The Great Predatory Birds of the Pleistocene of Cuba

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translated and amended by Storrs L. Olson

ABSTRACT

Recent paleontological investigations in Cuba have shown that the island was formerly inhabited by large populations of rodents and edentates. Based on discoveries of giant fossil raptorial birds (Strigiformes and Accipitriformes) in Cuba and other Antillean islands, the theory is put forth here that these predators were the principal agents in controlling the abundance of these native mammals. Details are given of the discovery in Cuba of the gigantic owl *Ornimegalonyx,* two species of giant barn owls (*Tyto*), a giant species of eagle (*Aquila borrasi*), and a vulture (*Antillovultur*) similar in size to the Andean Condor (*Vultur gryphus*). The relationships and possible origins of gigantism in these birds are discussed. Descriptions, geographic distribution, tables of measurements, and a list of the extinct faunas found in each of the type-localities are offered for each species.

Se expone la tesis, basada en los últimos descubrimientos realizados en Cuba y otras Antillas sobre aves fósiles gigantes de los órdenes Strigiformes y Accipitriformes, de que dichos táxones constituyeron el elemento faunístico primoridal que controlara con su acción predatora a roedores y desdentados que en estas islas existían, manteniendo asi el equilibrio biológico necesario. Se ofrecen datos concretos probatorios de la extremada abundancia en las Antillas de poblaciones de roedores y desdentados. Se dan detalles del descubrimiento en Cuba del gigantesco buho *Ornimegalonyx,* de dos especies gigantes de lechuzas del género *Tyto,* de una especie de águila gigante y de un buitre similar en talla a *Vultur gryphus.* Se plantea una discusión sobre el motivo que pudo originar el gigantismo en estas aves. Se ofrecen descripciones específicas de todas estas grandes aves predatoras, incluyéndose, distribución geográfica, tablas de medidas y una relación de la fauna extinguida hallada asociada en las localidades típicas.

Introduction

Recent studies of fossil material from numerous caves in Cuba have convincingly demonstrated the former extraordinary abundance of endemic mammals there. These include rodents of the genera *Heteropsomys, Capromys* (including *Geocapromys*), and *Macrocapromys*; ground sloths (Edentata) of the genera *Cubanocnus, Miocnus, Mesocnus,* and *Megalocnus*; and insectivores of the genera *Solenodon* and *Nesophontes.* These genera were represented throughout the island by species very numerous in terms of individuals. From such caves as Paredones and El Túnel in the province of Habana it is no exaggeration to say that tens of thousands of mandibles of *Capromys pleistocenicus* can be extracted from a single small chamber, although most of these specimens are poorly preserved. An examination of only a part of the fossil material taken from a small cave in Cayo Salinas, a few miles east-southeast of Caibarién, Las Villas, yielded the remains of over 200 individuals of the edentate genus *Mesocnus* (Acevedo, Arredondo, and Gonzalez, 1975). Further confirming the former abundance of native mammals is the widespread occurrence in Cuba of remains of blood-eating vampire bats of the genus *Desmodus* (Koopman, 1958; Arredondo, 1958b; Woloszyn and Mayo, 1974). These bats would necessarily have required numerous, large, warm-blooded mammals to sustain them. Similar abundant faunas of large rodents and ground sloths are also known from cave deposits in Hispaniola and Puerto Rico.

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Obviously, some natural regulator must have acted to maintain a biological equilibrium between these prolific herbivorous mammals and the vegetation on which they fed. In the Antilles, however, there are virtually no native carnivorous mammals. Exceptions are *Cubacyon transversidens* (Arredondo and Varona, 1974), a canid known from a single fragment of maxilla found in association with extinct vertebrates in a cave in the province of Habana, and the extant populations of *Procyon* known from the Bahamas, Barbados, and Guadeloupe, some or all of which may have been introduced to these islands by man (Varona, 1974; Arredondo and Varona, 1974). A mandible found in an Indian midden in Camagüey, Cuba, and attributed to *Procyon lotor* by the naturalist Andrés Poey (Harrington, 1935), may similarly have pertained to an introduced animal; the record is dubious in any case, since the specimen can no longer be found. Regardless, small procyonids could not have been an influential factor in the control of the endemic Antillean rodents and edentates.

The numerous and dense deposits of smaller vertebrates (Table 1) frequently found in Cuban caves abound with remains of the rodents [1] *Capromys pleistocenicus, Capromys nanus, Heteropsomys torrei,* and *H. offella;* the insectivores *Nesophontes micrus* and *N. major;* several genera of bats; passeriform birds, particularly of the genera *Mimocichla, Quiscalus* and *Dives;* as well as nonpasserines such as *Crotophaga* and *Glaucidium.* These remains are certainly attributable to the actions of medium-sized owls still existing in the island such as *Tyto alba* and *Asio stygius,* and perhaps to others now extinct, such as *Pulsatrix arredondoi* (Brodkorb, 1969).

The most outstanding accumulations of bones, however, are those of the larger mammals (Table 1) such as *Capromys pilorides, C. columbianus, Macrocapromys acevedo,* and occasional examples of *Cubanocnus gliriformis,* as well as large birds of various orders. Such remains suggest that many larger predators were once active in Cuba.

Much of the accumulation of vertebrate remains in cave deposits in Haiti was attributed to the depredations of the extinct giant barn owl *Tyto ostologa,* first described by Wetmore (1922). Another giant barn owl, *Tyto pollens* Wetmore (1937), first reported from Great Exuma and later from New Providence Island (Brodkorb, 1959), must have been an effective predator of *Capromys* in the Bahamas, as no doubt were the extinct diurnal raptors (Accipitridae) of the genera *Calohierax* and *Titanohierax* (Wetmore, 1937). The presence of such large raptors elsewhere in the Antilles suggested that the Cuban cave deposits might be attributable to similar avian predators. This was vividly confirmed by the discovery in Cuba of remains of five species of predatory birds of truly tremendous proportions. These birds occupied the niches which in continental areas are usually filled by various groups of carnivorous mammals. The absence of mammalian competitors, combined with a superabundance of large prey, are no doubt the principal factors contributing to the gigantism observed in these birds. The larger forms may have functioned particularly to keep the populations of edentates in check.

Brief History of Certain Discoveries

On 2 January 1954, the remains of a gigantic owl, the largest known, were discovered for the first time in the depths of a large cavern known as Pío Domingo Cave, located in the Sierra de Sumidero, opposite Pica-Pica Valley in Pinar del Río. These bones (Figure 5) were found in place, fastened to the calcareous surface of the floor by travertine, just as were those of the various edentates encountered in the immediate vicinity. This owl was described under the name *Ornimegalonyx oteroi* (Arredondo, 1958a) and was at first erroneously regarded as a member of the Phorusrhacidae, an extinct family of flightless South American carnivorous birds. Dr. Byran Patterson, who studied some of these remains, afterwards informed me (pers. comm.) of his belief that they actually pertained to a great owl, two times larger in linear dimensions than *Tyto ostologa* of Haiti. Brodkorb (1961), recognizing the validity of the nomenclature proposed in 1958, established that the species belonged in the family Strigidae, where he maintained it in later publications (Brodkorb, 1969, 1971). Addi-

[1] The mammalian classification used in this paper follows Varona (1974) and in some instances is at variance with Professor Arredondo's preferences.—Ed.

TABLE 1.—Associated fauna found in the type-localities of the large extinct species of Cuban birds of prey

Species	*Ornimegalonyx oteroi* Caverna de Pío Domingo, Pinar del Río	*Tyto riveroi* Cueva de Bellamar, Matanzas	*Tyto noeli* and *Aquila borrasi* Cueva del Túnel, Habana	*Antillovultur varonai* Cueva de Paredones, Habana
AMPHIBIA				
Bufo sp.	–	–	X	X
REPTILIA				
Iguanidae gen. and sp. indet.	–	–	X	–
Epicrates cf. *angulifer*	–	–	X	X
Geochelone cubensis	–	X	X	X
Crocodylus sp.	–	–	X	X
AVES				
Cathartes aura	–	–	X	–
Antillovultur varonai	–	–	–	X
Vulturidae gen. and sp. indet.	–	–	X	–
Aquila borrasi	?	–	X	X
Grus cubensis	?	–	–	–
Ornimegalonyx oteroi	X	–	X	X
Ornimegalonyx sp.	–	–	–	X
Pulsatrix arredondoi	–	–	–	X
Gymnoglaux sp.	–	–	–	X
Tyto alba	–	–	–	X
Tyto noeli	–	–	X	X
Tyto riveroi	–	X	–	–
MAMMALIA				
Solenodon cf. *cubanus*	X	–	X	X
Nesophontes micrus	X	–	X	X
Nesophontes major	–	–	–	X
Phyllonycteris poeyi	–	–	X	–
Natalus lepidus	–	–	X	–
Cubacyon tranversidens	–	–	X	–
Acratocnus sp.	–	–	X	–
Miocnus antillensis	X	–	X	X
Cubanocnus gliriformis	X	X	X	X
Mesocnus torrei	X	X	X	X
Mesocnus browni	–	–	X	X
Neomesocnus brevirostris	–	–	–	X
Megalocnus rodens	X	X	X	X
Megalocnus sp.	–	–	X	–
Capromys pilorides	X	–	X	X
Capromys prehensilis	X	–	–	–
Capromys nanus	–	–	–	X
Capromys columbianus	X	X	X	X
Capromys pleistocenicus	–	X	X	X
Capromys sp. A	–	–	X	–
Capromys sp. B	X	–	X	–
Capromys sp. C	–	–	X	X
Capromys sp. D	–	–	–	X
Macrocapromys acevedo	–	–	–	X
Heteropsomys torrei	X	–	X	X
Heteropsomys offella	X	–	X	X

X = present; ? = uncertain; – = not present.

tional fossils of this giant owl were later found in various caves in the provinces of Habana, Matanzas, Las Villas, and Camagüey, as well as in the Isle of Pines. It is possible that two unrecognized species of *Ornimegalonyx* may exist among these remains; one of these seems to be somewhat smaller than *O. oteroi,* while the other is larger. Considering the enormous size of this owl, particularly of its claws, it is quite conceivable that it could have made victims of juvenile edentates, notwithstanding the fact that *Ornimegalonyx* appears to have been incapable of flight.

In July 1954, explorations in the Cueva de Paredones in San Antonio de los Baños, revealed for the first time the fossil bones of an eagle larger than any of the living species of the family Accipitridae. Other bones of it were found a few years later in the Cueva del Túnel, La Salud, Habana. This eagle was named *Aquila borrasi* (Arredondo, 1970). According to its tarsometatarsus, it was very similar in size and morphology to the recently described species *Garganoaetus freudenthali* from the upper Miocene of Italy (Ballmann, 1973).

A fossil vulture from Cueva de Paredones was recently described as a new genus and species, *Antillovultur varonai* Arredondo (1971), and was the size of an Andean Condor. Various bones found in a cave in Habana and now under study, possibly indicate another large species of vulture.

Two species of giant barn owls of the genus *Tyto* were discovered a little later (Arredondo, 1972a, 1972b). One of these, *Tyto noeli,* founded on abundant bones from two caves in Habana, was similar in size to *Tyto ostologa* of Haiti. The other species, *Tyto riveroi,* based on the distal portion of a tarsometatarsus from Cueva de Bellamar, Matanzas, was truly gigantic, being larger than any of the fossil or living species of the genus. It is the one strigiform that most closely approaches the size of *Ornimegalonyx oteroi,* and like that species could also have captured small edentates. The eminent paleornithologist Alexander Wetmore (1959) was the first to report fossil remains of large barn owls from Cuba, but these were not named.[2]

[2] These specimens, a humerus and a femur, are still at the National Museum of Natural History. They are very much larger than *T. ostologa* or *T. noeli* and most probably pertain to the distinctive species *T. riveroi.* At a later date I hope to be able to describe these fossils further, along with abundant unpublished material of *T. ostologa.*—Ed.

The discovery of three species of tytonids in the upper Miocene of Italy (Ballmann, 1973), one of which, *Tyto robusta,* is equal in size to *T. noeli* and *T. ostologa,* and the other, *Tyto gigantea,* being only slightly smaller than *T. riveroi,* partly contradicts the hypothesis that gigantism in Antillean barn owls is attributable to insular evolution from smaller species that responded to the great abundance of food and the lack of competition from carnivorous mammals. The genus *Tyto* evidently had already evolved giant species in Europe, millions of years before the beginning of the Pleistocene. The following conclusions could therefore be drawn: (1) either the giant Antillean barn owls evolved in parallel with those of Europe, arriving through convergence at species of approximately the same size, or (2) the Antillean forms are descended from Tertiary European forms that established themselves in North America and colonized the Antilles before or during the Pleistocene. Against this last suggestion is the absence on the American continent of giant species of *Tyto.*

Ornimegalonyx is truly exceptional for its extremely large size. It appears to have evolved its gigantism in Cuba from some remote smaller ancestor. An affinity of *Ornimegalonyx* with any of the living genera of large continental owls is not clearly evident and its relationships may lie closer to some extinct form rather than with any presently living.

The study of the origins, evolution, and paleoecology of the giant raptorial birds of the Antilles is of great interest and significance to our understanding of the environment and evolution of many of the terrestrial vertebrates of those islands. It is hoped that this summary of what is known of the Cuban birds will aid in that understanding.

Abbreviations used are as follows: Academia de Ciencias de Cuba (ACC), Departamento de Paleontología de la Universidad de la Habana (DPUH), Museo del Grupo de Exploraciones Científicas "Pedro Borrás Astorga" (GEC), Museum of Comparative Zoology (MCZ), Museo Felipe Poey de la Academia de Ciencias de Cuba (MFP), Museo Montané de la Universidad de la Habana (MMUH), personal collection of Oscar Arredondo (OA), Sociedad Espeleológica de Cuba (SEC).

Order ACCIPITRIFORMES

Family VULTURIDAE

Genus *Antillovultur* Arredondo, 1971

Antillovultur varonai Arredondo, 1971

HOLOTYPE.—Proximal portion of left tarsometatarsus, DPUH 1254.

TYPE-LOCALITY.—Cueva de Paredones, San Antonio de los Baños, Habana, Cuba.

AGE.—Late Pleistocene.

OTHER MATERIAL.—GEC (unnumbered), distal portion of left humerus; OA 847, external trochlea of left tarsometatarsus; OA 848, body of seventh cervical vertebra. All specimens from the type-locality.

DESCRIPTION.—The type (Figure 1*a,b*) is a proximal portion of a tarsometatarsus, 42.5 mm in length, lacking the proximal articulating surface, hypotarsus, and slightly more than half the distal portion of the bone. The estimated total length is 141 mm, or about equal to that of *Vultur gryphus* and longer and slightly more robust than in *Gymnogyps californianus* (Figure 2, Table 2). From these two species and *Cathartes aura* it differs in having the groove in the anterior face of the bone narrower and deeper and the internal tubercle for M. tibialis anticus more expanded. In anterior view, the surface of the shaft between the internal border and the groove is notably thick and rounded, whereas in *Vultur, Cathartes,* and *Teratornis* it is narrower and sharp-edged. The surface of the shaft delimited by the external border and the groove is more slender than the internal ridge, contrary to the condition in the other genera mentioned. The shaft in medial view is proportionately more slender than in *Vultur* or *Cathartes.* These characters are considered to be of generic value.

The distance between the proximal border of the larger tubercle for M. tibialis anticus and the proximal extremity of the anterior groove is greater than in *Vultur* or *Teratornis* and equal to that in *Gymnogyps. Antillovultur* has an additional two proximal foraminae situated above the usual two. *Vultur* similarly possesses another aperture above the lateral proximal foramen but lacks the medial proximal foramen of *Antillovultur.*

FIGURE 1.—Specimens of *Antillovultur varonai,* Cueva de Paredones: *a,* holotype fragmentary proximal end of left tarsometatarsus (DPUH 1254), anterior view; *b,* same, posterior view; *c,* left humerus lacking proximal end (GEC unnumbered), palmar view. (Natural size.)

TABLE 2.—Measurements (mm) of the tarsometatarsus of *Antillovultur varonai* compared with other large New World vultures

Character	*Antillovultur varonai* Type, DPUH 1254	*Vultur gryphus*	*Gymnogyps californianus*	*Teratornis merriami*
Maximum length	141	141	124.2	132
Greatest proximal width	32.2	30.2	27	28
Least width of shaft (at break)	17	17	16.8	15
Length of outer trochlea from the angle of the middle trochlea	9	9.5	6	9
Greatest width of outer trochlea	8	8	8	8
Greatest width across trochlea	35*	35.4	30	29.5

* Estimated.

Cathartes aura has only two proximal foramina. *Teratornis* differs in having three great united foramina arranged so as to form a kind of circle. In *Antillovultur* the medial tubercle for M. tibialis anticus is better developed than in either *Vultur, Gymnogyps,* or *Cathartes,* and is situated over a slight protruberance on the internal border of the anterior groove. In posterior view the surface of the bone from the lateral foramen to the external border is flat and does not slope downward as in *Vultur*. On the opposite side, the surface from the medial foramen to the external border is very depressed compared to that in *Vultur*. An external trochlea from a left tarsometatarsus of this species is similar in size and shape to that of *Vultur*.

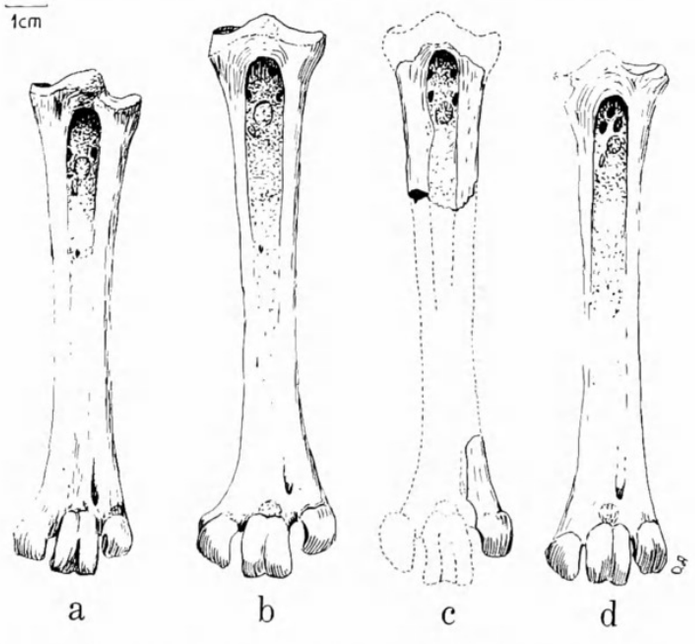


FIGURE 2.—Comparison of tarsometatarsi of New World vultures: *a, Gymnogyps californianus; b, Vultur gryphus; c, Antillovultur varonai; d, Teratornis merriami* (based on Wetmore, 1931). (Half natural size.)

A seventh cervical vertebra attributed to *Antillovultur* consists of the complete body lacking all of the processes. It is similar to vertebrae of *Vultur* in size and morphology.

A distal portion of a left humerus (Figure 1*c*) is from a specimen very similar in size to *Vultur*. This fragment has a length of 184 mm from the distal end to a point a little beyond the protruberance at the distal extremity of the deltoid crest. Taking this protruberance as a point of reference, the complete length of the bone can be estimated as 265 mm, which is about 20 mm less than in the specimens of *Vultur* compared. The least width of the shaft is 20 mm (21.7 in *Vultur*); the maximum distal width is 45.8 mm (54.3 in *Vultur*). The bone, although almost as large as that of *Vultur,* is more slender. The distal protruberance of the deltoid crest is at the same level as in *Vultur*. *Antillovultur* differs from *Vultur* in having the ectepicondylar prominence less pronounced, recalling that of *Cathartes*. The internal and external condyles are slightly smaller than in *Vultur* but with the distal borders more prominent. The internal condyle has a smooth and extensive depression on the entepicondylar side, which is present in *Cathartes* but absent in *Vultur*. The attachment of the anterior articular ligament is as large as in *Vultur,* but situated closer to the internal condyle, the space between them being less than in *Vultur* and more similar to *Cathartes*. The foramen located in this space is isolated from the brachial depression by a ridge that is absent in *Vultur* but somewhat evident in *Cathartes*. The brachial depression is deeper and more pronounced than in *Vultur,* particularly in the proximal region, but is notably less expanded than in either *Vultur* or *Cathartes*. The olecranal fossa is similar to that of *Vultur* and

less dilated than in *Cathartes*. The tricipital grooves are similar to those of *Vultur* but the external one is somewhat deeper and appears like that of *Cathartes*.

Family ACCIPITRIDAE

Genus *Aquila* Brisson

Aquila borrasi Arredondo, 1970

HOLOTYPE.—Left tarsometatarsus lacking trochleae, DPUH 1250.

TYPE-LOCALITY.—Cueva del Túnel, La Salud, Habana, Cuba.

OTHER LOCALITIES.—Cueva de Paredones, San Antonio de los Baños, Habana. Cueva de Pío Domingo, Sumidero, Pinar del Rio.

AGE.—Late Pleistocene.

OTHER MATERIAL.—Right femur lacking condyles, SEC P-26; ungual phalanges, SEC P-31, P-32, P-35, P-1147, and ACC 1000a; subterminal phalanx, ACC 1000b; distal end of tarsometatarsus, SEC P-40.

DESCRIPTION.—Tarsometatarsus (Figure 3) generally similar to that of *Aquila chrysaetos* but notably longer, since even without the distal end it measures 97.7 mm. The estimated total length of the bone is 130 mm, or 34 mm longer than that of *Aquila chrysaetos* and larger than that of any living species of eagle (Table 3). The proximal articular region is similar to that in *Aquila* but with the proximal foramina located only 5 mm from the internal cotyla, whereas in *A. chrysaetos* this distance is nearly twice as great. That which remains of the base of the hypotarsus in the type indicates that this process was probably similar to that of *A. chrysaetos*.

The tarsometatarsi of the fossil species *Buteo typhoius* and *B. contortus*, from the upper Miocene of Nebraska, and of *B. conterminus*, from the upper Pliocene of Nebraska (Wetmore, 1923), are larger than those of Recent species of *Aquila* and *Haliaeetus*, but are more slender proximally, the articular region in proximal view being of a different shape than in *Aquila* and also differing in the form and position of the middle trochlea. The tarsometatarsus of *B. contortus* measures 113 mm in length, which is 17 mm less than in *Aquila borrasi*. Although the Cuban species has certain similarities to *B. contortus* in the general structure of the tarsometatarsus, it is larger and more robust than that species and appears more like *A. chrysaetos*. According to the published figures, the recently described species *Garganoaetus freudenthali* Ballmann (1973), from the upper Miocene of Italy, is similar morphologically to *B. borrasi*, although its tarsometatarsus is slightly more robust. *Aquila borrasi* was a gigantic form within its genus, the only other known fossil forms of which are *Aquila delphinensis* and *A. pennatoides*, described by Gaillard (1939) from tarsometatarsi from the upper Miocene of France.

The femur of *Aquila borrasi* is larger and more robust than that of any living eagle. Although the one known specimen is incomplete, its maximum length is estimated at about 155 mm, as opposed to 125 mm in *Aquila chrysaetos*, 114 mm in *Haliaeetus leucocephalus*, and 96 mm in *Spizaetus ornatus*. This is even larger than in the two immense living eagles *Harpia harpyja* (131 mm)

FIGURE 3.—Holotype left tarsometatarsus of *Aquila borrasi* (DPUH 1250), Cueva del Túnel. (Anterior view at natural size.)

TABLE 3.—Measurements (mm) of the tarsometatarsus and claws of *Aquila borrasi* compared with other species of living eagles

Character	*Aquila borrasi*		*Pithecophaga jefferyi**	*Harpia harpyja**	*Aquila chrysaetos*	*Haliaeetus leucocephalus*	*Spizaetus ornatus*
TARSOMETATARSUS	Type, DPUH 1250						
Length from the upper border of the internal cotyla to the beginning of the scar for the hallux	97.7		80	70	64.5	55	68.2
Proximal width	22.4		24	36.6	21.5	20.5	18.5
Least width of shaft	13.2		13.2	19.3	10	10	9.6
UNGUAL PHALANX OF DIGIT I	SEC P-31	GEC (unnumbered)					
Dorsal arc	52.6	51.2	47	64	38.6	34.5	40.2
Ventral arc	46.7	47.2	39	51.5	33.5	31.2	33.5

* Measurements from specimens in the USNM collections. It can be seen that the tarsometatarsus of *Aquila borrasi,* while decidedly longer, is proportionately much more gracile than in either *Pithecophaga* or *Harpia*—Ed.

and *Pithecophaga jefferyi* (130 mm).[3] Other measurements (in mm) of this specimen are as follows: total length as preserved, 140, proximal width 45.4, vertical diameter of head 16.3, width of neck 17.2, maximum width of pneumatic foramen 8.0, length of pneumatic foramen 14.0, least width of shaft 19.8.

The femur differs from that of allied genera by the lesser projection of the trochanter above the head and by the greater width between the anterior border of the head and the apex of the trochanter (twice that of *Aquila chrysaetos* or *Haliaeetus leucocephalus*). The pneumatic opening is roughly oval in shape but wider distally. It is located at the base of the trochanter as in *Aquila* but differs in being not perfectly oval and in being oriented semiobliquely towards the external border of the trochanter. The foramina of the upper region of the trochanter are larger and deeper than in the other species compared. The rugose intermuscular line on the anterior face of the bone angles below and near the pneumatic opening along the external border of the shaft almost to its midpoint. In contrast, this line in *A. chrysaetos* originates farther above the upper border of the pneumatic opening and descends straight to the midpoint of the shaft. The head is massive and the neck is thick and oriented slightly upwards.

[3] Measurements supplied from specimens in the collections of the National Museum of Natural History, Smithsonian Institution.—Ed.

The ungual phalanges are very well developed (Figure 4), being almost two times larger than those of *A. chrysaetos*. They resemble those of *Harpia harpyja* in having the same degree of curvature. The ungual phalanx of digit IV is larger, while that of digit I is smaller than in *Harpia* (Table 3). The shape of the articular region and the ventral process of the first ungual phalanx of *A. borrasi* more closely resembles that of *Aquila* than *Haliaeetus, Spizaetus,* or *Buteo*. The ungual phalanges of digits II and IV are likewise similar to those of *Aquila* and differ from those of the other genera examined. The ungual phalanx of digit IV measures 33 mm through the ventral arc and 35 mm through the dorsal arc.

Order STRIGIFORMES

Family STRIGIDAE

Genus *Ornimegalonyx* Arredondo

Ornimegalonyx oteroi Arredondo, 1958a

SYNONYM.—*Ornimegalonyx arredondoi* Arredondo, 1958.

LECTOTYPE.—Left tarsometatarsus SEC P-383E. Lectotype designated by Brodkorb (1961); deposited in the Museum of Comparative Zoology, Harvard University.

TYPE-LOCALITY.—Caverna de Pío Domingo, Si-

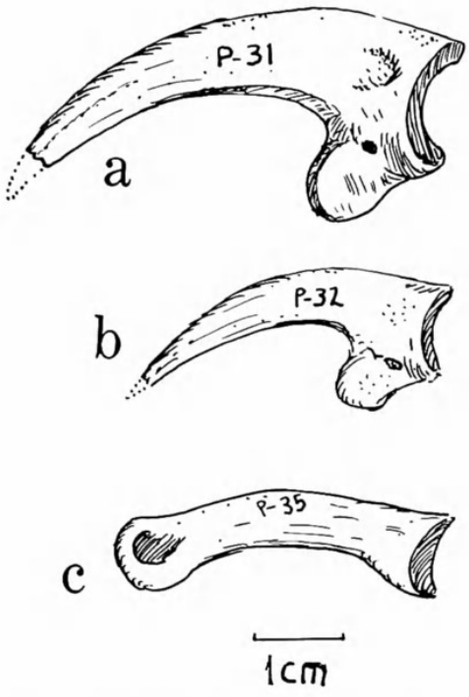


FIGURE 4.—Phalanges of *Aquila borrasi* from Cueva de Paredones: *a,* ungual phalanx of digit I (SEC P-31); *b,* ungual phalanx of digit II (SEC P-32); *c,* subterminal phalanx (SEC P-35). (Natural size.)

erra de Sumidero, Ensenada de Pica-Pica, Pinar del Rio, Cuba.

OTHER LOCALITIES.—Sierra de Anafe, Guanajay, Habana; Cueva de Paredones, San Antonio de los Baños, Habana; Cueva del Túnel, La Salud, Habana; Cueva de Isla, Punta del Este, Isla de Pinos; Cueva de Quinto, Boca de Camarioca, Mantanzas; Canteras de los Hornos de Cal, Sancti Spiritus, Las Villas; Sierra de Cubitas, Camagüey.

AGE.—Late Pleistocene.

OTHER MATERIAL.—Caverna de Pío Domingo, SEC P-383E, various pieces from the same individual as the lectotype as follows: left tarsometatarsus and fragments of the right, fragments of both tibiotarsi, left femur and fragments of the right, articular portions of the mandible, fragments of the sternum, scapula, carpometacarpus, and ungual and subterminal phalanges. From Paredones, El Túnel, Quinto, and Isla caves there are unnumbered pieces of tarsometatarsi, tibiotarsi, femora, phalanges, synsacra and other bones, all in private collections. From the collection of the author there are three subterminal phalanges from El Túnel and Paredones (OA 671, 676, 800).

DESCRIPTION.—Eight tarsometatarsi of *Ornimegalonyx* have come to light so far: the lectotype from Pío Domingo; one from Cueva de Quinto; two proximal halves from Paredones; a distal half from Cueva del Túnel and a proximal half from the same locality. Ultimately, two complete specimens from the same individual were found in a cave in the Sierra de Cubitas, Camagüey, along with other elements.

The dimensions of these bones indicate the enormous size that this bird had in relation to all other known Strigiformes, living or fossil (Figures 5–9, Tables 4–6). The tarsometatarsus is almost double the length of that of *Bubo bubo,* or more than double if one considers the specimen from Cueva de Quinto (GEC unnumbered) (Figure 7*a*) or that from Paredones. These bones are more than three times the size of the corresponding element of *Nyctea scandiaca,* more than four times that of *Asio otus,* and eight and a half times the size of *Glaucidium siju.*

In spite of its gigantic size, the tarsometatarsus of *Ornimegalonyx* is proportionately less robust than that of *Bubo, Nyctea,* or *Pulsatrix,* the difference being due to the relative lengthening of the shaft in *Ornimegalonyx.* If the tarsometatarsus of *Ornimegalonyx* were reduced to the length of that of *Asio otus,* the two elements would be seen to be very similar in proportion, whereas if one magnified the tarsometatarsi of *Bubo, Nyctea,* or *Pulsatrix* to the size of that of *Ornimegalonyx,* they would appear much stronger, wider, and more robust.

In *Ornimegalonyx* the internal trochlea is proportionately shorter and wider than in *Bubo, Nyctea,* or *Asio,* being more similar to *Pulsatrix.* The middle trochlea is narrow and placed very close to the outer trochlea. The distal foramen is somewhat lower than in *Bubo, Nyctea,* or *Asio,* and the ossified bridge on the anteroproximal region of the bone recalls that of *Bubo* and differs from *Nyctea* in that it is stronger and more circular. The internal cotyla is similar to that in *Bubo* and *Asio,* but somewhat lower than in *Nyctea.* The wide, deep groove on the posterior face of the bone is more pronounced than in *Bubo, Nyctea,* or *Asio.*

The tibiotarsi of the type individual are fractured into proximal and distal portions and shafts (Figure 5, Table 5). In a complete state they would have measured some 250 mm in length. The tibio-

TABLE 4.—Measurements (mm) of the tarsometatarsus of *Ornimegalonyx oteroi* compared with other owls

Character	*Ornimegalonyx oteroi*				*Bubo bubo*	*Nyctea scandiaca*
	SEC P-383.E Lectotype	SEC P-39	GEC (unnumbered)	MFP (unnumbered)		
Total length	147*	177	177	178	83.7	55.7
Proximal width	c. 32	36	35	–	22.6	19.9
Distal width across trochleae	c. 34	–	33	32	24.4	20.8
Least width of shaft	c. 15	c. 16	15	18	12.2	11.5
Length of middle trochlea from angle with inner trochlea	–	–	10	10	6.2	5.5
Least width of middle trochlea	–	–	13	13	8.9	8
Length of outer trochlea from angle with middle trochlea	c. 6	–	6	6	3	2.5
Width of outer trochlea	c. 9	–	8	9	5.4	6.8
Length of inner trochlea from angle with middle trochlea	–	–	9	9	6	5.5
Width of inner trochlea	–	–	14	c. 13	6.7	6

* Estimated.

tarsus from Cueva de Quinto has a length of 272 mm, which is almost twice that of *Bubo bubo* or *Nyctea scandiaca*. Its proximal width of 40 mm is likewise twice that of those species. The tibiotarsus of the lectotype individual appears to have been straight, while that from Cueva de Quinto is slightly curved and subtly twisted. Compared to the modern genera examined, the tibiotarsus of *Ornimegalonyx* (Figure 6*a*) has the fibular articulation more pronounced, the rotular crest, and the cnemial crest more elevated, and the fossa proximal to the condyles on the anterior face deeper.

Eight femora of *Ornimegalonyx* have been found so far. The left femur of the type individual is in the MCZ. Of the right, only a part of the proximal end remains in Cuba. The largest femur, represented by the proximal end only (Figure 7*d*), was found to the east of Sancti Spiritus and is deposited in the Museo Montané of the University of Havana (MMUH 3072). Two incomplete femora from Paredones (formerly SEC P-37 and SEC P-38, but now in the MCZ) are smaller than those of the type and for now are perhaps best referred to as *Ornimegalonyx* sp.

The femur of *Ornimegalonyx* differs principally from that of other owls in being much larger and notably more robust (Table 6). That of the type individual is almost one and a half times larger than the femur of *Bubo bubo,* while the large femur (MMUH 3072) from Sancti Spiritus is almost double the size of that of *Nyctea scandiaca*. It is curious that when reduced, the tarsometatarsi of *Ornimegalonyx* are less robust than in *Bubo* or *Nyctea,* while in the femora the opposite occurs.

Fragments of the sternum, as well as parts of the scapulae, ribs, vertebrae and carpometacarpi, were associated with the type individual in Pío Domingo cave. The most important sternal fragments are an anterior portion with the articulations for the coracoids, and another fragment of the left side containing four costal facets (the fifth having been fractured off). The costal facets vary slightly in size, the largest being 6 × 6 mm. Through these fragments it has been possible to reconstruct the sternum (Figure 8) as being wide, almost flat (both dorsally and ventrally), with a vestigial keel, which indicates that the bird was hardly able to fly. Its estimated length is 120 mm (vs. 47 mm in *Tyto alba*), the estimated width 75 mm (30 mm in *T. alba*); and the height at the keel some 30 mm (25 mm in *T. alba*). The similarity of this last measurement in two species which otherwise differ so greatly in size is a further indication of the great extent of the atrophy of the keel in *Ornimegalonyx*.

The carpometacarpus of *Ornimegalonyx* is small in proportion to the enormous size of the body. Its total length is estimated at about 90 mm whereas in *Bubo bubo,* a smaller volant species, it is 85 mm.

FIGURE 5.—Tibiotarsus, tarsometatarsus, femur, and phalanges (SEC P-383E) from the same individual as the lectotype of *Ornimegalonyx oteroi,* Caverna de Pío Domingo. The specimens are covered with calcareous concretions. (Natural size.)


1 cm

As with the other bones, the phalanges of *Ornimegalonyx* stand apart from those of other owls by their great size. The length of the ungual phalanges of digits II and III, measured through the dorsal arc, range from 37 to 39 mm, while that of digit I measures 40 mm. The proximal height of these phalanges ranges from 15–17 mm.

FIGURE 6.—Hindlimb elements of *Ornimegalonyx oteroi* from Cueva de Paredones: *a*, right tibiotarsus lacking distal end (SEC P-28); *b*, posterior view of left tarsometatarsus lacking distal end (SEC P-39). (Natural size.)

It was not until the beginning of 1969 that fragments of mandibles were found among the remains of the type individual of *Ornimegalonyx oteroi*. These consist of the two articular portions of both rami. These fragments permit for the first time a very approximate estimate of the size of the mandible and ultimately of the whole skull (Figure 9*a*). These mandibles are very similar in overall morphology to those of the diminutive genus *Glaucidium*. They differ from *Bubo bubo* in that the internal angular process is greatly lengthened. The posterior angular process, in comparison to that of *Bubo*, is notably more robust, and the portions that remain of the surangular and angular are greatly thickened at the point of the fracture. Judging by comparison with recent owls, the length of the entire mandible of *Ornimegalonyx oteroi* would have been some 115 mm and the distance between the external borders of the articulations was approximately 100 mm, or about two times larger than in *Bubo bubo*.

A portion of a cranium of *Ornimegalonyx* was

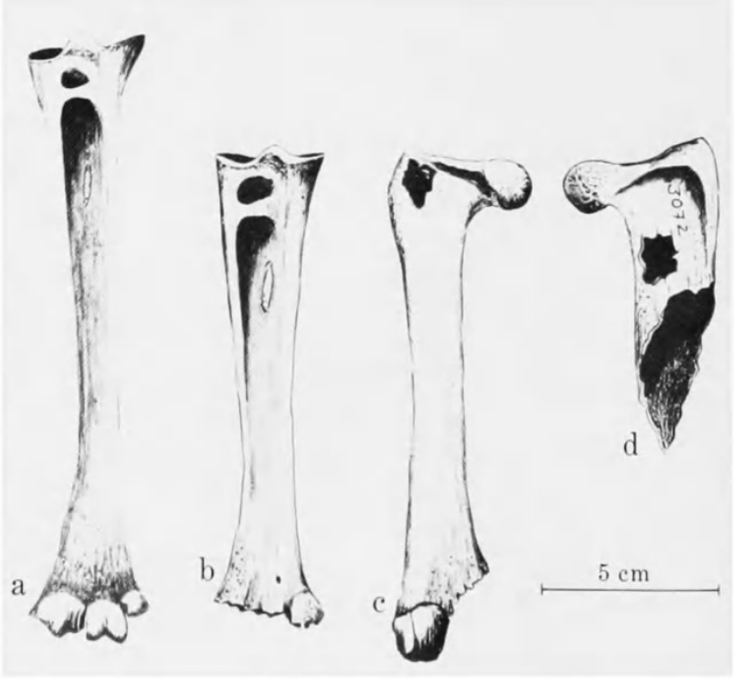


FIGURE 7.—Some variation in the hindlimb of *Ornimegalonyx*: *a*, *Ornimegalonyx* cf. *oteroi*, left tarsometatarsus (GEC unnumbered), Cueva del Quinto; *b*, *c*, *Ornimegalonyx oteroi*, left tarsometatarsus and right femur of the type individual (SEC P-38E), Pío Domingo cave; *d*, *Ornimegalonyx* sp., proximal end of left femur (MMUH 3072), Cantera de los Hornos de Cal, Sancti Spiritus.

TABLE 5.—Measurements (mm) of the tibiotarsus of *Ornimegalonyx oteroi* compared with other owls

Character	*Ornimegalonyx oteroi*					*Bubo bubo*	*Nyctea scandiaca*
	SEC P-383.E	SEC P-28	SEC P-29	MFP (unnumbered	GEC (unnumbered		
Total length	250*	–	–	–	272	155	129
Proximal width	c. 36	39	–	–	37	19	17.6
Least width of shaft	c. 13	14	15*	13*	c. 15	9.5	8
Distal width across trochleae	30	–	31	c. 30	c. 30	20.8	19.2

* Estimated.

TABLE 6.—Measurements (mm) of the femur of *Ornimegalonyx oteroi* compared with other owls

Character	*Ornimegalonyx oteroi*		*Ornimegalonyx* sp.	*Bubo bubo*	*Nyctea scandiaca*
	SEC P-383E	MFP (unumbered	MMUH 3072		
Maximum length	154	160	168*	108	96.4
Proximal width between antero-external border of head and postero-external border of trochanter	42	45*	46	23.7	20.5
Antero-posterior diameter of head	c. 11	12*	c. 12	7.5	8
Vertical diameter of head	15	–	c. 15	9	8.3
Least width of shaft	16	16*	20*	9.6	9.8
Distal width through condyles	35*	38*	–	22.5	21.5

* Estimated.

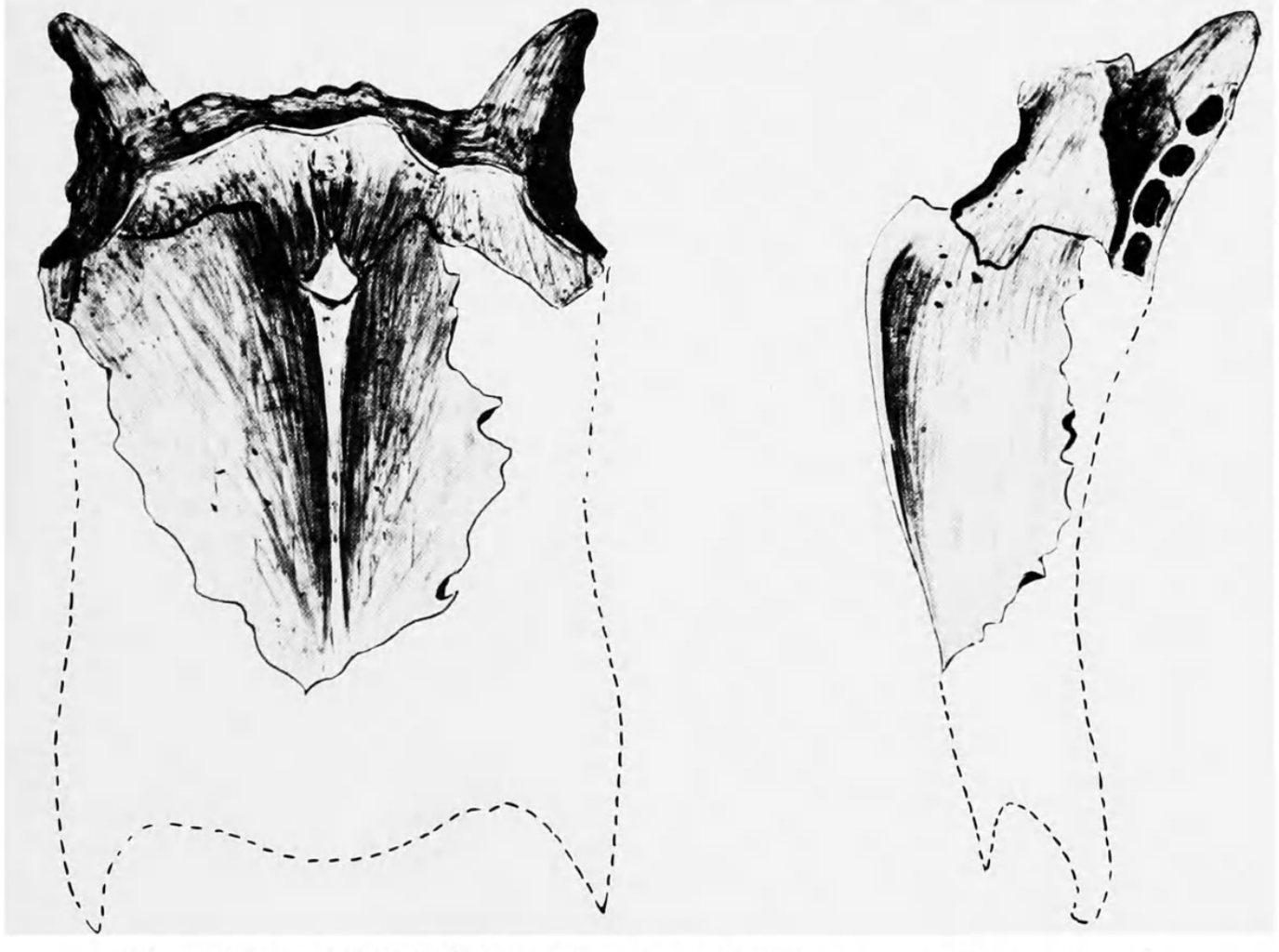
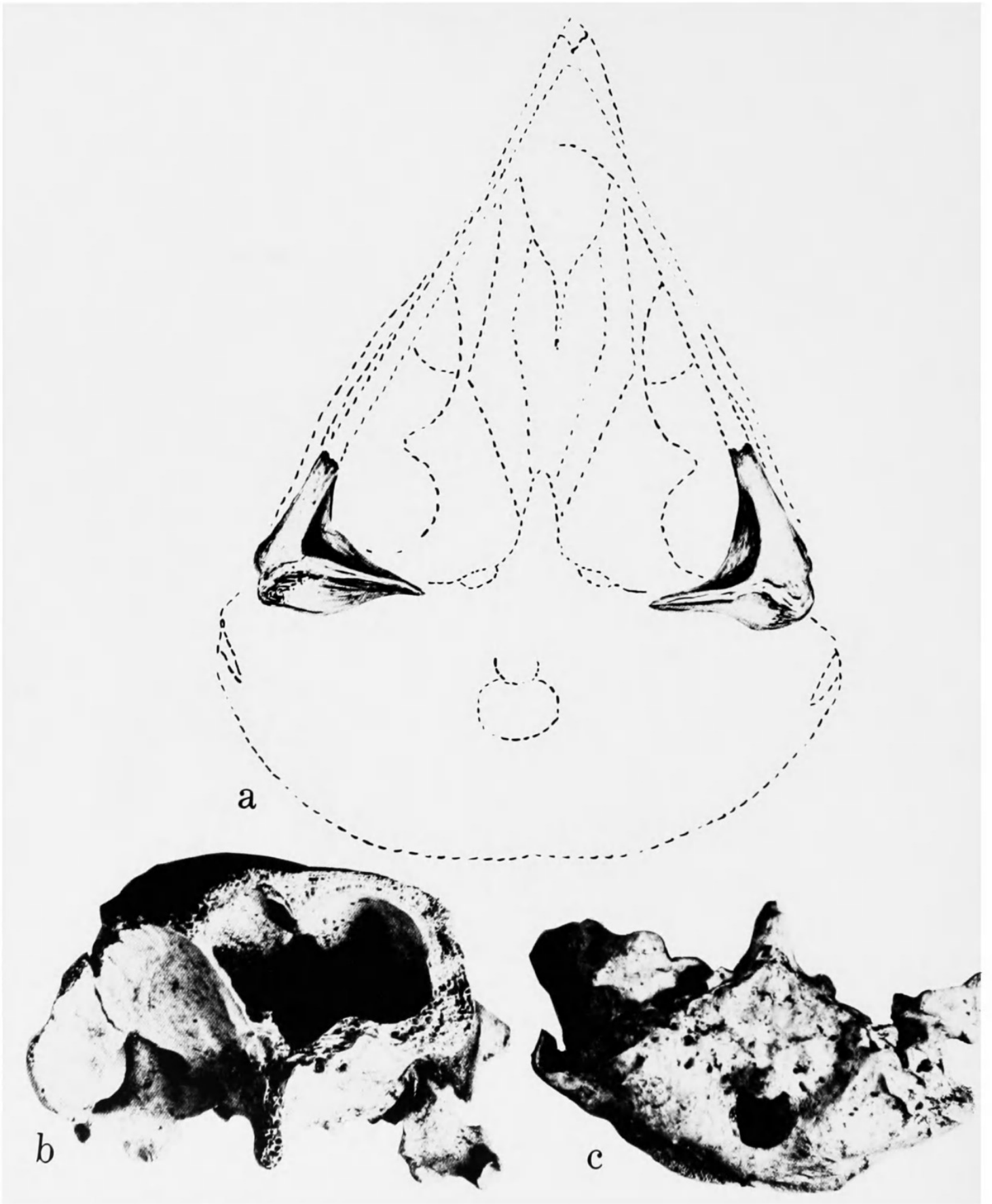


FIGURE 8.—Ventral and lateral views of the sternum of *Ornimegalonyx oteroi,* as reconstructed from two fragments from Pío Domingo and Paredones caves. (Natural size.)


a
b
c

found in Cueva de Paredones in 1959 (Figure 9*b,c*). For the time being it is best referred to only as *Ornimegalonyx* sp., for it is apparent that it does not correspond to the species *O. oteroi.* Rather, it appears to belong to a smaller form, as also evidenced by the femora found in the same locality. The specimen consists of the posterior portion of a cranium from the postorbital arc to the occiput and including the basisphenoid, the foramen magnum, and the occipital condyle. Viewed from the front, the great thickness of the walls of the cranium are seen in the region of the break. Compared to *Bubo bubo* it is larger, and in ventral view it has the postorbital process better developed. The opisthotic process is rather prominent and its extremity bends notably, hanging in the form of an ear. The basipterygoid processes are well developed. The foramen magnum is somewhat higher than wide, as opposed to *Glaucidium* and *Tyto* in which it is wider than high. As in *Nyctea,* the occipital condyle is very well developed in relation to the foramen magnum, whereas it is proportionately much smaller in *Glaucidium* and *Tyto.*

From the actual and estimated measurements of the various bones of *Ornimegalonyx* it can be established that this great owl stood some 1100 mm high in life. Although the general aspect of its skeleton is similar to that of living owls, it is distinguished from them by the long and robust hindlimbs, provided with long, heavy toes armed with the most powerful claws possessed by any strigiform bird. Although the sternum is larger than in any living owl, it is actually small in proportion to the rest of the bones of the skeleton. Its semiflat structure and reduced keel show that *Ornimegalonyx* was little or not at all capable of flight. In accordance with this, the bones of the wing are poorly developed, particularly the carpometacarpus.

Some of the differences in morphology and size that are observed between individuals of *Ornimegalonyx* are probably attributable to sexual dimorphism, since in other owls the females are larger than the males. Nevertheless, other bones that are either larger or smaller than those of the type individual and have distinct differences from it, probably indicate additional species—the cranium and femora from Paredones and the femur from Sancti Spiritus being examples.

Ornimegalonyx had to have been the scourge and terror of most of the larger mammals of the Pleistocene of Cuba and the claws and mandibles of this bird would have constituted a terrible combination of superior destructive power.

FIGURE 9.—Skulls of *Ornimegalonyx: a,* hypothetical reconstruction of the skull of *Ornimegalonyx oteroi* to show the size as extrapolated from the two mandibular articulations associated with the type; *b, c,* anterior and ventral views of the cranium (GEC unnumbered) of *Ornimegalonyx* sp. from Cueva de Paredones (the left quadrate is incorrectly articulated). (All figures natural size.)

Family TYTONIDAE

Genus *Tyto* Billberg

Tyto noeli Arredondo, 1972a

HOLOTYPE.—Right tarsometatarsus, DPUH 1251.

TYPE-LOCALITY.—Cueva del Túnel, La Salud, Habana, Cuba.

OTHER LOCALITIES.—Cueva de Paredones, San Antonio de los Baños, Habana; Cueva del Indio, Reparto El Globo, Calabazar, Habana; quarries near Sancti Spiritus, Las Villas.

AGE.—Late Pleistocene.

OTHER MATERIAL.—Cueva del Túnel: OA 818, right femur; OA 812, distal portion of left tibiotarsus; OA 804, distal portion of right humerus; OA 806, proximal fragment of right humerus; OA 822, shaft of right tibiotarsus; OA 815, distal portion of right ulna. Cueva de Paredones: OA 828, proximal portion of right tarsometatarsus; OA 827, proximal portion of right tibiotarsus; OA 839, right coracoid. Cueva del Indio: OA 1027, right femur.

DESCRIPTION.—Similar to the living species *Tyto alba* in its general skeletal configuration, but much larger (Figures 10, 11, Tables 7 and 8), equaling in size the extinct species *Tyto ostologa* of Haiti and *T. pollens* of the Bahamas. The tarsometatarsus was between 90 and 100 mm long and was similar to that of *T. pollens,* but more slender, even in specimens that are longer than in *T. pollens.* The tibiotarsus is likewise similar to that of *T pollens* but is less robust. This slenderness of the hindlimb is the most notable difference between the two species.

In the femur, humerus, ulna, coracoid, and claws, the only pronounced difference from *Tyto*

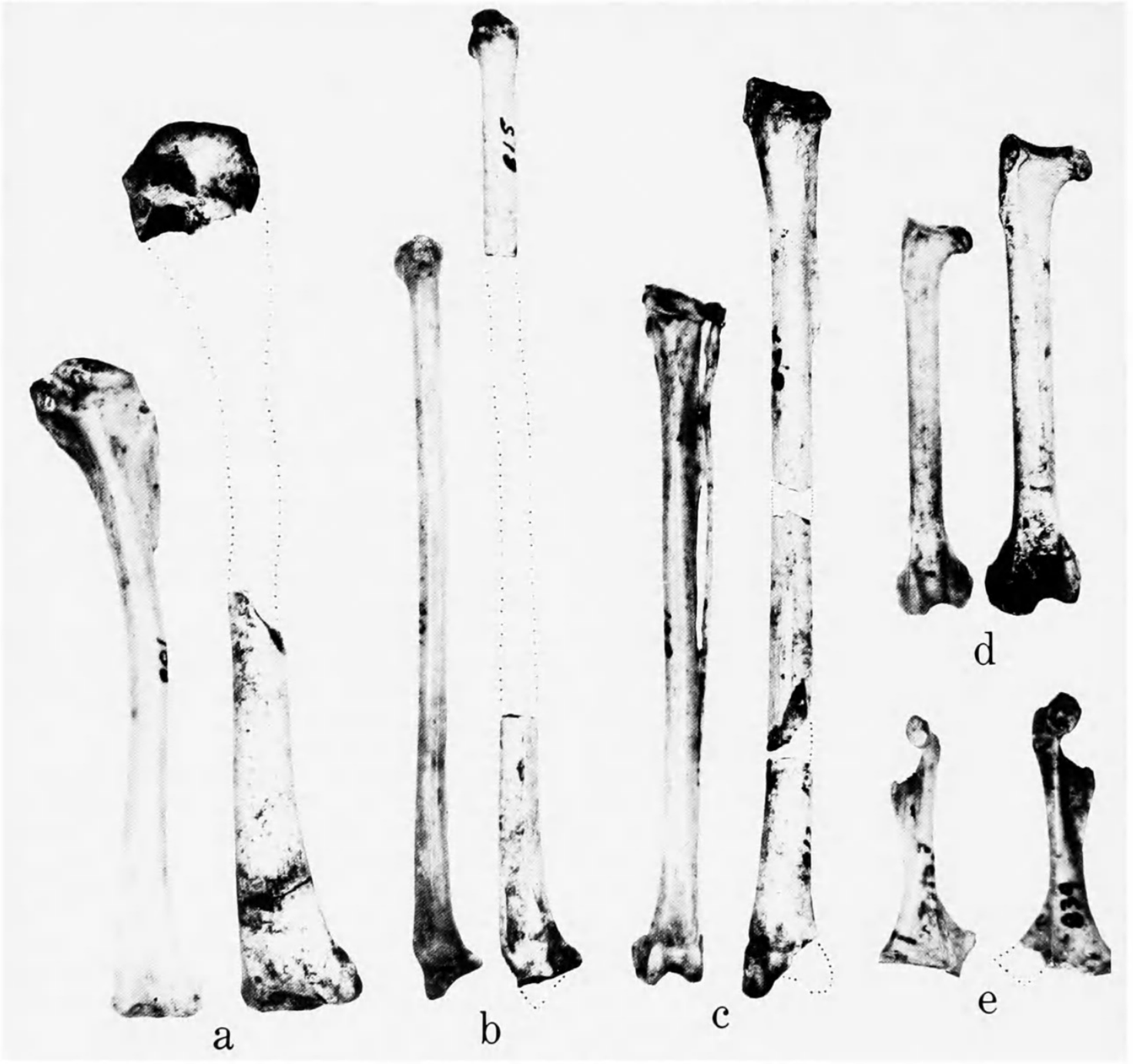


FIGURE 10.—Paratypes of *Tyto noeli* from Cueva del Túnel and Cueva de Paradones compared with a Recent specimen of *Tyto alba furcata* (on the left in each pair): *a*, fragments of right humerus (OA 804 and 826); *b*, fragments of right ulna (OA 806 and 815); *c*, fragments of tibiotarsus (OA 827, 812, and 822); *d*, right femur (OA 818); *e*, right coracoid (OA 839). (Natural size.)

alba is in size. Likewise, a fragment of the anterior portion of a sternum of *T. noeli* from quarries near Sancti Spiritus has the same conformation as that of *T. alba* but is larger. One might expect to find greater distinctions in the skull, but so far only fragments of the skull of *T. noeli* have been found.

Brodkorb (1959:357) suggested that *T. pollens* may possibly be differentiated from *T ostologa* only at the subspecific level. The same could be suggested for *T. noeli*. From the upper Miocene of Italy, a new species of giant barn owl, *Tyto robusta* Ballmann (1973), has been described that is near the size of *T. noeli*. The Cuban species is somewhat larger and heavier, however.

TABLE 7.—Measurements of limb bones of *Tyto noeli* compared with *Tyto alba*

Character	*Tyto noeli*			*Tyto alba furcata*
FEMUR	OA 818	OA 834	OA 1027	
Total length	74.3	73*	–	61
Proximal width	14.4	13.1	14	11.4
Antero-posterior diameter of head	5	5	5.5	3.2
Vertical diameter of head	5.8	5	5.7	4.6
Breadth through trochanter	9.2	8.2	9.2	6.8
Least width of shaft	6.4	6	6.5	5
Distal width	14.8	14	–	12.1
TIBIOTARSUS	OA 827	OA 831		
Total length	147*	–		108
Proximal width	16	–		10.9
Least width of shaft	6.4	–		5.5
Distal width	–	15		11.3
HUMERUS	OA 804	OA 826		
Total length	137*	–		100.1
Proximal width	–	23		16.9
Width of shaft	8.5	–		6.2
Distal width	20.5	–		15.7

* Estimated.

TABLE 8.—Measurements (mm) of the tarsometatarsi of the three Cuban species of *Tyto*

Character	*Tyto riveroi*	*Tyto noeli*		*Tyto alba furcata*
	DPUH 1252 Type	DPUH 1251 Type	OA 828	
Maximum length	125*	91.7	100*	78.4
Proximal width	22*	14.6	16	11.1
Distal width	22	17.4	–	13.7
Least width of shaft	9	6.7	7.3	5.2
Length of middle trochlea from angle of internal trochlea	6.8	5	–	2.5
Width of middle trochlea	8.5	6.4	–	4.8
Length of outer trochlea from angle of middle trochlea	11.5	c. 4	–	3
Width of outer trochlea	12.3	4.8	–	3.9
Length of inner trochlea from angle of middle trochlea	6.5	4.4	–	2.8
Width of inner trochlea	9.8	7.5	–	5

* Estimated.

Tyto riveroi Arredondo, 1972b

HOLOTYPE.—Distal portion of a left tarsometatarsus, DPUH 1252.

TYPE-LOCALITY.—Cueva de Bellamar, Mantanzas, Cuba.

AGE.—Late Pleistocene.

DESCRIPTION.—Tarsometatarsus with the general aspect of that of *Tyto alba* and still more similar to that of *T. noeli*. Except for size, significant morphological differences from the above species are almost absent; however, the measurements of the type of *T. riveroi* notably exceed the limits of either (Figure 11, Table 8). The estimated total length of this bone would be approximately 125

mm. The following slight morphological distinctions are also noted: greater separation of the internal and external trochleae from the middle trochlea, the intertrochlear spaces being narrower in *T alba* and *T noeli;* shaft proportionately wider and thicker. Compared with *T. pollens,* the same slight differences are apparent.

Tyto gigantea, recently described from the upper Miocene of Gargano, Italy (Ballmann, 1973), was an enormous barn owl, equal in size to *T. riveroi.* According to the published figures, the Italian species has the distal foramen somewhat more elevated and the middle trochlea lower and more elongate than in the Antillean species.

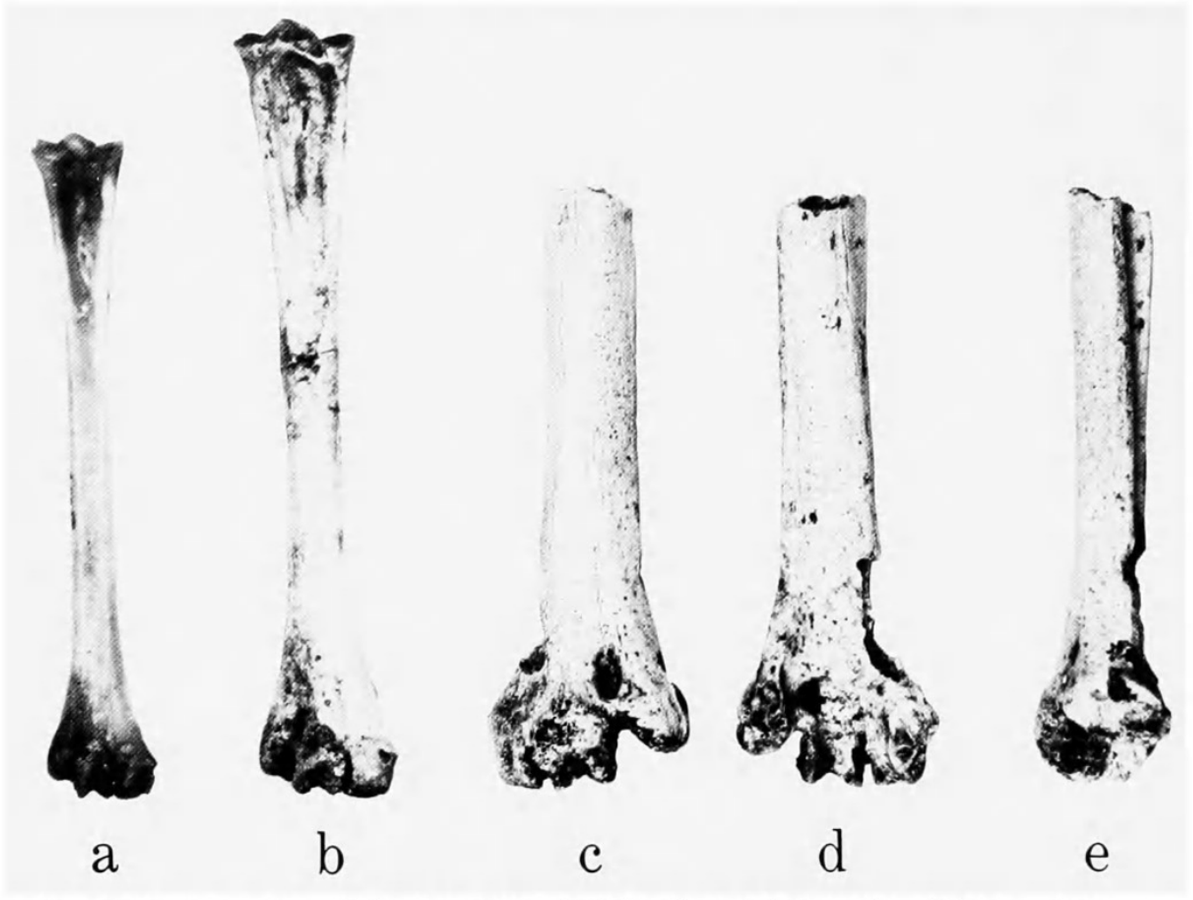


FIGURE 11.—Comparison of the tarsometatarsi of the three Cuban species of *Tyto: a,* Recent *Tyto alba furcata; b, Tyto noeli,* holotype (DPUH 1251), Cueva del Túnel; *c–e, Tyto riveroi,* holotype (DPUH 1252), Cueva de Bellamar, anterior, posterior, and lateral views. (Natural size.)

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