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Systematics and distribution of the giant fossil barn owls of the West Indies (Aves: Strigiformes: Tytonidae)

WILLIAM SUÁREZ¹ & STORRS L. OLSON²

¹P.O. Box 16477, West Palm Beach, FL 33416, U.S.A. E-mail: wsbirdingtours@birdlover.com

²Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, U.S.A.
E-mail: olson@si.edu

Abstract

After reviewing the systematics and distribution of the extinct West Indian taxa of Tytonidae (*Tyto*) larger than the living barn owl *Tyto alba* (Scopoli), we reached the following conclusions: (1) the species *T. ostologa* Wetmore (1922) is the only giant barn owl known so far from Hispaniola; (2) *T. pollens* Wetmore (1937) was a somewhat larger and even more robust representative of *T. ostologa* known from the Great Bahama Bank and Cuba; (3) the very rare species *T. riveroi* Arredondo (1972b) is here synonymized with *T. pollens*; (4) the smallest taxon of these giant barn owls is *T. noeli* Arredondo (1972a), which is widespread and abundant in Quaternary deposits of Cuba and is here reported for the first time from two cave deposits in Jamaica; (5) the only large barn owl named so far from the Lesser Antilles is *T. neddi* Steadman & Hilgartner (1999), which is here synonymized with *T. noeli*; (6) a new taxon from Cuba, *T. cravesae* new species, which in size approached the linear dimensions of *T. ostologa*, is named and described herein.

Key words: Giant Tytonidae, distribution, fossil birds, systematics, *Tyto*, West Indies

Introduction

The West Indies (in which we include the Bahamas), in particular the Cuban archipelago, was inhabited during part of the Quaternary by a diverse array of large predatory birds (Arredondo 1976; Olson 1978; Olson & Hilgartner 1982; Arredondo 1984; Arredondo & Olson 1994; Steadman & Hilgartner 1999; Arredondo & Arredondo 2002a, 2002b; Suárez & Emslie 2003; Suárez 2004a; Suárez & Olson 2007; Olson 2008; Suárez & Olson 2009) adapted for feeding on an equally diverse assemblage of endemic mammals (see Allen 1942; Angerbjörn 1985; Woods 1990; Alcover *et al.* 1998; MacPhee & Iturralde-Vinent 2000; White & MacPhee 2001; Dávalos 2004; Silva Taboada *et al.* 2008) and other vertebrates. Many of these species, both prey and predator, are now extinct (Olson 1978; Morgan & Woods 1986; Alcover & MacMinn 1994; Turvey 2009).

Among the nocturnal raptors were several species of barn owls (Tytonidae: *Tyto* Billberg) that were much larger than any extant form of the genus (for a summary see Steadman & Hilgartner 1999). We use the term “giant” to signify that all of these species were much larger than any extant species of Tytonidae although in weight there are a number of extant species of Strigidae that are larger than any of the West Indian barn owls would have been. Contrary to what has been written in some popular sources, none of these owls were flightless or even approaching flightlessness in their morphology.

Five species of these large barn owls have been named to date (Brodkorb 1971; Arredondo 1976; Olson 1978; Olson & Hilgartner 1982; Cuello 1988; Steadman & Hilgartner 1999). The systematics of this group of raptors began with the description of *Tyto ostologa* Wetmore, from Quaternary cave deposits in north-central Haiti, Hispaniola (Wetmore 1922). Additional specimens of that taxon were later collected at the type locality and nearby caves above L'Atalaye (Wetmore & Swales 1931) and in other parts of the island, including the Dominican Republic (Steadman & Hilgartner 1999). Following this discovery, *Tyto pollens* Wetmore was described as a species even larger than *T. ostologa*, from cave deposits thought to have come from the island of Great Exuma in the Bahamas (Wetmore 1937) but later determined to have come from Little Exuma (Hecht 1955). Years later,

Brodkorb (1959), and Olson & Hilgartner (1982), recorded *T. pollens* from deposits in Banana Hole, New Providence Island, also in the Bahamas.

Although Wetmore (1959) announced the presence of a very large form of *Tyto* from Baire, Santiago de Cuba Province, Cuba, the material, a humerus and a femur, was later identified and described as a new species of a large strigid owl in the genus *Bubo* Duméril (Arredondo & Olson 1994). Unequivocal proof of the existence of giant species of *Tyto* in Cuba was established with the description of *T. noeli* Arredondo, on the basis of postcranial elements from two Quaternary cave sites in the former La Habana Province (Arredondo 1972a). The distribution of this taxon in fossil deposits was later extended to other localities (e.g. Arredondo 1984; Jiménez *et al.* 1995; Suárez 2000, 2004b; Suárez & Díaz-Franco 2003), where it is common, especially in cave deposits at the Llanura Cárstica Meridional de La Habana-Matanzas (W. Suárez, pers. obs.). Nearly simultaneously, *Tyto riveroi* Arredondo was also described based on a single bone, the distal portion of a tarsometatarsus from Cueva de Bellamar, Matanzas Province. This barn owl was supposedly much larger than any other species known (Arredondo 1972a, 1972b, 1975, 1976, 1982, 1984), although this proves not to be correct (see *T. pollens*, this paper).

The only species of giant barn owl named so far from the Lesser Antilles is *Tyto neddi* Steadman & Hilgartner, known from few and very fragmentary postcranial remains collected in a cave deposit at Rat Pocket, Gun Shop Cliff, Two Foot Bay, island of Barbuda (Steadman & Hilgartner 1999). That species was described as being slightly larger than *T. noeli* from Cuba and smaller than *T. ostologa* from Hispaniola.

Only recently has it been possible to make direct comparisons of Cuban giant tytonids with other extinct taxa from elsewhere in the West Indies. This, plus discovery of new fossil material, provided the impetus for our review of this important group of nocturnal raptors.

Material and methods

Fossil specimens of *Tyto* from Cuba were examined in the following collections 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); Facultad de Biología, Universidad de La Habana (DPUH; formerly Departamento de Paleontología, Universidad de La Habana); Oscar Arredondo collection (OA); William Suárez collection (WS). This material includes the type series of *Tyto noeli* Arredondo and its holotypical right tarsometatarsus (DPUH 1251) as well as the holotypical distal portion of left tarsometatarsus (DPUH 1252) of *Tyto riveroi* Arredondo. Fossil strigid owls, including the type material of *Bubo osvaldoi* Arredondo & Olson, and most of the major skeletal elements of the Cuban Giant Owl *Ornimegalonyx oteroi* Arredondo were examined as well. We include skeletons of the living barn owls *Tyto alba* (Scopoli) and *Tyto furcata* (Temminck) (of Cuba and Jamaica, which we recognize as distinct from *T. alba*) and all modern genera of Strigidae present in the West Indies (*Megascops* Kaup, *Margarobyas* Olson & Suárez, *Bubo* Duméril, *Glaucidium* Siebold & Zucc, *Athene* (= *Speotyto*) F. Boie, *Pulsatrix* Kaup, *Asio* Brisson, and *Pseudoscops* Kaup), plus all the fossils of *T. ostologa* and *T. pollens* housed in the collections of the National Museum of Natural History, Smithsonian Institution (USNM; formerly United States National Museum), Washington D.C., including the holotypical proximal end of left tarsometatarsus (USNM 10746) of *T. ostologa*, and the holotypical distal fragment of right femur (USNM 359240) and all paratypes of *T. neddi* Steadman & Hilgartner. Additional material was also examined at the Florida Museum of Natural History (FLMNH), University of Florida, Gainesville (UF, acronym for catalogued fossils). Fossil species of *Tyto* discussed herein (see Fig. 1) are ordered according to their date of original description. Measurements were taken with digital calipers and rounded to the nearest 0.1 mm. Anatomical nomenclature is mainly that proposed by Howard (1929) and Baumel & Witmer (1993), modified in some instances. Under each species heading we have suggested English and Spanish vernacular names as well.

Results

Systematic Paleontology

Class AVES Linnaeus

Order STRIGIFORMES (Wagler)

Family TYTONIDAE Ridgway

Genus *Tyto* Billberg

The fossil material treated here is referable to the Tytonidae and to the genus *Tyto* (see Figs. 2–8), and differs from extinct and extant genera of Strigidae in the West Indies (see Materials and methods) by the following combination of osteological characters (see also Mourer-Chauviré 1987; Arredondo & Olson 1994; Steadman & Hilgartner 1999; Pavia 2004, among others): Coracoid less voluminous at the scapular end (much less deep) without pneumatic foramina; scapular facet, coracoidal foramen, and sternal facet, proportionately smaller; glenoid facet relatively larger; procoracoid large at base. Humerus less expanded proximally in palmar and anconal views; head proportionately small and less bulbous; bicipital furrow very deep; bicipital crest poorly developed; internal tuberosity reduced; impression of brachialis anticus much deeper. Ulna with prominence for anterior articular ligament more projected; impression of brachialis anticus deeper and more distally extended; bicipital attachment reduced; internal condyle better developed, and the sulcus intercondylaris much more extended into the internal side. Carpometacarpus with a deep fossa distad to the pisiform process (forming two marked ridges at the base of the latter); metacarpal II with internal border acute (less rounded); metacarpal III longer and well extended proximad. Femur with a more vertical trochanteric ridge (less inclined internally); distal end more flared; internal and external condyles more projected anteriorly, resulting in the rotular groove being much deeper; internal condyle larger in internal view; tuberculum M. gastrocnemialis lateralis distally located; popliteal area expanded. Tibiotarsus with slender shaft; inner cnemial crest shorter, but more projected anteriorly; sulcus intercnemialis very wide; fibular crest reduced and higher on shaft; distal fusion of fibular spine long and higher (proximad); distal portion of shaft less expanded bilaterally and less compressed antero-posteriorly; internal and external condyles projecting more posteriorly. Tarsometatarsus slender and convex anteriorly at the distal end, with lateral surface expanded (deeper); intercotylar prominence placed more anteriorly in relation to the position of anterior edges of both internal and external cotylae; ossified proximal supratendinal bridge absent (see also Brodkorb 1969:113); trochlea for digit IV massive; intertrochlear notch between trochleae for digits II and III reduced.

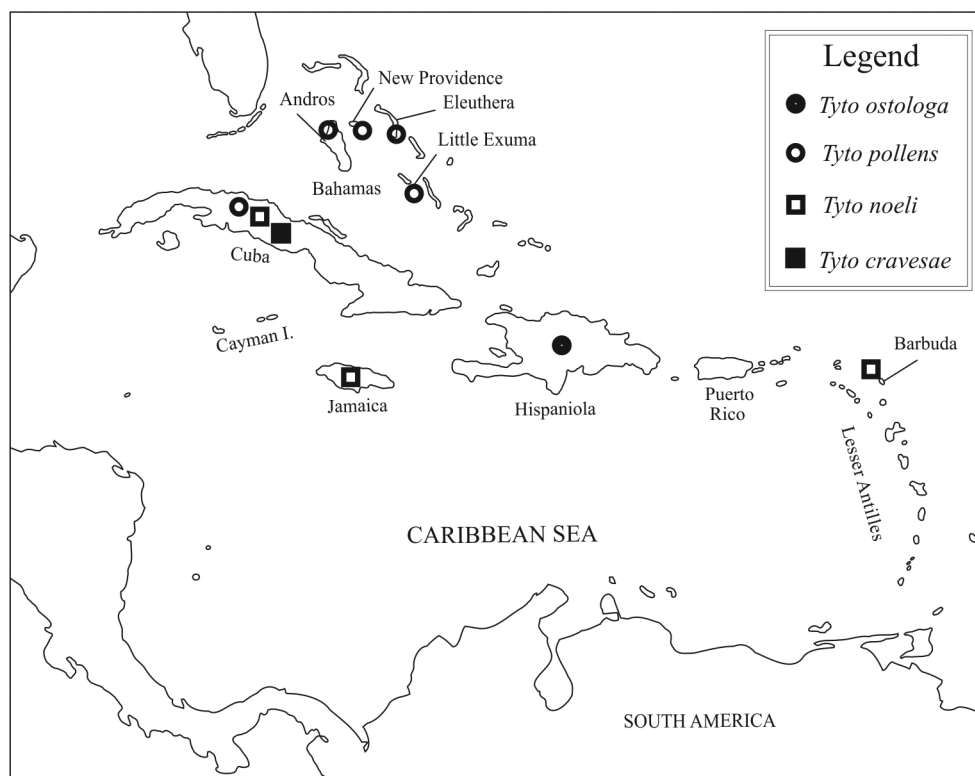


FIGURE 1. Map of the West Indies showing the distribution of giant fossil species of *Tyto*.



FIGURE 2. Left coracoids in dorsal view of *Tyto noeli* (A–C) compared with *T. cravesae*, new species: A, *T. noeli* (Jamaica) USNM 535720; B, *T. noeli* (Cuba) WS 909, image reversed to facilitate comparisons; C, *T. noeli* (Cuba) OA 3212; D, *T. cravesae* (paratype) OA 832. Scale = 1cm.

***Tyto ostologa* Wetmore**

Hispaniolan Giant Barn Owl; Lechuza Gigante de La Española
(Figs. 3D; 4B, F; 7F; 8B)

Tyto ostologa Wetmore, 1922: 2 (type locality “large cave [= Grotte San Francisco] northeast of St. Michel de L’Atalaye, Republic of Haiti”).

Holotype. Proximal end of left tarsometatarsus USNM 10746. Collected on 4–5 March 1921, by J. S. Brown and W. S. Burbank.

Material examined. *Grotte San Francisco, ca. 3 km northeast of St. Michel and caves above L’Atalaye, Haiti.*—Coracoid: complete left (USNM 543279; USNM 543360, fragmentary; USNM 543367), scapular half of left (USNM 543362–543363), scapular end of left (USNM 543364), shaft of left (USNM 543361), complete right (USNM 543278), scapular end of right (USNM 543365), sternal half of right (USNM 543366). Humerus: proximal third of left (USNM 543374–543375), proximal left (USNM 543376), shaft of left (USNM 543368), proximal third of right (USNM 543373), proximal shaft of right (USNM 543369), distal right (USNM 543370, with travertine—543372; USNM 543377, juvenile). Ulna: complete left (USNM 543327), proximal third of left (USNM 543330–543331, USNM 543343), proximal left (USNM 543344), distal left (USNM 543334, USNM 543336–543338, USNM 543340, USNM 543342), complete right (USNM 543326; USNM 543328, with travertine), proximal half of right (USNM 543333, with travertine and lacking proximal end), proximal right (USNM 543332), distal half of right (USNM 543329), distal right (USNM 543335, USNM 543339, USNM 543341). Carpometacarpus: nearly complete left (USNM 543378–543379, both abraded and lacking metacarpal III), proximal half of left (USNM 543384–543385), right (USNM 543282, lacking metacarpal III and part of distal symphysis), proximal half of right (USNM 543380–543382), proximal right (USNM 543383), distal half of right (USNM 543386–543387, both abraded and lacking metacarpal III). Femur: complete left (USNM 543284; USNM 543301, with travertine), nearly complete left (USNM 543293, lacking proximal end), proximal half of left (USNM 543290, juvenile–543291;

USNM 543295, without trochanter), proximal end of left (USNM 543288, fragmentary—543289; USNM 543299–543300), proximal fragment of left (USNM unnumbered, juvenile), distal left (USNM 543287; USNM unnumbered, without condyles), complete right (USNM 543277, abraded; USNM 543283, abraded; USNM 543286; USNM unnumbered, juvenile), incomplete right (USNM 543285, lacking distal end), proximal right (USNM 543296), distal right (USNM 543281; USNM 543294, with travertine; USNM 543297, fragmentary lacking condyles—543298). Tibiotarsus: proximal half of left (USNM 543346, lacking cnemial crests—543347), proximal third of left (USNM 543349, fragmentary), proximal left (USNM 543348, fragmentary; USNM 543350, lacking inner cnemial crest), distal half of left (USNM 543351; USNM 543353, lacking posterior portions of external condyle), distal left (USNM 543356–543357, lacking posterior portions of condyles; USNM 543279), proximal right (USNM 543345, lacking distal third and cnemial crests), distal right (USNM 543355; USNM 543358, juvenile and fragmentary). Tarsometatarsus: nearly complete left (USNM 543276, lacking inner calcaneal ridge; USNM 543302, lacking fragments of shaft and part of trochleae for digits II and IV), proximal third of left (USNM 543311, with travertine), proximal left (USNM 10746, holotype; USNM 543310, lacking external cotyla and intercotylar prominence; USNM 543312, lacking inner calcaneal ridge), distal half of left (USNM 543306, partially abraded and lacking trochlea for digit—IV 543307, external side only preserved), distal left (USNM 543303–543304; USNM 543308–543309, with travertine), nearly complete right (USNM 543313, juvenile, lacking trochlea for digit III and inner calcaneal ridge—543314, lacking proximal end and trochlea for digit III; 543317, lacking external cotyla and trochleae, with travertine), proximal half of right (USNM 543318), proximal third of right (USNM 543315, lacking intercotylar prominence and inner calcaneal ridge), proximal right (USNM 543320, fragmentary; USNM 543322–543324, all fragmentary), distal right (USNM 543316, lacking trochlea for digit IV, with travertine; USNM 543319; USNM 543321; USNM 543325, lacking trochlea for digit IV), trochleae for digits II and IV (USNM 10747, paratypes).

We have also examined uncatalogued fossils of various elements of this species from three localities in the Dominican Republic in the collections of the Florida Museum of Natural History, Gainesville (see Steadman & Hilgartner 1999).

Emended diagnosis. Larger than *Tyto noeli*, slightly smaller, or similar in size to some specimens of *T. pollens*, but consistently less robust, carpometacarpus proportionately shorter than in other species, tarsometatarsus with expanded fossa parahypotarsalis medialis.

Measurements. See Table 1–2.

TABLE 1. Measurements (mm) of pectoral elements of *Tyto cravesae*, new species, compared with other large fossil tytonids from the West Indies.

| Measurement | <i>Tyto cravesae</i> (Cuba) Range (mean) n | <i>Tyto ostologa</i> (Hispaniola) Range (mean) n | <i>Tyto pollens</i> (Bahamas) Range (mean) n | <i>Tyto noeli</i> (Cuba) Range (mean) n |
|---|--|--|--|---|
| Coracoid | | | | |
| Length of glenoid facet | 12.8 | 13.1–14.3 (13.8) 9 | — | 11.0–11.9 (11.5) 3 |
| Width of glenoid facet | 4.4 | 5.0–5.8 (5.4) 9 | — | 3.9–4.0 (3.95) 2 |
| Humerus | | | | |
| Depth of the head | 6.1–6.2 (6.15) 2 | 6.3–6.8 (6.6) 5 | 6.9 | 4.8–5.9 (5.5) 6 |
| Proximal width | 21.8–22.5 (22.1) 2 | 22.4–23.1 (22.8) 3 | 24.0 | 18.3–21.0 (19.6) 2 |
| Shaft width distal to deltopectoral crest | 9.4–9.7 (9.5) 2 | 9.6–9.8 (9.7) 2 | 10.8 | 7.3–9.1 (8.4) 5 |
| Shaft depth distal to deltopectoral crest | 9.2–9.3 (9.25) 2 | 9.2–9.6 (9.4) 2 | 10.7 | 7.1–8.3 (7.8) 5 |
| Shaft width at midpoint | 9.0 | 8.9–9.2 (9.0) 3 | 9.8 | 6.8–8.2 (7.7) 6 |
| Shaft depth at midpoint | 8.5–8.8 (8.6) 2 | 8.1–8.4 (8.3) 3 | 9.1 | 6.5–7.6 (7.3) 6 |
| Distal width | 20.5 | 21.3–21.8 (21.6) 5 | 23.1 | 18.3–18.5 (18.4) 2 |
| Ulna | | | | |
| Proximal depth | 13.7 | 13.5–14.2 (13.8) 4 | — | 11.2–13.0 (12.0) 3 |
| Carpometacarpus | | | | |
| Length | 70.0 | 68.1–68.6 (68.3) 2 | 74.8 | 66.3 |
| Proximal width | 7.2 | 6.9–8.0 (7.5) 8 | 8.4 | 6.2–6.7 (6.4) 2 |
| Proximal depth | 15.3 | 15.2–16.2 (15.7) 6 | — | — |

TABLE 2. Measurements (mm) of pelvic elements of *Tyto cravesae*, new species, compared with other fossil large tytonids from the West Indies.

| Measurement | Tyto cravesae (Cuba) Range (mean) n | Tyto ostologa (Hispaniola) Range (mean) n | Tyto pollens (Bahamas) Range (mean) n | Tyto noeli (Cuba) Range (mean) n |
|-------------------------------------|---|---|---|--|
| Femur | | | | |
| Proximal width | 15.5–16.1 (15.8) 3 | 15.0–17.3 (16.4) 12 | 15.9–16.8 ^c (16.3) 2 | 12.5–14.5 (13.6) 10 |
| Proximal depth | 9.6–9.9 (9.7) 3 | 9.1–10.2 (9.7) 9 | — | 7.8–8.9 (8.3) 9 |
| Depth of head | 6.6 | 6.6–7.4 (6.9) 13 | 7.0 | 5.5–6.2 (5.9) 5 |
| Shaft width at midpoint | 6.7–6.8 (6.75) 2 | 6.6–7.4 (7.0) 10 | 8.1–8.2 ^c (8.15) 2 | 5.6–6.3 (6.0) 12 |
| Shaft depth at midpoint | 7.9–8.1 (8.0) 2 | 5.9–7.2 (6.7) 10 | 7.5 | 5.5–6.7 (6.1) 12 |
| Distal width | 16.3 | 16.5–18.3 (17.3) 9 ^a | 18.1 ^c | 13.4–15.4 (14.4) 10 |
| Depth of internal condyle | 10.5–10.8 (10.7) 2 | 10.9–11.9 (11.5) 8 | — | 8.6–10.0 (9.3) 10 |
| Depth of external condyle | 12.9+ | 13.7–15.2 (14.5) 9 | — | 11.4–12.5 (12.0) 11 |
| Tibiotarsus | | | | |
| Shaft depth at midpoint | 7.3 | 6.8–7.5 (7.2) 6 | 7.5 (7.5) 2 | 5.8–6.4 (6.0) 4 |
| Shaft width proximal to condyles | 12.0 | 10.8–13.3 (12.7) 13 | 14.5–15.0 (14.7) 2 | 9.3–11.2 (10.2) 11 |
| Distal width | 15.1–15.3 (15.2) 2 | 16.0–17.6 (16.9) 12 ^b | 16.7 ^b | 13.0–14.2 (13.6) 6 |
| Tarsometatarsus | | | | |
| Length | 93.7 | 91.4–96.2 (94.0) 3 | 98.6–98.8 (98.7) 2 | 84.6–91.5 (88.5) 4 |
| Proximal width | 15.2–15.9 (15.6) 2 | 16.1–17.8 (17.3) 9 | 17.6–18.0 (17.8) 2 ^b | 12.5–14.5 (13.6) 10 |
| Depth of external cotyla | 10.3–10.5 (10.4) 2 | 9.5–11.2 (10.5) 6 | 10.6–12.6 (11.6) 2 | 8.2–9.3 (8.9) 5 |
| Depth of internal cotyla | 9.7–10.2 (9.9) 2 | 9.4–11.2 (10.4) 12 | 10.7–10.8 (10.75) 2 | 8.3–9.5 (8.9) 4 |
| Depth through inner calcaneal ridge | 11.5–11.9 (11.7) 2 | 11.3–13.5 (12.3) 5 | 13.1 | 10.5–10.9 (10.7) 3 |
| Shaft width at midpoint | 6.8–7.2 (7.0) 4 | 5.7–7.7 (7.2) 6 | 8.4–8.7 (8.5) 2 | 5.3–6.7 (6.1) 16 |
| Shaft depth at midpoint | 5.7–6.4 (6.1) 4 | 5.0–6.6 (6.2) 6 | 6.6–6.9 (6.7) 2 | 4.9–6.7 (5.4) 16 |
| Distal width | 17.3–18.2 (17.8) 5 | 18.4–20.4 (19.7) 9 | 20.2–21.1 ^b (20.6) 2 | 14.4–17.3 (15.7) 12 |
| Width of trochlea for digit III | 6.6 | 6.4–7.7 (7.1) 12 | 7.2–7.7 (7.4) 3 | 5.5–6.2 (5.8) 7 |
| Depth of trochlea for digit IV | 12.6–12.8 (12.7) 2 | 9.8–13.5 (12.4) 8 | 14.9–15.0 (14.95) 2 ^b | 9.5–12.0 (10.5) 10 |

^aSteadman & Hilgartner (1999:79, table 2).

^bOlson & Hilgartner (1982:37, table 8).

^cWetmore (1937:438).

+ Abraded.

Distribution. Hispaniola in north-central and southern Haiti and southern Dominican Republic.

Remarks. *Tyto ostologa* was described from three fragments of a single tarsometatarsus and the distal end of a right radius collected in Quaternary cave deposits in north-central Haiti in 1921 (Wetmore 1922). It was later noted that the name of the cave from which the type material was obtained was Grotte San Francisco (Wetmore & Swales 1931: 237). The postcranial elements obtained at the type locality and nearby caves above L'Atalaye in 1925 and 1927–1928 (Miller 1926, 1929; Wetmore & Swales 1931; Wetmore 1959) are at USNM and are mostly fragmentary and often still incrustated with travertine (see Material examined). Although this additional material was never described and has remained uncatalogued, it provided the basis for later comparisons of *T. ostologa* (Wetmore 1937; Olson & Hilgartner 1982; Steadman & Hilgartner 1999), and the present study. In the collections of the Florida Museum of Natural History, there is fossil material of *T. ostologa* from at least five cave localities, excavated from 1978 to 1984 by C. A. Woods & colleagues (see Woods *et al.* 1985) in southern Haiti and southern Dominican Republic (Steadman & Hilgartner 1999: 76), so the species probably occurred throughout the island of Hispaniola in pre-human times.



FIGURE 3. Left humeri in anconal view (A, B) and right carpometacarpi in external view (C, D) of giant species of *Tyto* from the West Indies: A, *T. cravesae*, new species (holotype) MNHNCu 75.590; B, *T. noeli* (large) WS 980; C, *T. cravesae*, new species (holotype) MNHNCu 75.590; D, *T. ostologa* USNM 543378, image reversed to facilitate comparisons. Scale = 1cm.

***Tyto pollens* Wetmore**

Bahaman Giant Barn Owl; Lechuza Gigante de Las Bahamas (Fig. 6D)

Tyto pollens Wetmore, 1937: 436 (type-locality “cave deposits on Great Exuma, Bahama Islands” = Little Exuma Island *vide* Hecht, 1955).

Tyto riveroi Arredondo, 1972b: 131, **new synonymy** (type-locality “Cueva de Bellamar, poco más de 1 Km. al Sur de la costa interior de la Bahía de Matanzas, Municipio de Matanzas,” Matanzas Province, Cuba).

Holotype. Left femur MCZ 2262. Collected by Vivienne Knowles in 1937.

Material examined. *Hendry Cave, Royal Island, Eleuthera, Bahamas.*—Coracoid: incomplete right (USNM 615825). Carpometacarpus: nearly complete right (USNM 615826). Tarsometatarsus: incomplete left (USNM 615827, lacking fragments of midshaft).

Banana Hole, New Providence, Bahamas.—Femur: proximal right (UF 41807). Tibiotarsus: distal half of left (UF 41804). Tarsometatarsus: complete left (UF 3196), incomplete left (UF 41808, lacking proximal end and trochlea for digit IV).

Cueva de Bellamar, Municipality of Matanzas, Matanzas Province, Cuba.—Tarsometatarsus: distal half of left (DPUH 1252, holotype of *T. riveroi*), proximal half of right (CZACC unnumbered), proximal end of right (OA 3215).

There also exist specimens from Andros, Bahamas, in the Florida Museum of Natural History (D. W. Steadman, pers. comm.).

Measurements. See Tables 1–2. Measurements of the three fragmentary tarsometatarsi of *T. riveroi* are here compared with those of *T. pollens* from the Bahamas (in parentheses, from Brodkorb 1959: 357, table 2): least width of shaft 8.4, 8.5 (8.6); width through trochleae, 21.5 (21.2); width of shaft at level of distalmost proximal foramen 13.6, 14.4 (13.7), depth through calcaneal ridge 13.9 (13.4).

Distribution. Bahamas, islands of the Great Bahama Bank; Cuba, Matanzas Province (see Fig. 1).

Remarks. This is the rarest, largest, and most robust of the Antillean barn owls, as well as being the largest representative of the genus *Tyto* in the New World. The species was originally named from a nearly complete femur (the holotype), an incomplete coracoid, the shaft of a major metacarpal, and the “head” of a tibiotarsus, from cave deposits thought to have come from the island Great Exuma in the Bahamas (Wetmore 1937). It was later determined that the cave was located on Little Exuma (Hecht 1955). The femur was characterized as slightly larger than that of *T. ostologa* of Hispaniola with the trochanteric ridge larger and more robust (Wetmore 1937: 436).

Brodkorb (1959) recorded *T. pollens* from deposits in Banana Hole, New Providence Island. Additional material from the same site was reported by Olson & Hilgartner (1982), who confirmed its distinction from *T. ostologa* and *T. noeli*. New material of *T. pollens* was collected by an expedition of the Smithsonian Institution in 1990 from Hendry Cave, Royal Island, Eleuthera, Bahamas. This consisted of a coracoid, carpometacarpus, tarsometatarsus, and few pedal phalanges. The owl remains were decidedly scarce in comparison with bones of its principal prey, the Bahaman hutia *Geocapromys ingrahami* (Allen). The carpometacarpus of *T. pollens* is much larger and more robust than in any specimen of *T. ostologa* available suggesting a proportionately larger wing in the former. Otherwise, the new material mentioned above provides evidence of overlap in size between *T. pollens* and *T. ostologa* (Table 1–2), but the former can be recognized by its decided robustness and other characters (see Wetmore 1937; Brodkorb 1959; Olson & Hilgartner 1982).

It is likely that *T. pollens* was present on all of the islands of the Great Bahama Bank inhabited by *Geocapromys* Chapman. There is as yet no evidence of the species from the islands of the Little Bahama Bank, where *Geocapromys* may not have existed until introduced by Amerindians (see Olson & Hilgartner 1982).

Arredondo (1972b) described a new species, *Tyto riveroi*, based on the distal half of a tarsometatarsus from a cave deposit in Matanzas Province, Cuba, that was much larger than *T. noeli*. For reasons discussed below, Arredondo was always under the impression that *Tyto noeli*, *T. ostologa*, and *T. pollens* were all of about the same size, therefore making *T. riveroi* distinctive by its greater size, which is not correct. We have located additional specimens from Cuba that are referable to *T. riveroi*. This material (topotypes) includes two proximal ends of right tarsometatarsi lacking articular surfaces (see Material examined), collected by Manuel Rivero de la Calle at the same time and place as the holotype. These fossils had never been mentioned in the literature, even though one of them was included in Arredondo’s paleontological collection. We were able to make direct comparisons of that specimen (OA 3215) with the tarsometatarsus of *T. pollens*. In size, *T. riveroi* is similar to *T. pollens* and there are no other distinctions to be made between them. Therefore we consider *Tyto riveroi* Arredondo 1972b, to be a junior subjective synonym of *T. pollens* Wetmore 1937. Fossils erroneously identified as *T. riveroi* by Salgado *et al.* (1992: 28, table 1) from cave deposits in Pinar del Río Province, were based on part of the type material of *Bubo osvaldoi*.

Brodkorb (1959:357) considered the possibility that *Tyto pollens* and *T. ostologa* were possibly differentiated only at the subspecific level but we agree with other authors (Wetmore 1922, 1937; Arredondo 1972a; Olson & Hilgartner 1984; Steadman & Hilgartner 1999) in considering them distinct at the species level, along with the other taxa recognized here. The rarity of *Tyto pollens* in Cuba is difficult to understand, although it could possibly be related to the much greater number of other avian predators on that island as opposed to the Bahamas.

***Tyto noeli* Arredondo**

Noel’s Giant Barn Owl; Lechuza Gigante de Noel
(Figs. 2A,B,C; 3B; 4A; 5A,B,C,D,G; 6A,E,F; 7A,B,C)

Tyto noeli Arredondo, 1972a: 416 (part). (type locality: “Cueva del Túnel, Término Municipal de La Salud, La Habana [now Mayabeque]” Province, Cuba).

Tyto noelli Arredondo, 1972a: 428, table 5 (lapsus).

Tyto neddi Steadman & Hilgartner, 1999: 76, **new synonymy** (type-locality: "Rat Pocket, Gun Shop Cliff, Two Foot Bay, Barbuda").



FIGURE 4. Right femora of giant species of *Tyto* from the West Indies in anterior view (A–D) and internal view (E–G): A, *T. noeli* (large) WS 894; B, *T. ostologa* USNM 543283; C, *T. cravesae*, new species (holotype) MNHNCu 75.590; D, *T. cravesae*, new species (paratype, proximal segment) MNHNCu 75. 594, image reversed to facilitate comparisons; E, *T. cravesae*, new species (paratype, distal segment) MNHNCu 75. 594, image reversed to facilitate comparisons; F, *T. ostologa* USNM 543283; G, *T. cravesae*, new species (holotype) MNHNCu 75.590. Scale =1cm.

Holotype. Right tarsometatarsus DPUH 1251. Collected March 3, 1968, by Noel González Gotera and Oscar Arredondo.

Emended diagnosis. The smallest and least robust of the fossil giant barn owls from the West Indies.

Material examined. *Cueva de Paredones, Ceiba del Agua, Municipality of Caimito, Artemisa (formerly La Habana) Province, Cuba.*—Coracoid: nearly complete left (OA 3212, lacking sterno-coracoidal process and procoracoid), nearly complete right (paratype OA 839, lacking sterno-coracoidal process). Humerus: distal end of left (WS 885, juvenile), proximal half of right (OA 3218). Ulna: incomplete left (WS 899, lacking distal end), distal half of left (OA 3016–3017), proximal half of right (OA 3210), proximal right (CZACC 400–624, lacking olecranon), distal half of right (OA 3022), shaft of right (WS 915). Femur: complete left (WS 913–914, both fragmentary), distal half of left (OA 3214), distal left (paratype OA 834, abraded), complete right (OA 3211). Tibiotarsus: distal half of left (OA 3213), distal left (CZACC unnumbered, juvenile), proximal half of right (paratype OA 827). Tarsometatarsus: complete left (WS 18A), distal half of left (OA 3112), distal left (WS 916, juvenile), incomplete right (OA 829, OA 3113; both lacking distal end), proximal shaft of right (OA 833), proximal right (OA unnumbered), distal right (OA 3119; WS 882, lacking wing of the trochlea for digit IV).

Cueva de Sandoval, Vereda Nueva, Municipality of Caimito, Artemisa (formerly La Habana) Province, Cuba.—Coracoid: complete left (WS 369), complete right (WS 368, WS 851), sternal half of right (WS 909). Humerus: incomplete left (WS 980, lacking distal end, portions of deltopectoral crest and bicipital surface), proximal left (WS 1112, fragmentary), proximal shaft of left (WS 348), distal half of left (WS 983), shaft of left

(WS 343, juvenile), distal shaft of left (WS 863, juvenile), distal left (WS 1108), proximal third of right (CZACC unnumbered), distal half of right (WS 342), distal portion of shaft of right (WS 371–372). Ulna: proximal half of left (WS 370), proximal left (WS 906–907, lacking olecranon), proximal right (WS 905, lacking most of the articular surface), distal right (WS 950, WS 1111). Femur: incomplete left (WS 373, lacking proximal end; CZACC unnumbered, lacking proximal third), proximal half of left (WS 1032), incomplete right (WS 894–895, lacking head; CZACC unnumbered, lacking head and internal condyle), proximal half of right (CZACC unnumbered), proximal right (WS 781; WS 841, juvenile), distal right (WS 1106, fragmentary). Tibiotarsus: incomplete left (WS 839, lacking proximal end, juvenile), distal half of left (WS 345), distal left (WS 902; WS 984, lacking internal condyle), incomplete right (WS 344, lacking distal end), distal right (WS 901; WS 903, lacking anterior portions of the lateral condyle—904, juvenile). Tarsometatarsus: complete left (WS 897E) and complete right (WS 898E) of the same individual, proximal left (WS 911, fragmentary), proximal right (WS 910, lacking inner calcaneal ridge), distal half of right (WS 846, lacking trochleae for digits II and III; CZACC unnumbered), distal right (WS 912, lacking trochlea for digit IV, juvenile).

Cueva del Indio, Calabazar, Municipality of Boyeros, Ciudad de La Habana Province, Cuba.—Femur: incomplete right (OA 1027, lacking condyles).

Cueva del Túnel, La Salud, Municipality of Quivicán, Mayabeque (formerly La Habana) Province, Cuba.—Humerus: distal shaft of left (OA 814), proximal right (WS 295–296, both fragmentary), distal shaft of right (WS 291, juvenile). Ulna: proximal left (OA 807), distal left (paratype OA 816), distal right (paratype OA 815). Femur: incomplete left (OA 819, lacking both ends), incomplete right (paratype OA 818, with fragmentary condyles). Tibiotarsus: proximal left (OA 809, lacking inner cnemial crest), distal half of left (WS 136), distal left (paratype OA 812), distal shaft of left (OA 810), proximal half of right (WS 213, lacking outer cotyla), proximal right (WS 214), distal half of right (OA 3118). Tarsometatarsus: complete right (holotype DPUH 1251), medial segment of right (OA 813, OA 821), distal right (OA 817).

Cueva de Insunza, La Salud, Municipality of Quivicán, Mayabeque (formerly La Habana) Province, Cuba.—Humerus: distal shaft of right (WS 268). Tarsometatarsus: nearly complete left (WS 15, lacking fragments of shaft posteriorly).

Cueva del Chicharrón, La Salud, Municipality of Quivicán, Mayabeque (formerly La Habana) Province, Cuba.—Carpometacarpus: incomplete left (CZACC unnumbered, lacking metacarpal III).

Cuevas Blancas, Aguacate, Municipality of Quivicán, Mayabeque (formerly La Habana) Province, Cuba.—Carpometacarpus: proximal left (CZACC unnumbered, CZACC unnumbered). Tibiotarsus: distal right (CZACC unnumbered). Tarsometatarsus: proximal half of left (CZACC unnumbered, lacking inner calcaneal ridge), distal left (CZACC unnumbered).

Cantera cerca de Loma de Mosas, 5 km Northeast of the city of Sancti Spiritus, Sancti Spiritus Province, Cuba.—Femur: proximal fragment of right (OA 3120).

Cueva de la Jutía, Loma de los Rubíes, Municipality of Florencia, Ciego de Ávila Province, Cuba.—Tarsometatarsus: distal left (CZACC unnumbered).

Skeleton (Goat Bone) Cave, Clarendon Parish, Jamaica.—Coracoid: left (USNM 535720).

Drum Cave, Clarendon Parish, Jamaica.—Tarsometatarsus: distal half of right (USNM 615828, lacking trochleae for digits II and III), distal left (USNM 615829, lacking trochlea for digit IV).

Rat Pocket, Gun Shop Cliff, Two Foot Bay, Barbuda.—Coracoid: humeral end of left (paratype of *T. neddi* USNM 359245). Femur: distal right (holotype of *T. neddi* USNM 359240, fragmentary). Additional type material of *T. neddi*, not listed herein, includes a few pedal and ungual phalanges (see Steadman & Hilgartner 1999).

Distribution. Cuba, from the province of Pinar del Río (see Suárez & Díaz-Franco 2003, Suárez 2004b) to Ciego de Ávila; also south-central Jamaica and Barbuda (see Fig. 1).

Remarks. *Tyto noeli* is the commonest extinct large barn owl in the Quaternary of Cuba, its type series being the largest (Arredondo 1972a) for any fossil tytonid described from the West Indies. This taxon was originally known from two Quaternary cave sites in the former La Habana Province (now split in two provinces: Artemisa to the west, and Mayabeque to the east). Although Arredondo (1972a: 416) commented on the abundance of postcranial elements of *T. noeli* in his collection (at least 23 specimens), in the original description only ten were used, plus three others that appeared only in tables and figures (for a total of 13; note that the legends to figures 2 and 4 are reversed in the original description). At that time, Arredondo (1972a) could rely only on the little published information on *T. ostologa* and *T. pollens* for comparison with *T. noeli* and hence was under the

impression that *T. noeli* was about the same size, or even larger than those two species, which is not the case, however (for a correct size correlation see Olson & Hilgartner 1982: 36; Steadman & Hilgartner 1999: 79). Confusion arose because the type series was a composite which included a large and robust tarsometatarsus (and other specimens) lacking the distal end (OA 828), referred herein to a new species described below. In Table 2 of the original description Arredondo estimated the total length of this specimen at 100 millimeters, much larger even than *T. pollens*, which was incorrect. Arredondo did not consider that the holotypical tarsometatarsus of *T. noeli* had a shorter shaft when compared with the equivalent element in *T. furcata*, the species used by him as a model for his hypothetical reconstructions (O. Arredondo pers. comm. to W. Suárez in 1999). Overestimation is evident also in the length of the tibiotarsus reconstructed, based on fragments from different individuals (see Arredondo 1972a, figs. 4, 3). A relatively shorter shaft of the tarsometatarsus, compared with *T. alba* or with *T. furcata*, is a shared character of all the giant *Tyto* species from the West Indies (see Wetmore & Swales 1931: 237; Brodkorb 1959: 357). That mistake is what led Arredondo to consider that *T. noeli*, *T. ostologa*, and *T. pollens* were about the same size in all his subsequent publications (Arredondo 1972b; Acevedo-González *et al.* 1975; Arredondo 1976, 1982, 1984). Furthermore, and as result of that confusion, some fossils described herein as a new species, larger than *T. noeli*, provided the basis for speculations about the presence of *T. riveroi* in cave deposits in the former La Habana Province (see Suárez & Arredondo 1997: 101).

A few fragments (see Material examined; Figs. 2A, 7B) from two caves in the Portland Ridge area of southern Jamaica collected in 1995 establish that *T. noeli* also occurred on that island. These bones probably date from well into the Holocene as surface material from Drum Cave had a radiocarbon age of 3700±150 yr and the lower level of Skeleton Cave dated to 6410±110 yr (McFarlane *et al.* 2002). In contrast, the only bones of this tytonid yet dated directly are from the Cueva El Abrón deposit in Pinar del Río Province, Cuba, of late Pleistocene (17, 406 ±161yr) age (Suárez & Díaz-Franco 2003).

We also compared the holotypical fragmentary distal end of a femur (USNM 359240) and the paratypical fragment of a coracoid (USNM 359245) of *Tyto neddi* from the island of Barbuda (Steadman & Hilgartner 1999) with equivalent material of *T. noeli* from Cuba and could find no quantitative or qualitative characters by which the two could be separated (Fig.5A, C; Table 3). These two species had never been compared directly before. Although it is possible that more material of this owl from the Lesser Antilles might reveal some differences from *T. noeli* of Cuba and Jamaica, there is no basis for making a distinction at present. The characters proposed by Steadman & Hilgartner (1999: 77) in the diagnosis of *Tyto neddi* are found in our series of *T. noeli*. Therefore we provisionally consider *Tyto neddi* Steadman & Hilgartner (1999) to be a junior subjective synonym of *T. noeli* Arredondo (1972a).

TABLE 3. Measurements (mm) of elements of *Tyto noeli* from Cuba, Jamaica, and Barbuda.

| Measurement | Cuba Range (mean) n | Jamaica Range (mean) n | Barbuda Range (mean) n |
|---|------------------------|---------------------------|---------------------------|
| Coracoid | | | |
| Length of glenoid facet | 11.0–11.9 (11.4) 3 | 10.9 | 11.5 |
| Width of shaft at narrowest point | 5.3–5.9 (5.5) 4 | 5.4 | — |
| Depth of shaft at narrowest point | 3.4–3.7 (3.6) 4 | 3.6 | 3.4 |
| Femur | | | |
| Distal width | 13.4–15.4 (14.4) 10 | — | 15.3 |
| Depth of internal condyle | 8.6–10.0 (9.3) 10 | — | 9.9 |
| Tarsometatarsus | | | |
| Shaft width at midpoint | 5.3–6.7 (6.1) 16 | 5.9 | — |
| Shaft depth at midpoint | 4.9–6.7 (5.4) 16 | 4.8+ | — |
| Width through trochleae for digits II and III | 11.2–12.5 (11.9) 4 | 10.8+ | — |
| Depth of trochlea for digit II | 8.4–10.7(9.5) 8 | 9.3 | — |

+ Abraded.

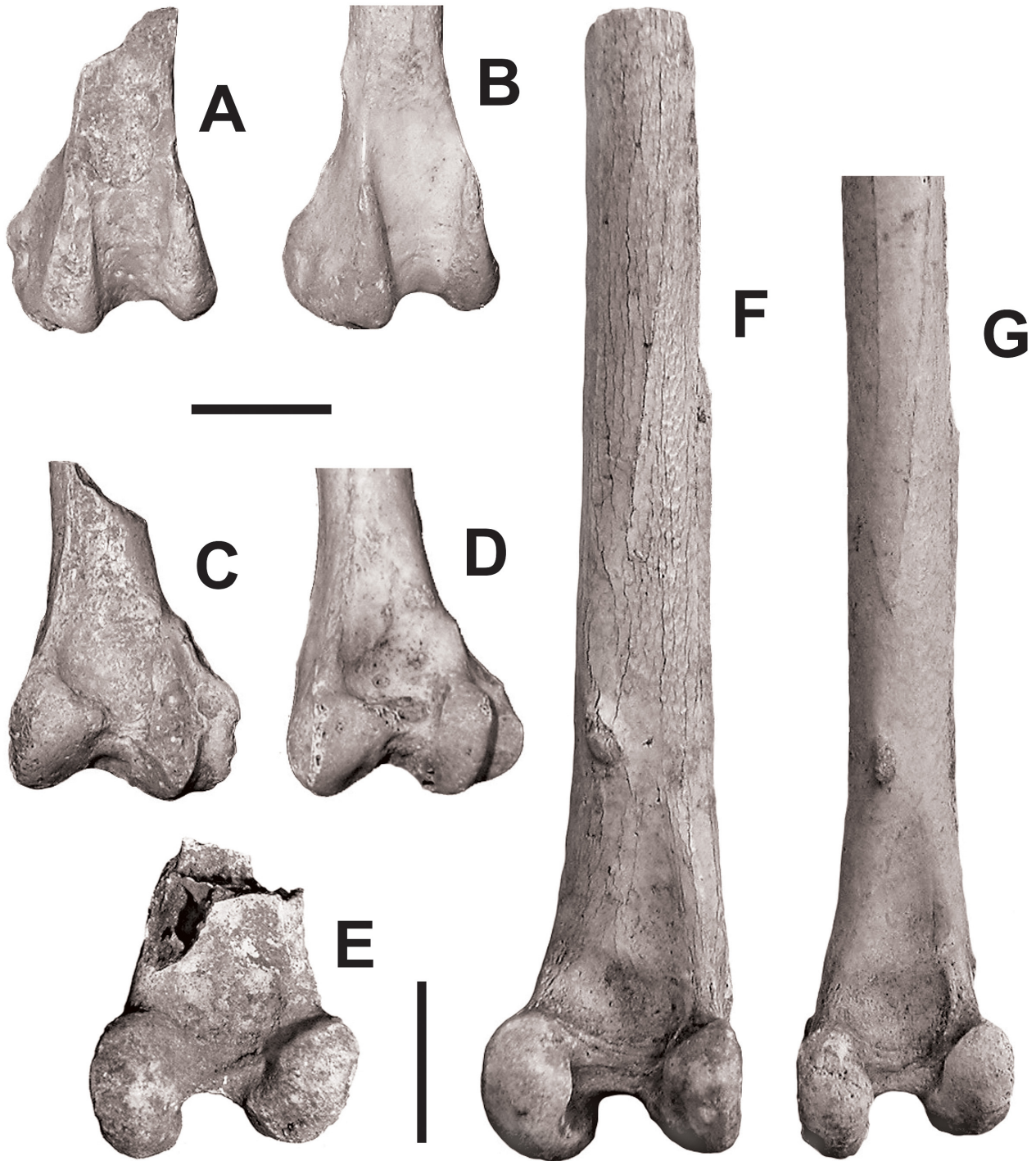


FIGURE 5. Distal ends of right femora in anterior (A, B) and posterior (C, D) views and distal ends of left tibiotarsi in anterior view (E–G) of giant species of *Tyto* from the West Indies: A and C, *T. noeli* (Barbuda, holotype of *T. neddi*) USNM 359240; B and D, *T. noeli* (Cuba) WS 894; E, *T. cravesae*, new species (paratype) OA 831; F, *T. cravesae*, new species (paratype) MNHNCu 75.593; G, *T. noeli* (large) WS 345. Scale =1cm.

The series of *Tyto noeli* we examined increases our knowledge of the size range for this species, providing evidence of marked sexual dimorphism, as can be expected in a large nocturnal raptor, in agreement with material of the other species described from the West Indies (Olson & Hilgartner 1982; Steadman & Hilgartner 1999). From Barbuda, two different-sized species of *Tyto* were recorded by Steadman & Hilgartner (1999), the smaller being about the size of the living *Tyto alba* and identified as *Tyto* sp. Pavia (2004: 635) interpreted these differences in size as sexual dimorphism of a single species of *Tyto* that occurred in that island. The series of large Tytonidae from

the West Indies we examined does not support Pavia's point of view, and we agree with Steadman & Hilgartner (1999) in recognizing two species from Barbuda. Similarly, remains of *Tyto furcata* and *T. noeli* can also be found in association in Cuban cave deposits (Arredondo 1972a, 1975, 1976, 1982, 1984; Suárez 2000). Specimens of *Tyto noeli* are consistently larger and more robust than those of *T. furcata* (Arredondo 1972a), and smaller and more gracile than in *T. ostologa*, *T. pollens* (Table 1–2; see Olson & Hilgartner 1982; Steadman & Hilgartner 1999), or in the new species described below.



FIGURE 6. Proximal ends of right tarsometatarsi in anterior view (A–D) and distal ends of left (E, F) and right (G, H) tarsometatarsi in anterior view of giant species of *Tyto* from Cuba. A, *T. noeli* (adult) WS 15, image reversed to facilitate comparisons; B, *T. cravesae*, new species (juvenile, paratype) MNHNCu 75.595; C, *T. cravesae*, new species (adult, paratype) MNHNCu 75.596; D, *T. pollens* (adult), OA 3215; E, *T. noeli* (adult) WS 18A; F, *T. noeli* (juvenile) WS 916; G, *T. cravesae*, new species (juvenile, paratype) WS 09I; H, *T. cravesae*, new species (adult, paratype) MNHNCu 75.592. Scale =1cm.

Tyto cravesae, new species

Craves's Giant Barn Owl; Lechuza Gigante de Craves
(Figs. 2D; 3A,C; 4C,D,E,G; 5E,F; 6B,C,G,H; 7D,E; 8A)

Holotype. Associated postcranial elements of a single individual MNHNCu 75. 590 (original numbers in collection of William Suárez are indicated in parentheses), consisting of the proximal half of a left humerus (WS 1026E"), proximal end of a right ulna (WS 1114E"), nearly complete right carpometacarpus (WS 1027E"), and a nearly complete right femur (WS 1025E"). Collected by William Suárez on 5 June 1998.



FIGURE 7. Right tarsometatarsi in anterior view of giant species of *Tyto* from the West Indies: A, *T. noeli* (small specimen) WS 15, image reversed to facilitate comparisons; B, *T. noeli* (Jamaica) USNM 615828; C, *T. noeli* (large specimen) WS 898E; D, *T. cravesae*, new species (paratype) MNHNCu 75.596; E, *T. cravesae*, new species (paratype) OA 878; F, *T. ostologa* USNM 543276, image reversed to facilitate comparisons. Scale = 1cm.

Type locality and age. Cueva de Paredones, about 3 km SW of Ceiba del Agua, Municipality of Caimito, Artemisa (formerly La Habana) Province, Cuba (see Arredondo 1961, 1970, 1971, 1982, 1984; Brodkorb 1969; Morgan & Ottenwalder 1993; Gutiérrez 2010). The type material was collected within the cave and near the place known as “Salón del Pozo” (see Morgan & Ottenwalder 1993), in an amoeboid-shaped patch of red clay matrix (ca. 50 cm in its greatest diameter) in a wall cavity about 1.5 m from the floor of the cave. Quaternary, probably late Pleistocene but not dated (see Morgan & Ottenwalder 1993 for discussion of the age of deposits in Cueva de Paredones). This is the type locality of other Cuban fossil birds such as *Pulsatrix arredondo* Brodkorb, *Gymnogyps varonai* (Arredondo), *Ornimegalonyx “minor”* Arredondo, and *Oscaravis olsoni* (Arredondo & Arredondo) (see Brodkorb 1969; Arredondo 1971, 1976, 1982, 1984; Arredondo & Arredondo 2002b, Suárez & Olson 2009).

Measurements (mm) of holotype. Humerus: proximal width 22.5, depth of head 6.2, width of shaft at level of distal end of deltopectoral crest 9.7, depth of shaft at level of distal end of deltopectoral crest 9.3, depth of midshaft 8.8. Ulna: proximal depth 13.7. Carpometacarpus: length 70.0, proximal width 7.2, proximal depth 15.3. Femur: length through internal condyle 79.5+ (abraded), proximal width 15.5, proximal depth 9.7, shaft width at midpoint 6.8, shaft depth at midpoint 7.9, depth of internal condyle 10.8.

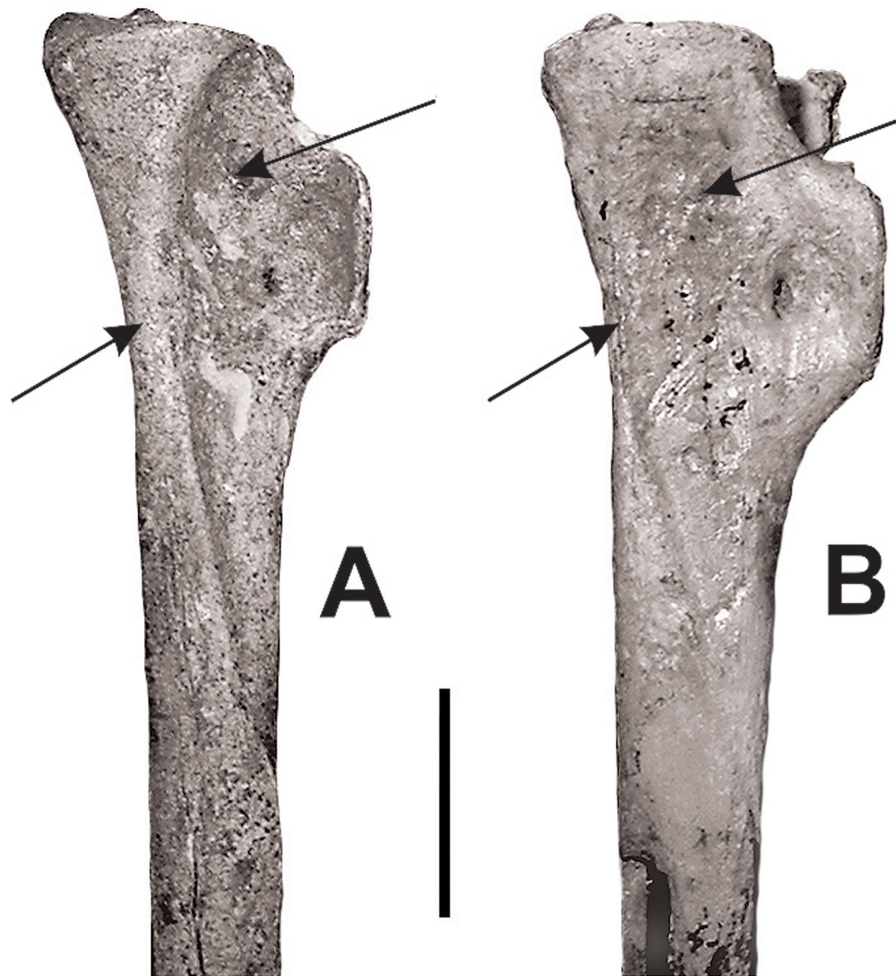


FIGURE 8. Right tarsometatarsi in internal view of giant species of *Tyto* from the West Indies: A, *T. cravesae*, new species (paratype) MNHNCu 75.596; B, *T. ostologa* USNM 543302, image reversed to facilitate comparisons. Arrows indicate characters discussed in text. Scale = 1 cm.

Paratypes. Topotypes.—Coracoid: sternal end of left (OA 832). Humerus: shaft of left (WS 077). Tibiotarsus: distal end of left (OA 831, paratype of *T. noeli*). Tarsometatarsus: complete right (MNHNCu 75.596), right lacking distal end (OA 828, paratype of *T. noeli*), proximal end of right (MNHNCu 75.595, juvenile, formerly WS unnumbered), distal end of right (WS 09I, juvenile).

Cueva del Campo de Tiro, Meseta de Anafe, Municipality of Caimito, Artemisa (formerly La Habana) Province, Cuba.—Femur: left lacking a proximal portion of the shaft (MNHNCu 75.594, formerly WS 218E).

Cueva del Túnel, La Salud, Municipality of Quivicán, Mayabeque (formerly La Habana) Province, Cuba.—Humerus: proximal end of right (OA 826, paratype of *T. noeli*), distal half of right (OA 804, paratype of *T. noeli*). Tibiotarsus: distal half of left (MNHNCu 75.593, formerly WS 216). Tarsometatarsus: distal end of left (MNHNCu 75.591, formerly WS 137), distal end of right (MNHNCu 75.592, formerly WS 215).

Cuevas Blancas, Aguacate, Municipality of Quivicán, Mayabeque (formerly La Habana) Province, Cuba.—Femur: Proximal end of left (CZACC unnumbered). Tarsometatarsus: shaft of right (CZACC unnumbered).

Las Breas de San Felipe, Martí, Municipality of Martí, Matanzas Province, Cuba.—Tarsometatarsus: distal end of left (MNHNCu 75.4801) (see Iturralde-Vinent *et al* 2000).

Measurements of paratypes. See Table 1–2.

Distribution. Fossil localities in Western Cuba, from Artemisa to Matanzas Provinces.

Etymology. After Julie Craves, of the University of Michigan-Dearborn, for her dedication to avian conservation and her boundless appreciation of Cuban friends and birds.

Diagnosis. A species of the genus *Tyto* that is larger than *T. noeli* and smaller than *T. pollens*, about the size of

some specimens of *T. ostologa* but less robust, differing from that species by the longer carpometacarpus, deeper and more ovoid shaft of the femur, tarsometatarsus distinctly flared at the ends, and fossa parahypotarsalis medialis smaller.

Description and comparisons. Specimens referred to *Tyto cravesae* are consistently larger and more robust than the equivalent elements in the skeleton of *T. noeli*, and smaller and much more gracile than those of *T. pollens*. Juvenile specimens of *T. cravesae* are also consistently larger and more robust than juveniles or adults of *T. noeli* (Fig. 6). Qualitative characters in comparison with *T. noeli* include: femur with a much deeper shaft (Fig. 4), being ovoid in cross section (cylindrical or less ovoid with much less deep shaft in *T. noeli*); distal end with posterior articular surface of the internal condyle larger and more expanded (smaller in *T. noeli*); distal end of tibiotarsus (Fig. 5) with shaft greatly expanded bilaterally and with the tendinal groove wider (shaft not expanded, tendinal groove thinner in *T. noeli*); tarsometatarsus (Figs. 6–8) with shaft relatively shorter but more robust, with anterior metatarsal groove expanded and relatively shallow (shaft relatively longer and thinner, with anterior metatarsal groove thinner and deeper in *T. noeli*), tubercle for tibialis anticus distally placed (this character can be variable) being separated from the proximal metatarsal foramina (consistently proximad and closer to proximal metatarsal foramina in *T. noeli*), distal end proportionately less massive (in some individuals) than in *T. noeli*.

Bones of *T. cravesae* are less robust, but similar in linear dimensions to some specimens of *T. ostologa* (Figs. 3, 4, 7, 8; Table 1–2). Most of the pectoral elements of *T. cravesae*, including coracoid, humerus, and ulna, are very similar in characters when compared with *T. ostologa*; in contrast, the carpometacarpus and hindlimb elements show consistent diagnostic characters including carpometacarpus (Fig. 3; Table 1) longer with a more slender metacarpal II (shorter and more robust metacarpal II in *T. ostologa*); femur (Fig. 4, Table 2) with the shaft more ovoid in cross section, so that it is much wider in either lateral or medial view (shaft more cylindrical, less ovoid in *T. ostologa*); tarsometatarsus (Figs. 6–8, Table 2) with proximal half of shaft relatively more expanded or wider, flaring more gradually proximad (shaft less expanded, flaring more abruptly at the proximal articulation in *T. ostologa*), anterior metatarsal groove also relatively wider (narrower in *T. ostologa*), fossa parahypotarsalis medialis smaller (internal view), resulting the medial (inner) border of shaft at this level wider (usually larger, greatly expanded and with thin medial border in *T. ostologa*), distal end less developed and smaller (much more developed, larger and massive in *T. ostologa*).

Compared with *T. pollens*, the femur of *T. cravesae* has the shaft deeper and ovoid (less deep or ovoid in *T. pollens*); tarsometatarsus relatively more elongated with the shaft less constricted bilaterally at midpoint (very wide and robust, relatively shorter, greatly constricted shaft bilaterally at midpoint in *T. pollens*). Other comparable elements of these two species are very similar in qualitative characters, being distinguishable mostly by the discrepancies in size and robustness mentioned above, *T. pollens* being the largest (Tables 1–2).

Remarks. The species *Tyto cravesae* seems to be more closely related to *T. noeli* than to *T. ostologa* of Hispaniola, which is different in the morphology of the carpometacarpus and proximal end of the tarsometatarsus. *Tyto cravesae* is, after *T. pollens* (including *T. riveroi*), the rarest species of barn owl in the fossil record of Cuba. A deposit formed from ancient pellets of this new species was discovered and excavated by WS in January of 1992, in a cave named Cueva del Campo de Tiro, in the eastern extremity of Meseta de Anafe, near Cayaguasal, Caimito. This deposit was located in a small depression about one meter in diameter and 9 cm at its deepest point, embedded in a dry red-orange soil (see Paratypes of *T. cravesae*). The deposit was filled with fragmentary material, including bones of juveniles of the extant rodent *Capromys pilorides* (Say) and juveniles and adults of the extinct *Geocapromys columbianus* (Chapman), plus scarce remains of *Tyto cravesae* (W. Suárez unpubl. data). The existence in Cuba of large members of *Tyto* such as *T. cravesae* and strigid owls of about the same size and larger (Arredondo 1976, 1982, 1984; Arredondo & Olson 1994) probably contributed to the rarity of *T. pollens* there in the late Pleistocene, but just how the almost staggering diversity of avian raptors may have partitioned their potential resources of prey remains to be explored.

Discussion

The present revision of the extinct giant barn owls from the Quaternary of the West Indies decreases the number of previously recognized species from five to three, with *Tyto riveroi* of Cuba being synonymized with *T. pollens* of the Bahamas, and *T. neddi* of Barbuda with *T. noeli* of Cuba. An additional new species, *Tyto cravesae*, is described

here from Cuba, to bring the total to four. These giant barn owls have the following distribution in the Antillean Subregion: *Tyto ostologa* Wetmore 1922, endemic to Hispaniola; *T. pollens* Wetmore 1937, Bahamas and Cuba; *T. noeli* Arredondo 1972a, Cuba, Jamaica, and Barbuda; *T. cravesae*, new species, endemic to Cuba (see Fig. 1).

We speculate that more than one invasion of the genus *Tyto* occurred in the West Indies to give rise to these large species. It appears that *T. ostologa* may have been derived from an earlier stock because of the unique morphology of the proximal end of the tarsometatarsus, which is distinct from other biogeographically related large barn owls (Figs.7,8), although this might also be the result of some particular specialization to conditions in Hispaniola. Equally distinctive is the more ovoid and deeper shaft of the femur in *T. cravesae* as compared with all the other large barn owls. The reduction of distal wing elements, such as the carpometacarpus, which is relatively shorter in *T. ostologa*, may be related to a number of variables such as maneuverability and load bearing capacity.

Most barn owls (*Tyto*) feed on a variety of vertebrate prey but are heavily dependent upon mammals, their exceptionally acute directional hearing being an adaptation for feeding on animals moving about at night, which means mostly mammals. Populations of Tytonidae on islands are almost invariably linked to mammalian prey, and endemic species or subspecies of *Tyto* on islands are almost without exception an indication of the presence of an endemic mammal (Olson unpubl. data). Understanding the distribution and evolution (of size, for example) of giant barn owls in the West Indies is therefore dependent upon knowledge of the distribution and size of their mammalian prey species, most of which are now also extinct or nearly so.

The largest of all the West Indian barn owls was *Tyto pollens*, and where it existed on the Great Bahama Bank, there is no question about its principal prey—the Bahaman hutia *Geocapromys ingrahami*. This was the only terrestrial mammal on the bank and the remains of the owl are always associated with those of the hutia. Most of the sediment in the deposits of Hendry Cave, Royal Island, Eleuthera, for example, consisted of tightly packed bones of the hutia that must have accumulated over many generations of owls. The only naturally occurring remaining population of *G. ingrahami* is confined to tiny East Plana Cay, although the species was known historically elsewhere on the Great Bank. The maximum recorded weight of extant individuals is 1050g (Howe & Clough 1971) but that population may have been dwarfed by the very small land area and high population densities because most fossil material from elsewhere appears to include larger individuals than represented by modern comparative skeletons (Olson unpubl. data).

In Cuba, where *Tyto pollens* (“*T. riveroi*”) was rare, it would have had a much greater choice of prey. We consider that Arredondo’s hypothesis (1976, 1982, 1984) that it captured small individuals of Cuban edentates is unlikely, so that it probably preyed mainly on some species of rodents. *T. pollens* probably evolved in Cuba and subsequently colonized the Bahamas. The Bahamas would have experienced their greatest contraction in land area about 400 thousand years ago (Olson & Hearty 2009), suggesting that *Geocapromys* may have colonized the archipelago during a subsequent glacial period when the Cuban and Bahaman archipelagos were much closer geographically, to be followed shortly afterwards by its only nocturnal predator, *Tyto pollens*.

The smallest of the giant barn owls, *Tyto noeli*, doubtless originated in Cuba, where it was abundant and widespread. The species evidently spread to islands where mammalian prey of suitable size occurred. In the Lesser Antilles it is known so far only from Barbuda (*T. “neddi”*) where its main prey would have been the extinct giant rice rat *Megalomys audreyae* Hopwood. Several species of giant rice rats (Sigmodontinae: Orizomyini) are known from fossil and archeological deposits throughout the Lesser Antilles, including Barbados, and they were also known historically from Martinique and St. Lucia, although there is as yet no evidence of rice rats on Dominica (Turvey *et al.* 2010, 2012). The islands from St. Vincent through Grenada are exceptional as much smaller rice rats (*Oligoryzomys* Bangs) once occurred there along with the diminutive Lesser Antillean Barn Owl *Tyto insularis* Pelzeln (Olson & Suárez unpub. data). *Tyto noeli* probably occurred throughout the rest of the Lesser Antilles where giant rice rats occurred but where there has been insufficient paleontological exploration to document its former distribution.

The colonization of Jamaica by *T. noeli* was probably a relatively recent event. Two endemic land mammals are known historically from Jamaica (Pregill *et al.* 1988; Woods 1989); the hutia *Geocapromys brownii* (Fischer), which, with a weight of 1000 to 2000 g (Anderson *et al.* 1983), adults of which would have been much too large for *T. noeli* to take, and the now extinct rice rat *Oryzomys antillarum* Thomas which was very similar in size and morphology to mainland rice rats such as *O. palustris* (Harlan), which weighs from 45 to 80 g (Wolfe 1982). The fossil record in Jamaica indicates that *Oryzomys* Baird did not colonize Jamaica until the end of the Pleistocene, about 11,000 years ago (see McFarlane *et al.* 2002; Silva Taboada *et al.* 2008). Therefore, the colonization of Jamaica by *Tyto noeli* probably took place following the arrival of the rice rat.

Steadman & Hilgartner (1999) speculated that *Tyto ostologa* preyed on monkeys and ground sloths in Hispaniola. *Tyto ostologa* appears to have been the Hispaniolan representative of *T. pollens* (Olson & Hilgartner 1982: 36), but was not as robust. This suggests that its principal prey may have been somewhat smaller than adults of the rodent *Geocapromys ingrahami*, the principal prey of *T. pollens* in the Bahamas. The most likely candidate as prey for *T. ostologa* would have been the extinct rodent *Isolobodon portoricensis* Allen, a species widespread in fossil deposits in Hispaniola but first described from archeological material from Puerto Rico, where it had been taken as a domesticate by Amerindians and where it never occurred in the wild (Olson & Maíz López 2008). The fact that there is no evidence of a giant barn owl in the extensive fossil record of Puerto Rico is further testimony that *Isolobodon* Allen was never native there. On the other hand, the considerable diversity of mammals in the fossil record of Hispaniola would suggest that the island could have harbored more than one species of giant *Tyto*, yet the only one known at present is *T. ostologa*.

In Cuba three species of large tytonids (one smaller, one about the size of, and another larger than *T. ostologa*) were sympatric, and deposits formed by pellets of at least two of them (*T. noeli* and *T. cravesae*) are known (see Arredondo 1976, 1982; Suárez 2000, 2004b; Suárez & Díaz-Franco 2003; W. Suárez unpubl. data). *Tyto pollens* is extremely rare in Cuba and deposits formed there by this barn owl are totally unknown. Knowledge of the exact species composition of the prey of large tytonids is derived from isolated deposits where no remains of the strigid owl *Ornimegalonyx oteroi* occur. *Ornimegalonyx* Arredondo is mainly responsible for the presence of remains of large members of Capromyidae Smith (see Silva Taboada *et al.* 2008) in Cuban deposits, especially those found at low elevations. Sites occurring relatively high in the mountains, sometimes with difficult access, provide the best opportunity to find isolated prey remains of *Tyto noeli*, *T. cravesae* and the living barn owl *Tyto furcata* (Suárez unpubl. data).

In some localities such as Cueva El Abrón (see Suárez & Díaz-Franco 2003, Suárez 2004b, Silva Taboada *et al.* 2008), remains of *Tyto noeli* are mixed with its principal prey, juveniles of *Geocapromys columbianus* and *Boromys offella* Miller. The only known isolated deposit formed by *T. cravesae* (see the account of that species above) contains scarce remains of native rodents including juveniles of *Capromys pilorides* and *G. columbianus*. The latter, in different growth stages, seems to be the most important prey component of all large nocturnal raptors in Cuba. On the other hand, some small species of extinct terrestrial mammals, such as *Nesophontes micrus* Allen and *Boromys torrei* Allen, were extensively preyed upon by the living barn owl *Tyto furcata*. After the European colonization and introduction of rodents in the genera *Mus* Linnaeus and *Rattus* Fischer, those taxa replaced the native Antillean mammals in the diet of the living barn owl (Jiménez *et al.* 2005).

We know little for certain about the timing and causes of the extinction of any of the forms of giant barn owls in the West Indies, although there is no reason to believe that any of them disappeared prior to the arrival of humans. There is some evidence to suggest that these large raptors may have persisted into historical times. In Hispaniola *Tyto ostologa* likely persisted as late as the 18th century as Wetmore & Swales (1931: 238–239) relate that on 1 Feb 1788 three French residents of Haiti climbed to the summit of La Selle where at night they heard “hollow cries imitating the human voice that they attributed to some nocturnal bird, as they had seen feathers resembling those of a swan at the edge of sort of a den or cavern.” In modern times, Arredondo (1975: 184) described a sighting of a very large and dark-colored barn owl made by the Cuban mammalogist Gilberto Silva Taboada in Haiti, while Silva was searching for bats in a cave. In Cuba there are legends of a very large, white-colored barn owl in the countryside of Camagüey Province (Arredondo 1975: 184), but these have never been corroborated. Equally intriguing is the folklore from Andros Island, Bahamas, of a mysterious, large and white nocturnal entity called the “chickcharnie” that occurred in old-growth Caribbean Pine *Pinus caribaea* Morelet, which has been interpreted as possibly referring to *Tyto pollens* in historical times (Marcot 1995; White 1998; Hume & Walters 2012).

The disappearance of the giant species of *Tyto* had to have been closely tied to the reduction and extinction of their principal mammalian prey. As shown by midden deposits throughout the Caribbean, rodents were a favored food item of the islands’ first human colonizers (see Silva Taboada *et al.* 2008). With the advent of European settlers in the 16th century, hunting pressure would have increased (although probably offset by the extermination of aboriginal human populations), and predators such as rats, cats, dogs, and pigs were introduced, doubtless to the detriment of owls and their prey. Added to this was the usual habitat destruction, begun by Amerindians, but exacerbated by clearing for farming and European settlements. The principal prey of *Tyto pollens*, the Bahaman hutia, still existed historically at least on Crooked Island and Great Abaco, but become extinct in modern times and

the species now occurs only as a relict on East Plana Cay (see Olson & Pregill 1982; Morgan 1989; Woods & Kilpatrick 2005; Turvey & Dávalos 2008; Borroto-Páez *et al.* 2012).

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