F. & Winker, K. 2012. Fifty-third supplement to the American Ornithologists' Union *Check-list of North American birds*. *Auk* 129: 573–588.
- Emslie, S. D. 1995. An early Irvingtonian avifauna from Leisey Shell Pit, Florida. *Bull. Fla. Mus. Nat. Hist.* 37: 299–344.
- Emslie, S. D. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida peninsula. *Orn. Monogr.* 50: 1–113.
- Emslie, S. D. & Czaplewski, N. J. 1999. Two new fossil eagles from the late Pliocene (late Blancan) of Florida and Arizona and their biogeographic implications. *Smiths. Contrib. Paleobiol.* 89: 185–198.
- Friedmann, H. 1950. The birds of North and Middle America, pt. 11. *US Natl. Mus. Bull.* 50.
- Howard, H. 1929. The avifauna of Emeryville Shellmound. *Univ. Calif. Publ. Zool.* 32: 301–394.
- Howard, H. 1932. Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea. *Contrib. Palaeont. Carnegie Inst. Wash.* 429: 1–82.
- Lerner, H. R. L., Klaver, M. C. & Mindell, D. P. 2008. Molecular phylogenetics of the buteonine birds of prey (Accipitridae). *Auk* 125: 304–315.
- Miller, L. H. 1911. A series of eagle tarsi from the Pleistocene of Rancho La Brea. *Univ. Calif. Publ. Bull. Dept. Geol.* 6: 305–316.
- Miller, L. H. 1915. A walking eagle from Rancho La Brea. *Condor* 17: 179–181.
- Miller, L. H. 1925. The birds of Rancho La Brea. *Carnegie Inst. Wash. Publ.* 349: 63–106.
- Miller, L. H. 1928. Generic re-assignment of *Morphnus daggetti*. *Condor* 30: 255–256.
- Morgan, G. S., Ray, C. A. & Arredondo, O. 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. *Acad. Nat. Sci. Phil., Spec. Publ.* 13: 99–117.
- Olson, S. L. 1985. A new species of *Siphonorhis* from Quaternary cave deposits in Cuba (Aves: Caprimulgidae). *Proc. Biol. Soc. Wash.* 98: 526–532.

- Olson, S. L. 2006. Fossil evidence of the Rufous Crab-Hawk (*Buteogallus aequinoctialis*) in Jamaica. *J. Raptor Res.* 40: 284–287.
- Olson, S. L. 2007. The “walking eagle” *Wetmoregyps daggetti* Miller—a scaled-up version of the Savanna Hawk *Buteogallus meridionalis*. *Orn. Monogr.* 63: 110–113.
- Olson, S. L. & Hilgartner, W. B. 1982. Fossil and subfossil birds from the Bahamas. *Smiths. Contrib. Paleobiol.* 48: 22–56.
- Olson, S. L. & Wiley, J. W. 2016. The Blue-headed Quail-dove (*Starnoenas cyanocephala*): an Australasian dove marooned in Cuba. *Wilson J. Orn.* 128: 1–21.
- Peters, J. L. 1931. *Check-list of birds of the world*, vol. 1. Harvard Univ. Press, Cambridge, MA.
- Phillips, R. 2012. An active nest of the rare Solitary Eagle *Harpyhaliaetus solitarius* discovered in Belize. *Spizaetus* 13: 2–8.
- van Rossem, A. J. 1948. A race of *Urubitornis solitaria* from northwestern Mexico. *Proc. Biol. Soc. Wash.* 61: 67–68.
- Seminario, Y., Phillips, R. & Curti, M. 2011. Observations of the post-fledging behavior and prey of the Solitary Eagle. *J. Raptor Res.* 45: 261–264.
- Seymour, K. L. 2015. Perusing Talara: overview of the late Pleistocene fossils from the tar seeps of Peru. *Nat. Hist. Mus. Los Angeles County Sci. Ser.* 42: 97–109.
- Sharpe, R. B. 1874. *Catalogue of the birds in the British Museum*, vol. 1. Trustees of the Brit. Mus., London.
- Silva Taboada, G., Suárez Duque, W. & Díaz Franco, S. 2007. *Compendio de los mamíferos terrestres autóctonos de Cuba, vivientes y extinguidos*. Ed. Boloña, La Habana.
- Steadman, D. W., Almonte Milan, J. N. & Mychajliw, A. M. 2019. An extinct eagle (Aves: Accipitridae) from the Quaternary of Hispaniola. *J. Raptor Res.* 53: 319–333.
- Suárez, W. 2000. Fossil evidence for the occurrence of Cuban Poorwill *Siphonorhis daiquiri* in western Cuba. *Cotinga* 14: 66–68.
- Suárez, W. 2004. The identity of the fossil raptor of the genus *Amplibuteo* (Aves: Accipitridae) from the Quaternary of Cuba. *Carib. J. Sci.* 40: 120–125.
- Suárez, W. 2020. The fossil avifauna of the tar seeps Las Breas de San Felipe, Matanzas, Cuba. *Zootaxa* 4780: 1–53.
- Suárez, W. & Arredondo, O. 1997. Nuevas adiciones a la paleornitología cubana. *El Pitirre* 10: 100–102.
- Suárez, W. & Olson, S. L. 2008 [2007]. The Cuban fossil eagle *Aquila borraasi* Arredondo: a scaled-up version of the Great Black-Hawk *Buteogallus urubitinga* (Gmelin). *J. Raptor Res.* 41: 288–298.
- Suárez, W. & Olson, S. L. 2009a. A new genus for the Cuban teratorn. *Proc. Biol. Soc. Wash.* 122: 103–116.
- Suárez, W. & Olson, S. L. 2009b. The generic position of *Miraquila terrestris* Campbell: another addition to the Buteogalline radiation from the Pleistocene of Peru. *J. Raptor Res.* 43: 250–254.
- Suárez, W. & Olson, S. L. 2014. A new fossil species of small crested caracara (Aves: Falconidae: *Caracara*) from the Pacific lowlands of western South America. *Proc. Biol. Soc. Wash.* 127: 299–310.
- Suárez, W. & Olson S. L. 2015. Systematics and distribution of the giant fossil barn owls of the West Indies (Aves: Strigiformes: Tytonidae). *Zootaxa* 4020: 533–553.
- Wetmore, A. 1937. Bird remains from cave deposits on Great Exuma Island in the Bahamas. *Bull. Mus. Comp. Zool.* 80: 427–441.
- Wetmore, A. 1965. The birds of the Republic of Panamá, pt. 1. *Smiths. Misc. Coll.* 150: 1–483.
- Woods, C. A. 1980. Collecting fossil mammals in the Greater Antilles: an immense journey. *Plaster Jacket* 34: 4–13.

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