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

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A new fossil vulture (Cathartidae: *Cathartes*) from Quaternary asphalt and cave deposits in Cuba

by William Suárez & Storrs L. Olson

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SUMMARY.—A new small fossil species of vulture from Quaternary asphalt and cave deposits in western Cuba is described herein. Some specimens of this taxon are the smallest known in the genus *Cathartes*, including the modern Lesser Yellow-headed Vulture *C. burrovianus*. The extinction of the Cuban megafauna, coupled with the loss of open habitats once dominated by grassland savannas, contributed to the population decline and final extinction of endemic vultures in Cuba during the Holocene.

Two species of New World vultures (Cathartidae) form part of the modern avifauna of Cuba: the common Turkey Vulture *Cathartes aura* (Linnaeus, 1758), and Black Vulture *Coragyps atratus* (Bechstein, 1793), which is very rare (Kirkconnell *et al.* 2020). Vultures were better represented in Cuba's fossil record during the late Pleistocene and part of the Holocene (Arredondo 1976, 1984, Suárez 2001, Suárez & Emslie 2003) and included Cuban Condor *Gymnogyps varonai* (Arredondo, 1971) and two smaller species of *Cathartes* Illiger, 1811, and *Coragyps* Le Maout, 1853 (Suárez 2000a, 2001, 2020). Although some remains from Cuba have been referred also to *Sarcoramphus* Duméril, 1805, and *Cathartes aura* (*cf.* Arredondo & Varona 1974, Acevedo González *et al.* 1975, Acevedo-González & Arredondo 1982, Arredondo 1984, Jiménez & Valdés 1995, Arredondo & Arredondo 2002a,b), these represent misidentified specimens, or modern bones of the latter species (Suárez 2001).

Fossils of *Cathartes* from Quaternary deposits in Cuba include an undescribed species (Suárez 2000a, 2001, 2004, 2020). The first specimen of this taxon to be identified was the proximal half of a right tarsometatarsus from an immature individual (Fig. 3A, D), collected in 1997 by WS when excavating Quaternary cave deposits in Cueva de Sandoval, near Vereda Nueva, municipality of Caimito, La Habana (now Artemisa) province (see Suárez 2000b). This cave is the type locality of Cuban Falcon *Falco kurochkini* (Suárez & Olson 2001a) and Suárez's Giant Eagle *Gigantohierax suarezi* (Arredondo & Arredondo 2002a). Given its small size, the bone of the new *Cathartes* was not referable to *C. aura* (W. Suárez & O. Arredondo unpubl.) and was believed to belong to either a new species or Lesser Yellow-headed Vulture *C. burrovianus* Cassin, 1845, which is close in size and was erroneously listed for Jamaica historically (Sharpe 1873: 133). Material of the new vulture has been recovered also from a cave deposit at Cueva del Indio, municipality of San José de las Lajas, La Habana (now Mayabeque) province, Cuba. One specimen, a distal fragment of a left humerus, was identified as *C. aura* by Jiménez & Valdés (1995) in a short list of vertebrates published in an abstract, but was re-identified by WS. It differs from *C. aura* by its much smaller size and some qualitative characters (WS unpubl.). More recently, additional and better preserved material was collected in asphalt deposits at Las Breas de San Felipe, Matanzas, Cuba (Suárez 2020). Here, we compare, describe and name these fossils as a new species of *Cathartes* endemic to the Greater Antilles.

Methods

Comparative modern and fossil (see Systematic paleontology) material examined for this study is held in the National Museum of Natural History, Smithsonian Institution (USNM), Washington DC; American Museum of Natural History (AMNH), New York; Royal Ontario Museum (ROM), Toronto; Los Angeles County Natural History Museum (LACM), California; Museo Nacional de Historia Natural de Cuba (MNHNCu), La Habana; and the William Suárez (WS) collection, La Habana, respectively. Skeletons examined include: *Coragyps atratus* (USNM 16646, 288760–761, 289772, 320020, 321771, 498693, 500989, 559658–659, 560278, 610724, 613352, LACM 86818, ROM 92440, 112189, 112334, 112399); *Cathartes aura* (USNM 18184, 19774, 346785, 490864, 500990, 559147, 562524, 610725–727, 612254, 621554); Greater Yellow-headed Vulture *C. melambrotus* Wetmore, 1964 (USNM 559319, 621939); *C. burrovianus* (USNM 227374, 431336, 622341, 627472, AMNH 1264, 8630, 12094, ROM 115856); Andean Condor *Vultur gryphus* Linnaeus, 1758 (USNM 346631, 430210); California Condor *Gymnogyps californianus* (Shaw, 1797) (USNM 13823, 17033, 17946–950, 345225, 346582, 489359, 489406, 489755, 492447); and King Vulture *Sarcoramphus papa* (Linnaeus, 1758) (ROM 32251, 94585, 115643). Osteological terminology is modified from Howard (1929) and Baumel & Witmer (1993). Measurements were taken with digital callipers to the nearest 0.1 mm.

Results

Systematic paleontology

Class AVES Linnaeus

Order CATHARTIFORMES Coues

Family CATHARTIDAE Lafresnaye

Genus *Cathartes* Illiger

The new species agrees with the genus *Cathartes* and differs from *Coragyps* by having tarsometatarsus with short and relatively wider shaft, more compressed anteroposteriorly, anterior metatarsal groove well extended distad, and trochleae shorter and flaring abruptly from shaft. It differs from *Gymnogyps* Lesson, 1842, which is known from the Cuban fossil record, and agrees with *Cathartes*, in characters described by Emslie (1988).

Cathartes emsliei sp. nov.

Emslie's Vulture; Aura de Emslie

(Figs. 1–4, Table 1)

References:

'*Cathartes?* sp.': Suárez (2000a: 120).

'referable to *Cathartes*': Suárez (2001: 110).

'a small species of vulture': Suárez (2004: 124).

'*Cathartes* sp.': Suárez (2020: 14).

Holotype.—Proximal half of left tarsometatarsus MNHNCu 75.4752 (Fig. 3B–E), collected by WS and S. Díaz Franco on 27 December 2002, at San Felipe I (see Type locality).

Paratypes.—*San Felipe I*: right tibiotarsus without proximal end, MNHNCu 75.4750 (Fig. 2A); distal right tibiotarsus, MNHNCu 75.4754; distal left, MNHNCu 75.4748, and right, MNHNCu 75.4749 (Fig. 2C), tibiotarsi; proximal right tarsometatarsi, MNHNCu 75.4745, MNHNCu 75.4753; distal half of right tarsometatarsus, MNHNCu 75.4746 (Fig. 3H–J); proximal half of left tarsometatarsus, MNHNCu 75.4747; distal half of left tarsometatarsus,



Figure 1. Right scapulas (A–B, ventral view) and left coracoids (C–D, dorsal view) in two species of the genus *Cathartes*. *C. burrovianus*: USNM 622341 (A, C); *C. emslii*: paratype MNHNCu 75.692 (B); paratype MNHNCu 75.4755 (D). Scale = 1 cm (William Suárez)



Figure 2. Right tibiotarsi (A–C, anterior view) in two species of the genus *Cathartes*. *C. emslii*: paratype MNHNCu 75.4750 (A), paratype MNHNCu 75.4749 (C); and *C. burrovianus*: USNM 622341 (B). Scale = 1 cm (William Suárez)

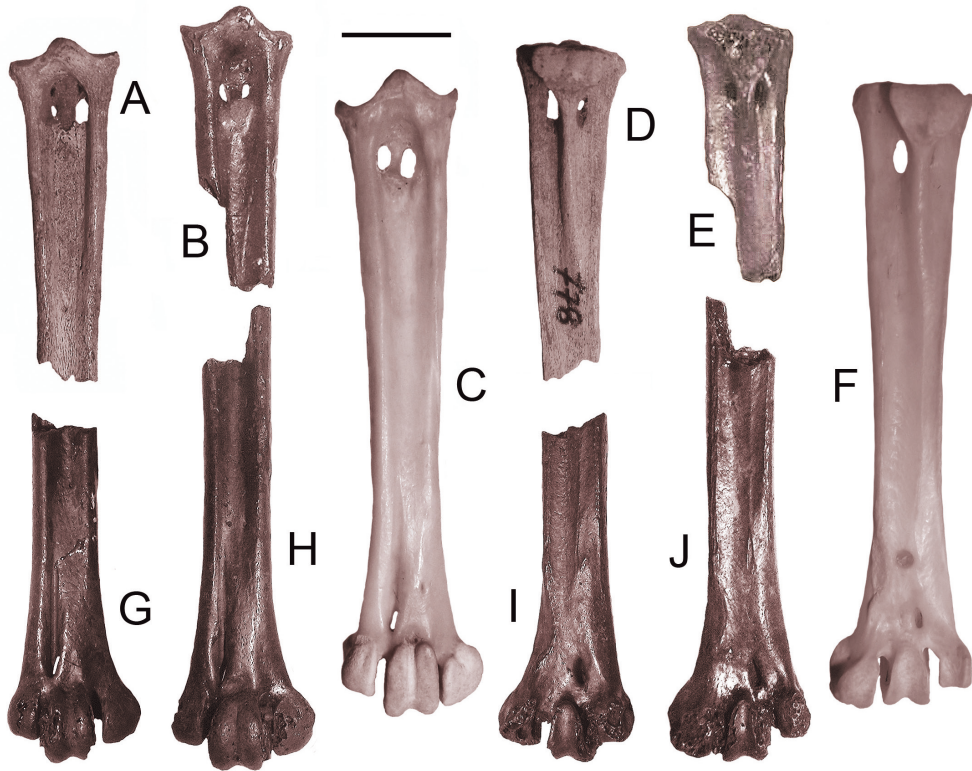


Figure 3. Tarsometatarsi in two species of the genus *Cathartes*, in anterior (A–C, G–H) and posterior (D–F, I–J) views. *C. emsleyi*: paratype proximal right (A, D) WS 778, holotype proximal left (B, E) MNHNCu 75.4752, paratype distal left (G, I) MNHNCu 75.4751, paratype distal half of right (H, J) MNHNCu 75.4746 (images E, G and I are reversed to facilitate comparisons). *C. burrovianus*: right (C, F) USNM 622341. Scale = 1 cm (William Suárez)

MNHNCu 75.4751 (Fig. 3G–I). *San Felipe II*: right scapula, MNHNCu 75.692 (formerly P-692, Fig. 1B); fragmentary left coracoid, MNHNCu 75.4755 (formerly P-691, Fig. 1D). *Cueva de Sandoval*: proximal right tarsometatarsus, WS 778, immature.

Diagnosis.—A small species of *Cathartes* differing from *C. burrovianus* by having coracoid with reduced glenoid facet, wider and deeper anterior intercondylar fossa of the tibiotarsus, and tarsometatarsus with base of trochlea II wider in posterior view.

Measurements.—See Table 1.

Type locality.—Asphalt deposits at Las Breas de San Felipe (c.22°57'N, 80°58'W), 5.5 km west of the town of Martí, San Felipe Valley, municipality of Martí, Matanzas province, Cuba. The asphalt seeps of Las Breas de San Felipe are the only known productive fossil tar seeps in the Greater Antilles and contain two productive fossil sub-localities, San Felipe I and San Felipe II, respectively (for a detailed description see Iturralde-Vinent *et al.* 2000, and for the fossil avifauna present there, see Suárez 2020). This is the type locality of Cuban Caracara *Milvago carbo* Suárez & Olson, 2003, and some other Cuban extinct raptors (Suárez 2020).

Other localities.—Cueva de Sandoval (Sandoval III low deposit; see Suárez 2000b, 2004, Suárez & Olson 2001a), c.4 km south of Vereda Nueva, municipality of Caimito, Artemisa province, Cuba.

TABLE 1
Measurements (mm) of skeletal elements of *Cathartes emsliei*, compared to those of living species of the genus *Cathartes*. Range (mean, sample size).

Element and Character	<i>Cathartes emsliei</i> sp. nov.	<i>C. burrovianus</i>	<i>C. melambrotus</i>	<i>C. aura</i>
<i>CORACOID</i>				
Shaft width at midpoint	6.9	6.8–8.6 (7.6, <i>n</i> = 5)	8.7–9.5 (9.1, <i>n</i> = 2)	8.1–9.6 (9.3, <i>n</i> = 10)
Depth at midpoint of glenoid facet	8.0	9.5–10.2 (10.0, <i>n</i> = 5)	11.3–12.1 (11.7, <i>n</i> = 2)	11.1–13.2 (11.6, <i>n</i> = 10)
<i>SCAPULA</i>				
Proximal width	11.1	12.4–12.9 (12.4, <i>n</i> = 5)	13.8–14.1 (13.95, <i>n</i> = 2)	15.9–17.0 (16.3, <i>n</i> = 10)
Shaft width at midpoint	4.4	5.2–5.7 (5.3, <i>n</i> = 5)	6.1–6.3 (6.2, <i>n</i> = 2)	6.3–6.8 (6.6, <i>n</i> = 10)
<i>TIBIOTARSUS</i>				
Shaft width at midpoint	5.6–5.8 (5.7, <i>n</i> = 2)	5.8–6.4 (5.9, <i>n</i> = 5)	7.0–7.2 (7.1, <i>n</i> = 2)	6.6–7.4 (7.0, <i>n</i> = 10)
Distal width	9.7–10.2 (9.8, <i>n</i> = 4)	9.9–10.3 (10.1, <i>n</i> = 5)	12.1–12.4 (12.25, <i>n</i> = 2)	11.1–12.6 (12.2, <i>n</i> = 10)
Depth of internal condyle	9.9	9.6–10.0 (9.8, <i>n</i> = 5)	10.5–11.0 (10.75, <i>n</i> = 2)	10.7–11.1 (11.0, <i>n</i> = 10)
Depth of external condyle	9.1–9.5 (9.3, <i>n</i> = 2)	9.2–9.7 (9.5, <i>n</i> = 5)	10.7–11.1 (10.9, <i>n</i> = 2)	11.0–12.4 (11.5, <i>n</i> = 10)
<i>TARSOMETATARSUS</i>				
Proximal width	10.6–11.4 (10.0, <i>n</i> = 3)	10.7–12.1 (11.5, <i>n</i> = 5)	14.5–15.3 (14.9, <i>n</i> = 2)	13.0–15.5 (14.2, <i>n</i> = 11)
Depth of internal cotyla	5.2	5.6–6.3 (6.0, <i>n</i> = 5)	7.8–8.3 (8.05, <i>n</i> = 2)	10.3–11.2 (10.9, <i>n</i> = 10)
Depth of external cotyla	4.8–5.6 (5.2, <i>n</i> = 3)	5.1–5.7 (5.5, <i>n</i> = 5)	8.0–8.2 (8.1, <i>n</i> = 2)	8.5–10.6 (9.4, <i>n</i> = 10)
Min. width of shaft	5.9–6.4 (6.2, <i>n</i> = 3)	6.1–6.7 (6.5, <i>n</i> = 5)	7.4–7.7 (7.55, <i>n</i> = 2)	7.3–7.7 (7.5, <i>n</i> = 11)
Distal width	13.0–13.2 (13.1, <i>n</i> = 2)	13.1–13.6 (13.5, <i>n</i> = 5)	15.8–16.3 (16.05, <i>n</i> = 2)	15.0–16.6 (15.6, <i>n</i> = 10)

Status and distribution.—Extinct, known only from Quaternary asphalt deposits at Las Breas de San Felipe and cave deposits in western Cuba.

Chronology.—Late Pleistocene to Holocene. Radiocarbon dates (^{14}C) based on humeral material of the extinct Cuban sloth *Parocnus browni* from Las Breas de San Felipe yield ages ranging from $4,960 \pm 280$ years BP to $11,880 \pm 420$ years BP (Jull *et al.* 2004, Steadman *et al.* 2005). In addition, three species of extinct birds from San Felipe II ranged (^{14}C) from 22,000 \pm 2,600 years BP to >41,000 years BP (Suárez 2020: Table 2).

Description and comparisons.—The fossil specimens in this study from tar seeps and cave deposits are heavily mineralised, black-brown and beige in colour, respectively. Specimen WS 778 is not completely ossified, having a porous surface, but with proximal epiphysis present, representing an immature. *Cathartes emsliei* is much smaller than *C. melambrotus* or *C. aura*, being similar to *C. burrovianus* in size, but tending to be slightly smaller, and more gracile, in some specimens than the latter (Table 1). *C. emsliei* differs from *C. burrovianus* by the presence of the following qualitative characters (Figs. 1–3): coracoid having glenoid facet reduced; external border very sharp, with dorsal and ventral surfaces of the shaft flattened (glenoid facet large, external border rounded and both surfaces less flattened in *C. burrovianus*); scapula similar in morphology but more flattened dorso-ventrally (less flat in *C. burrovianus*); tibiotarsus with supratendinal bridge wider and flattened, located proximad and mediad; anterior intercondylar fossa wide and deep (supratendinal bridge thin, less flattened, distad and more laterad, intercondylar fossa thinner, or less expanded and less deep in *C. burrovianus*); tarsometatarsus with intercotylar prominence smaller, or

reduced, and thinner; shaft more compressed bilaterally at midpoint; anterior metatarsal groove thinner but deeper; internal and external anterior metatarsal ridges better defined with sharp edges; metatarsal facet tending to be deeper and expanded (this character is variable); base of trochlea II wide (posterior view); trochlea III more distally projected with posterior groove thin and deep (intercotylar prominence larger and wider, shaft relatively broader at midpoint, anterior metatarsal groove wider and less deep, internal and external anterior metatarsal ridges less defined, being more rounded, base of the trochlea II thin and trochlea III not as distally projected with a wider groove posteriorly in *C. burrovianus*). The immature specimen (WS 778) possesses a posterior metatarsal ridge more distally extended than in specimens of *C. burrovianus*, or the other fossil tarsometatarsi available in the series to evaluate this character.

Etymology.—Named for our esteemed colleague and friend, Dr Steven D. Emslie, University of North Carolina Wilmington, USA, in recognition of his contribution to the knowledge of New World vultures, including those from Cuba.



Figure 4. Hypothetical reconstruction of Emslie's Vulture *Cathartes emsliei* (William Suárez)

Discussion

Cuban scavengers (see Hertel 1992, 1994, 1995) were highly specialised, evolving in the complete absence of carnivorous mammals (Arredondo 1976, Silva *et al.* 2007), and becoming extinct during the Holocene. Emslie's Vulture (Fig. 4) appears to be derived from a Central American ancestor (probably one related to the smaller living species *C. burrovianus*) rather than from North America, unlike the two other extinct Cuban taxa in the genera *Coragyps* and *Gymnogyps* (Suárez & Emslie 2003, Suárez 2020). Skulls with massive and large bills, compared to continental congeners, are common adaptations in Cuban carrion-eaters (Suárez & Olson 2001b, 2003, Suárez & Emslie 2003). Currently, the cranial anatomy is unknown in *C. emsliei*. Special attention is needed when identifying isolated fragmentary cranial (including rostral) material of the genus *Cathartes* in Quaternary deposits in Cuba, or elsewhere in the West Indies. *C. emsliei* can be confused with remains of the modern and common *C. aura*. The new taxon appears closer in affinity to *C. burrovianus*, with a preference for grassland, savanna and open habitats in marshes and mangroves, rather than forests (see Houston 1994a,b, Griffiths & Bates 2002).

Until the present, remains of *C. aura* have been unknown in Cuban fossil deposits dating from the Pleistocene (WS pers. obs.), apparently as a result of colonisation during the Holocene (see Santana *et al.* 1986), following the decline and extinction of the endemic, highly specialised carrion-eating taxa (see Suárez 2000a, Suárez & Olson 2001b, 2003, 2009, 2014, Suárez & Emslie 2003). In fact, the presence of *C. aura* (see Wotzkow & Wiley

1988) and *Coragyps atratus* in Cuba today (Kirkconnell *et al.* 2020) represent species that replaced endemic West Indian specialists in their respective genera (Suárez 2020), with the latter taxon being very rare (González Rossell *et al.* 2013, Kirkconnell *et al.* 2020) and not yet well established. No direct ^{14}C dating of specimens of *C. aura* is available from Cuban deposits. Endemic vultures, as well as the relatively varied native megafauna they relied on, are absent from Quaternary deposits in the Bahamas (Olson & Hilgartner 1982). *C. aura* has been reported as a fossil there (Olson *et al.* 1990, Steadman *et al.* 2015). There was virtually no competition (only *Caracara creightoni* Brodkorb, 1959) for *C. aura* in the Lucayan Archipelago during colonisation from North America in the late Pleistocene / Holocene. Large reptiles seem to have been an important source of carrion (Olson *et al.* 1990). The same lack of competition in Cuba, during part of the Holocene, attracted scavengers from the mainland, including *C. aura* and Crested Caracara *Caracara cheriway* (von Jacquin, 1784). Resident *C. aura* in the Greater Antilles have pre-orbital facial caruncles like those of populations breeding in eastern North America and Central America (Graves 2019), from where the Antilles were colonised (Santana *et al.* 1986; see comments on its distribution in the Antilles in Gundlach 1876, 1893). *Caracara cheriway*, in contrast, is represented by disjunct populations in Cuba, the Isle of Pines, and Florida (see Suárez & Olson 2014). Like *C. aura*, this caracara is also not recorded in Florida from deposits older than the late Pleistocene (Brodkorb 1964, Emslie 1998); it probably represents a recent (Holocene) invasion from the peninsula to Cuba following extinction of the regional endemic and highly specialised *Caracara creightoni* (Suárez & Olson 2001b, 2003). The successful expansion of *C. aura* in the Greater Antilles (AOU 1998, Raffaele *et al.* 1998) after colonisation was greatly facilitated by increasing forest clearance and the food sources afforded by the introduction of domestic stock by the Spanish colonists, which replaced native megafauna (*cf.* giant terrestrial tortoises, sloths, monkeys, large rodents, etc.; see Silva *et al.* 2007). For the introduction of *C. aura* to other islands in the Caribbean, see Santiago Valentín (1998).

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Addresses: William Suárez, P.O. Box 16477, West Palm Beach, FL 33416, USA, e-mail: ws@wsbirdingtours.com. Storrs L. Olson, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA, e-mail: olsons@si.edu

