

A PALEONTOLOGICAL PERSPECTIVE OF WEST INDIAN BIRDS AND MAMMALS

STORRS L. OLSON

*National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20560*

ABSTRACT.—The Pleistocene and Holocene fossil record of West Indian birds and mammals is briefly reviewed, with emphasis on the Greater Antilles; as yet, almost nothing is known of vertebrate fossils in the Lesser Antilles. Extinct faunas in the Greater Antilles are generally characterized by an abundance of rodents, insectivores, and edentates, and numerous species of raptorial birds, often of great size, which evolved in response to the lack of mammalian predators. The Antillean bird and mammal faunas appear to be an accumulation resulting from many over-water colonizations during several geologic epochs. The most distinctive, and hence probably the oldest of West Indian homeotherms, the insectivores and todies, appear to be most similar to taxa in the Oligocene of North America. Other colonizations probably took place subsequent to the Oligocene, the mammals having stronger affinities with South America and the birds with North America.

Studies of vertebrate paleontology in the West Indies have only begun to scratch the surface of the knowledge potentially available there. The present fossil record in many respects tends more to illustrate the state of our ignorance than to elucidate particular zoogeographic problems. Nevertheless, there are a number of fascinating fossils from the West Indies and elsewhere that bear on the subject of this symposium.

I have arranged this presentation in two sections. The first deals with the late Pleistocene to Recent fossils that have been found within the Antilles. These do not provide a great store of information on the origins of the Antillean avifauna, but they do yield some interesting facts about inter-island distributions. The second section treats the significance of certain fossils found outside the West Indies to the zoogeography of the area and also the relative antiquity of certain groups of Antillean birds and mammals. I am including some discussion of West Indian mammals other than bats, only because they are not being treated elsewhere in this symposium and because in some cases they do have a bearing on avian zoogeography.

In dealing with fossil species, one is always called upon to provide some theory for the cause of their extinction. Concerning the Antillean

fossil forms to be discussed here, we can identify three probable periods of extinction. The first of these consist of what has often been referred to as the "vicissitudes" of the Pleistocene. Post-glacial rise in sea level, with its consequent inundation of low-lying areas, greatly reduced the size of some islands and obliterated others. This, coupled with changes in climate, would have been one cause of extinction. However, many of the Antillean birds and mammals known only from fossils appear to have survived these vicissitudes. The second period of extinction probably came with the arrival of Amerindians. Although there is as yet little to document it, there can be little doubt that at least the edentates and flightless birds of the West Indies were directly affected by predation by early man. The final period of extinction came with the arrival of Europeans. The effect of subsequent alteration of habitat, and introduction of predators such as the mongoose and rats, is too well known to need further discussion here.

With the exception of a very few specimens of mammals known from Tertiary marine beds, all the bird and mammal fossils from the West Indies are from Pleistocene or Recent deposits, a number of significant specimens even being discovered in Amerindian middens. Most of this material has been found in caves or sinkholes and much of the accumulation of bones here may be attributed to the work of cave-roosting owls.

The Lesser Antilles are virtually unknown from a paleontological standpoint. Brodkorb (1965) described a small collection of avian fossils from Barbados. This included a new species of goose, *Neochen barbadiana*, related to the Orinoco Goose, *N. jubata*, of South America, thus reflecting another South American element in the avifauna of the Lesser Antilles. A new species of coot, *Fulica podigrica*, was also named, but I believe that the material used to define this species is of a composite nature, the type being a humerus of a coot only doubtfully distinct from extant coots in the Caribbean (*F. americana* and *F. caribaea*), while the leg elements may possibly be from an endemic species of rail of some other genus (Olson, 1974).

From the islands of Anguilla and St. Martin, Cope (1868, 1869) described the gigantic, almost bear-sized rodent *Amblyrhiza inundata* of the endemic Antillean family Heptaxodontidae. If such an incredible creature existed on these small islands it certainly gives one cause to expect other spectacular discoveries in the remainder of the Lesser Antilles. Associated with the remains of *Amblyrhiza* were two bones of birds which Cope (1883) illustrated and described but did not specifically identify. I recently located these specimens in the Ameri-

can Museum of Natural History and identified one as an imperfect coracoid of a Brown Pelican (*Pelecanus occidentalis*) and the other as a humerus of Audubon's Shearwater (*Puffinus lherminieri*), neither unexpected. These records, along with Brodkorb's Barbadian study, Wetmore's (1952) report of the Black-capped Petrel, *Pterodroma hasitata*, from a midden on Martinique, and a few bones from middens on St. Kitts and Antigua (Wing, 1973; Wing, et al., 1968), are all that is known of the fossil birds of the Lesser Antilles. Clearly there is much room for improving our knowledge in this area.

In contrast, there have been numerous discoveries of fossils in the Greater Antilles (including the Bahamas), although Jamaica still remains very poorly known.* Attention has been devoted chiefly to mammals. Until recently, virtually all of what was known of the fossil birds could be attributed to the efforts of three men — Alexander Wetmore, Pierce Brodkorb, and Oscar Arredondo.

The long isolation of the Antilles is particularly exemplified by its mammalian fauna. Apart from bats and a few recent colonizers in the Lesser Antilles and Bahamas, some of which may have been introduced by man, there are only four orders of native land mammals in the West Indies: insectivores, edentates, rodents, and primates.

It is particularly noteworthy that aside from extant populations of raccoons (*Procyon*) in the Lesser Antilles and Bahamas, carnivores are absent. Recently, a new genus and species of canid, *Cubacyon transversidens*, has been described from a fragment of maxilla with a single tooth that was found encrusted with lime and associated with extinct mammals in a cave in Cuba (Arredondo and Varona, 1974). Due to the rapidity with which bones may at times be coated with lime, the intimate association of dogs with man, and the extreme variability of domestic canids, I detect among my colleagues an air of skepticism concerning this record. The absence of carnivorous mammals in the West Indies, as Arredondo (1976) has noted, is no doubt responsible for the appearance in the fossil record of numerous and truly enormous raptorial birds — both diurnal and nocturnal.

The most intriguing of the West Indian mammals are the insectivores. The largest forms of these are the two living species of *Solenodon*, known from Cuba and Hispaniola. A third fossil species has also been described from the latter island. The smaller insectivores in the genus *Nesophontes* are known only from fossil remains, but some of

*After this paper was presented, a new genus and species of flightless ibis and certain other fossil birds were reported from Jamaica (Olson and Steadman, 1977).

these are so recent as to suggest the strong possibility that a living individual may yet come to light. Four species of *Nesophontes* have been described from Cuba, two from Hispaniola, one from Puerto Rico, and one unidentified form has been reported from Cayman Brac. Recent unpublished studies indicate that there will be additions to and deletions from the list of species of *Nesophontes* so far known (C. A. Woods, pers. comm.; and S. Olson, new specimens from Puerto Rico). *Solenodon* and *Nesophontes* were formerly considered as forming two quite distantly related families, but McDowell (1958) challenged this view and presented evidence that the two genera are more closely related than previously suspected. He maintained that they formed a single family and considered the differentiation between the two genera to have taken place in the West Indies. The Antillean insectivores are unquestionably of North American origin since this order is not known in South America except for a few montane sbrews of recent arrival there.

A prominent element among the fossil mammals of the Greater Antilles were the members of two subfamilies of ground sloths belonging to the family Megalonychidae. Six species in five genera have been named from Cuba, two species in two genera from Hispaniola, and one genus and species from Puerto Rico. According to the classification of Paula Couto (1967) and Varona (1974), none of these genera is shared between islands. All the species are, of course, extinct. It may at first seem strange that such seemingly sedentary creatures as ground sloths should figure so prominently in the fauna of the Antilles. Yet megalonychid sloths appear to have had a more than ordinary ability to cross water barriers. Of the endemic South American mammals, the megalonychids were the first to enter North America and are known from deposits there that are older than the late Pliocene land connection between North and South America (Hirschfeld and Webb, 1968). The former abundance of some of the species must have been incredible. Just part of the material from one small pocket of a Cuban cave is reported to have yielded remains of over 200 individuals of the genus *Mesocnus* (Acevedo, et al., 1975).

But the truly predominant mammalian element in the Antilles was the rodents. Recently extinct cricetids of the genus *Oryzomys*, based on skins, are known in the Lesser Antilles from St. Vincent, St. Lucia, and Martinique. A fossil species is known from Barbuda and imperfectly known forms evidently occurred on Barbados and St. Kitts (C. E. Ray, pers. comm.). These are descended from *Oryzomys* arriving from the South American mainland. Another recently extinct species of

Oryzomys from Jamaica probably represents an independent invasion from Central America. The remaining rodents of the West Indies all belong to the suborder Caviomorpha. A few of these are known from living examples, but the remainder, many of them quite large, are known only as fossils. A multiplicity of genera and species has been named from the Greater Antilles, the taxonomy of which is in such a state of flux that it is not practical to list them here (see Varona, 1974; and a recent revision of Hispaniolan forms by Rímoli, 1976). Additional taxa are known from the Virgin Islands, Cayman Brac, Little Swan, Bahamas, Martinique, and, of course, *Amblyrhiza* from Anguilla and St. Martin. Many of these rodents in the Greater Antilles were once very abundant, some cave deposits being made up of thousands of specimens.

The most enigmatic of Antillean mammals is the monkey *Xenothrix* (Williams and Koopman, 1952) known from a single jaw fragment from Jamaica. Despite re-examination by several workers, attempts to place this form with any existing monkeys have failed and the consensus is that *Xenothrix* is a valid and highly distinctive genus of primate with no obvious close mainland relatives.

In contrast to most of the avifauna, the land mammals of the West Indies, with the exception of the insectivores, are not of North American, but ultimately of South American origin. Paula Couto (1967) concluded that the West Indian edentates have their closest relationships with genera from the Miocene of South America. As Simpson (1956) has pointed out, the Antillean sloths are too radically different to have evolved since the late Pliocene from any of the known North American forms. The caviomorph rodents colonized the West Indies on several occasions. Their ancestors are of South American origin, but it is possible that some of these forms had moved into Central America in the Pliocene or Pleistocene and from there proceeded to the Antilles. Simpson (1956) considered direct colonization from South America to be more likely. The absence of carnivores, ungulates, lagomorphs and marsupials is good evidence of the long isolation of the Antillean islands and of the fact that the mammalian fauna that is found there did not arrive via land connections.

Turning next to birds it is perhaps most logical to begin with the raptors, since these were the principal predators on the West Indian mammals and were responsible for much of what we know of the fossil record. From Cuba, Arredondo (1971) has described a new genus and species of condor, *Antillovultur varonai*. I entertain some reservations about the validity of the genus, since the published illustrations

and descriptions indicate a strong similarity to the modern genus *Gymnogyps*. The California Condor, *G. californianus*, now restricted to California, is known to have ranged across the entire Southern United States as far as peninsular Florida in the Pleistocene. The Cuban bird appears to differ from this species, however, and it may well have been an endemic form. A possible source of food for this bird would have been the carcasses of large edentates.

Wetmore (1937b) named a new genus and species of large eagle, *Titanohierax gloveralleni*, and a new genus and species of large hawk, *Calohierax quadratus*, from Pleistocene deposits on Great Exuma in the Bahamas. The latter species was subsequently reported from New Providence by Brodkorb (1959). More spectacular is Arredondo's (1970) discovery of a truly enormous eagle in Cuba, which he has named *Aquila borraasi*, though I doubt that the species is actually referable to that genus. This species was larger than any living eagle. The identification by Wetmore (1928) of a fragmentary carpometacarpus from Cuba as the living South American Gray Buzzard-eagle (*Geranoaetus melanoleucus*), is open to question. I regard the systematics of fossil, and even living, hawks and eagles as being in a very unsatisfactory state. Many of the fossil forms have not been compared with one another or with adequate material of modern forms, skeletons of some of which are still not available. Until a thorough revision of this group is undertaken we cannot be certain of the relationships or origins of the fossil accipitrids so far known from the Antilles. That there are no large accipitrids yet known from Hispaniola is almost surely due to inadequate knowledge of the fossil record.

In the Falconidae, the modern caracara *Polyborus plancus* now occurs from southwestern United States through most of Central and South America, with obviously relict populations in south Florida, Cuba, and the Isle of Pines. Two fossil species based on very poor material have been named from Puerto Rico and New Providence. I do not regard these forms as being sufficiently distinct to merit specific status (Olson, 1976a), but the fossils do indicate that *P. plancus* once had a wider range in the Antilles. The species is as yet unknown from Hispaniola. However, from some fossil material collected in a cave in Haiti in the 1920's, I have recently described a new species of the related genus *Milvago* (Olson, 1976a). The modern forms of this genus range from Argentina north to Costa Rica but are not known elsewhere in Central America or the Antilles. Thus it might appear that the Hispaniolan species (*Milvago alexandri*) colonized the island directly from northern South America. This is a false impression, how-

ever, since Pleistocene fossils of *Milvago* have recently been discovered in Florida (Kenneth E. Campbell, pers. comm.), indicating that these falcons have retreated from a formerly more extensive range.

With the nocturnal raptors we come to some of the most interesting of West Indian fossil birds. Today, fairly typical barn owls (*Tyto alba*) occur in the Bahamas, Cuba, and Jamaica, while two quite distinct forms are found in Hispaniola (*T. a. glaucops*) and in Dominica and St. Vincent through Grenada (*T. a. insularis* and *nigrescens*). Wetmore (1920) named a new form of this general size, *T. cavatica*, from a cave deposit in Puerto Rico and it may be anticipated that similar tytonids may well occur in fossil deposits throughout the Lesser Antilles. Whether *T. cavatica* deserves specific rank can be better determined with additional material. Its status also depends upon whether one chooses to recognize *T. glaucops* and *T. insularis* as full species (as I feel increasingly inclined to do) or as races of *T. alba*.

Of further interest is a giant barn owl, *Tyto ostologa*, described by Wetmore (1922b) from Haiti. Although originally known only from the proximal end of a tarsometatarsus, there is now available much additional material representing most of the skeleton from many individuals. A barn owl of similar size but more robust, *T. pollens*, was described from Great Exuma (Wetmore, 1937b) and later from New Providence (Brodkorb, 1959). More recently, Arredondo (1972a) has named a similar form, *T. noeli*, from Cuba. Whether these three forms are entirely distinct from one another remains to be determined and it seems quite possible that at least *T. pollens* and *T. noeli* may prove to be conspecific.

Arredondo (1972b) discovered in Cuba yet another barn owl of truly enormous proportions which he named *Tyto riveroi*. This was based on the distal end of a tarsometatarsus. Arredondo's diagnosis is substantiated by a femur and humerus sent to Dr. Wetmore a number of years ago but which were never described. These are indeed much larger than *T. pollens* — *noeli* — *ostologa*. Thus we see that there once were three distinct size classes of barn owls in the West Indies. An amazingly parallel situation has been reported from the Miocene of the Gargano Peninsula in Italy, where Ballmann (1973, 1976) has identified three species of *Tyto* of virtually the same sizes as the three Cuban species. In the Miocene the Gargano Peninsula was separated from the mainland and its mammalian fauna was characterized by an absence of carnivores and a great proliferation of rodents, some of which attained considerable size. The similarity of this fauna to that of Cuba is thus very striking.

Gigantism in Antillean owls does not stop with *Tyto riveroi*. In 1958, Arredondo described what he first thought to be a new form of the Tertiary South American carnivorous birds of the family Phorusracidae. It was subsequently shown that this new form, which he called *Ornimegalonyx oteroi*, was actually a titanic owl. *Ornimegalonyx* is now known from several localities in Cuba and exhibits such variation as to suggest that there are two distinct species (Kurochkin and Mayo, 1973). The specimens of *Ornimegalonyx* show such a reduction of the sternum and wing that Arredondo has suggested this owl was flightless. I rather imagine that these birds could fly or glide to some extent, but it may have taken very little flying ability to capture juvenile ground sloths, which this great owl was fully large enough to do. *Ornimegalonyx* is a strigid rather than a tytonid owl and E. N. Kurochkin (in litt. 28 March 1975) informs me that he believes the genus to be not far removed from such mainland genera as *Ciccaba* and *Strix*.

From Cuba, Brodkorb (1969) has described a new species, *arredondoii*, in the Neotropical genus *Pulsatrix*, to add another group of owls to the Antillean fauna. From the Bahamas he has also named a new species of pygmy owl, *Glaucidium dickensoni*, a genus represented elsewhere in the Antilles only in Cuba, and a new screech owl, *Otus providentiae*, a genus with Antillean representatives in Cuba, Puerto Rico and the Virgin Islands. Hispaniola lacks any sort of small owl other than the Burrowing Owl, *Speotyto cunicularia*, and none has turned up in the abundant fossil material from Haiti I have examined. I can offer no explanation for this puzzling absence.

Leaving the raptors, we will turn next to the Gruiformes. There is presently a living form of the Sandhill Crane (*Grus canadensis*) found in Cuba and the Isle of Pines, which is only subspecifically different from the populations of North America. The discovery of what appears to be a distinct new species, *Grus cubensis* (Fischer, 1968; Fischer and Stephan, 1971a) in Pleistocene deposits from Pinar del Rio therefore was somewhat of a surprise. *Grus cubensis* differs from *G. canadensis* in its much broader bill, stockier hindlimb, and reduced wing and pectoral girdle, characters suggesting that it may have been flightless. Thus, Cuba must have experienced two invasions of cranes from North America, the last one being very recent.

Members of the family Rallidae, or rails, are perhaps the most characteristic land birds of oceanic islands. Any such island without an endemic flightless rail of some sort is potentially a source of fossil material of undescribed species. Therefore, there may well be many

species as yet undetected in the Antilles alone. The first extinct West Indian rail was described by Wetmore (1918) as a new genus and species, *Nesotrochis debooyi*, from abundant material found in Amerindian middens in the Virgin Islands. Remains of this species were later found in caves and middens in Puerto Rico. A second species of *Nesotrochis* was discovered a few years ago in cave deposits in Cuba (Olson, 1974), although it was first incorrectly diagnosed as a coot under the name *Fulica picapicensis* (Fischer and Stephan, 1971b). I have described a third species, *Nesotrochis steganinos* (Olson, 1974), from the same deposits in Haiti in which *Tyto ostologa* was found. All of these species were flightless. The genus *Nesotrochis* is very distinctive and its affinities remain obscured. For the present, nothing can be said of its geographical origins.

In the 1920's, three new genera and species of living birds were discovered in the Zapata Swamp of Cuba — a nearly flightless rail, *Cyanolimnas cerverai*, a finch, *Torreornis inexpectata*, and a wren, *Ferminia cerverai*. Barbour (1928) believed that these species had evolved in the Zapata Swamp, but the discovery of a well-marked subspecies of *Torreornis* in the arid regions of extreme eastern Cuba clearly quashed this notion. I now understand that another race of *Torreornis* has recently been taken on islets off northern Camagüey. The fossil record has played a part in this story as well. Remains of the rail *Cyanolimnas* have been found in Pinar del Rio (incorrectly identified as a new species of *Rallus* by Fischer and Stephan, 1971b), and I reported on a large series from a cave on the Isle of Pines (Olson, 1974). It is obvious that the three fascinating "endemic" birds of the Zapata Swamp are relicts rather than autochthons.

Included among five fossil birds that Wetmore described from Puerto Rican caves in 1920 was an extinct snipe, *Capella anthonyi*. I had rather expected to find that this was some weakly differentiated form of the migrant North American snipe *Capella gallinago* that occurs in Puerto Rico today. Instead, on examining the type material, I discovered that this is a very distinct species. However, it is not a snipe. Rather, it is a woodcock, belonging to the genus *Scolopax* (Olson, 1976c). The only other woodcock in the New World is *Scolopax minor* of eastern North America, there previously being no indication of this group in the Antilles. A woodcock in Puerto Rico is not too surprising when one considers that several distinctive insular derivatives of the European Woodcock (*Scolopax rusticola*) are found in the East Indies and elsewhere (Java, Sumatra, Celebes, New Guinea, the Moluccas, and the Riu Kius). It seems to have escaped notice that in the

American Woodcock, which until very recently was placed in a separate genus, *Philohela*, the wing elements are highly specialized, the carpometacarpus in particular being extremely lengthened and tapered. In this regard, the Puerto Rican woodcock is most interesting in that its wing elements are much more similar to those of the more primitive Old World species than to the American one. This indicates that *Scolopax anthonyi* probably arrived in the West Indies before the American woodcocks had acquired distinctive specializations of the wing.

The only other fossil shorebird of note here is the thick-knee *Burhinus nanus* from the Pleistocene of New Providence Island. *Burhinus* occurs elsewhere in the West Indies only on Hispaniola, where an endemic race of the Neotropical species *Burhinus bistriatus* is found.

Wetmore (1920) described a fossil quail-dove, *Geotrygon larva*, from Puerto Rico and suggested that this may have been a representative of *Geotrygon caniceps*, a species now found in Cuba and Hispaniola but not in Puerto Rico.

Three genera of parrots inhabit the West Indies. Gaps in their distribution suggest a number of extinctions and indeed there are no less than 10 names proposed for West Indian parrots that are based solely on drawings or descriptions from early literature. Some, such as the supposed species of *Amazona* from Guadeloupe and Martinique, are very likely valid, since parrots of this genus occur on St. Vincent, St. Lucia, and Dominica, as well as throughout the Greater Antilles. In the West Indies the only macaw to survive long enough for specimens to be preserved was the Cuban species *Ara tricolor*, which is now extinct. Old accounts suggest the possibility of there having been 7 or 8 other macaws in both the Greater and Lesser Antilles. The only paleontological confirmation of this to date is a single tibiotarsus from a midden on St. Croix in the Virgin Islands. This was described by Wetmore (1937a) as a new species, *Ara autochthones*. The bone is indeed that of a macaw (although from an immature individual) and does not appear to be referable to any known species. However, since Indians elsewhere are known to have kept and traded live macaws, often transporting them long distances, the actual provenance of the species *Ara autochthones* may be subject to doubt.

A new genus of woodpecker, *Bathoceleus*, described by Brodkorb (1959) from New Providence, is founded on a single coracoid and is somewhat problematical. It may possibly be related to the endemic Antillean genera *Xiphidiopicus* and *Chryserpes*, of Cuba and Hispaniola, respectively, which I believe to be the oldest of the West Indian woodpeckers (Olson, 1972).

Living crows in the West Indies are represented by species in two size classes. A large form with two races, *Corvus leucognaphalus*, inhabits Cuba, North Caicos, Hispaniola, and has only recently been extirpated on Puerto Rico. The fossil record shows that this species once extended to the Virgin Islands, and bones of a crow of this size are also known from Exuma, Crooked Island, and New Providence in the Bahamas, although Brodkorb (1959) has designated the specimens from the last island as a new species, *Corvus wetmorei*. Smaller crows are represented by a species endemic to Jamaica, *Corvus jamaicensis*, and by *Corvus palmarum* from Cuba and Hispaniola. The fossil record shows that a small crow also occurred in Puerto Rico and the Virgin Islands, Wetmore (1920) having designated this as a new species, *Corvus pumilis*.

This completes our brief examination of the birds and mammals known as fossils from the West Indies. It should be evident that any meaningful zoogeographic analysis of the distribution of these organisms within the Antillean region will have to take into account the repeated extinctions that have taken place there.

The West Indies have evidently been islands throughout their existence, as there appears to be no sound evidence of their having been connected with any continental area. Naturally, these islands could have received colonizing birds and mammals through the entire period of their existence. Inasmuch as the islands would have been less strenuously affected by the various faunal upheavals and replacements that took place on the continents during the Tertiary, one could expect that the descendants of colonizers from various geological periods might have persisted as relicts in the West Indies while their continental ancestors perished. Thus, much as Madagascar is home to several primitive and anomalous groups, the West Indies, too, present a similar though not as striking example of this phenomenon.

The two seemingly most ancient groups of higher vertebrates in the West Indies are the solenodontid insectivores and the todies (Todidae), neither of which now occur outside the Greater Antilles. The todies are coraciiform birds that are most closely related to the motmots (Motmotidae) of the Neotropics. Fifty years ago, Chapman (1923) showed that the motmots are primarily a Central American group that have only secondarily invaded South America. Thus their origins appeared to be in North America. Recently, I have identified a previously described fossil from the Oligocene of Switzerland as a motmot (Olson, 1976b), which shows that the Motmotidae were likely derived in turn from the Old World, where all the remaining families of the

order Coraciiformes occur. Furthermore, I have also described a new genus and species of today from the Oligocene of Wyoming (Olson, 1976b) which provides evidence for the suggestion that the Todidae are of North American origin.

Much new material of fossil insectivores has come to light since McDowell wrote on the subject in 1958. He believed at the time that the North American Oligocene fossils previously assigned to the Solenodontidae were in fact not at all closely related to that family. He considered the closest living relatives of the Solenodontidae to be the shrews, and pointed out that the most primitive known shrew at that time was from the Oligocene of North America. Since then, McKenna (1975) has found the genus *Apternodus* (Apternodontidae), also from the Oligocene of North America, to be related to solenodons and shrews. While the fossil record of the Todidae is too incomplete to allow generalizations, that of the insectivores indicates that there are no known North American forms younger than the Oligocene that were sufficiently primitive to have given rise to the Antillean forms. Because two of the oldest families of homeotherms in the West Indies were derived from groups that were prevalent in North America in the Oligocene, it is quite possible that members of these groups colonized the West Indies during that epoch.

Both Simpson (1956) and Paula Couto (1967) contend that the endentates must have reached the West Indies in Miocene or, at the latest, early Pliocene time.

The relative antiquity of other groups of living West Indian homeotherms can only be guessed at on the basis of their morphology. I would suggest that the nightjars of the genus *Siphonorhis* are also among the older inhabitants of the West Indies. This genus includes the recently extinct species *Siphonorhis americana* of Jamaica and the living species *Siphonorhis brewsteri* of Hispaniola. It has long been held that *Siphonorhis* is related to the Central and South American genus *Nyctidromus*, but this conclusion appears to have been based entirely on the fact that both of these genera have a relatively long tarsus. It has not been stressed that the bill structure of *Siphonorhis* is quite different from that of any of the other caprimulgids, being very broad and heavy. In fact, the bill shape of *Siphonorhis* (Fig. 1) is actually more similar to that of the owlet-frogmouths, Aegothelidae, of Australasia, which also have a fairly long tarsus. While *Siphonorhis* is definitely not an aegothelid, its bill structure is probably more primitive than the weak and specialized structure of typical caprimulgids. *Siphonorhis* may well be one of the most primitive of the Caprimulgidae,

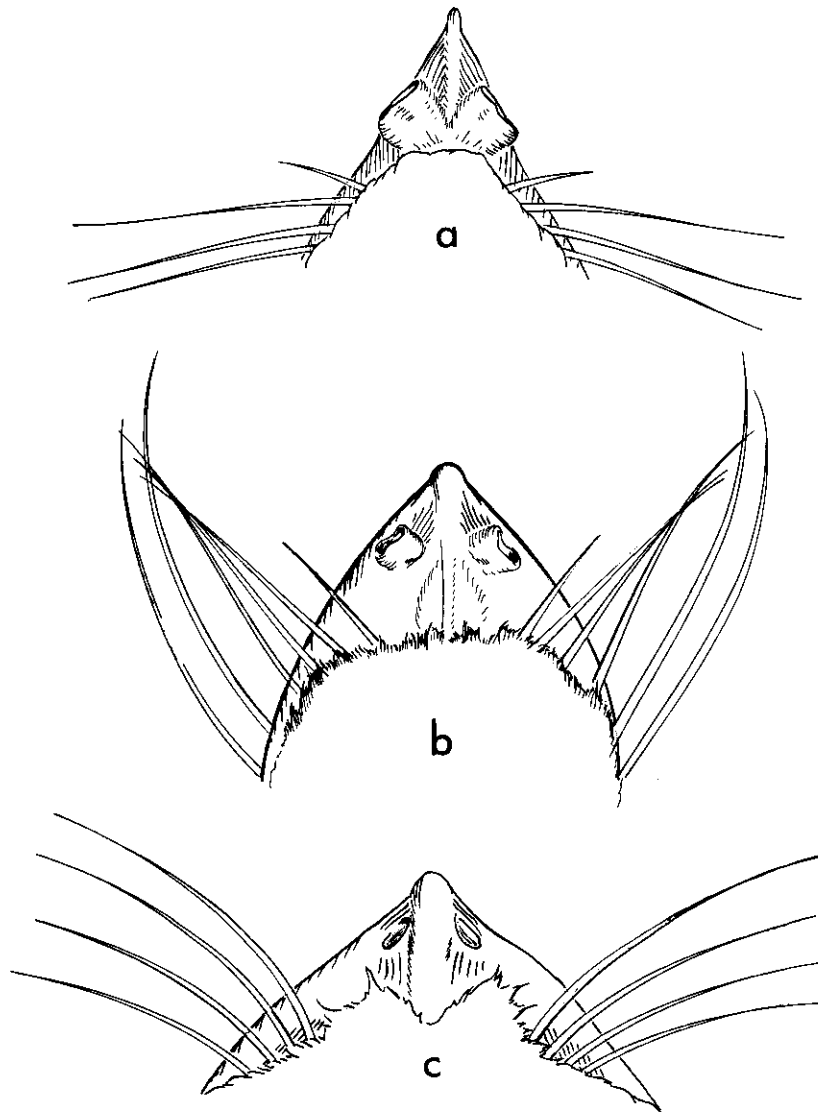


FIGURE 1. — Dorsal view of bills of three species of Caprimulgiformes: *a*, *Nyctidromus albicollis* (Caprimulgidae); *b*, *Siphonorhis brewsteri* (Caprimulgidae); *c*, *Aegotheles cristatus* (Aegothelidae).

and if so, one of the more ancient members of the Antillean avifauna.

Another distinctive West Indian bird is the Hispaniolan Piculet, *Nesocittes micromegas*. This genus has no close relative among mainland piculets and Short (1974) has even proposed tribal status for it. Piculets are among the least specialized members of the woodpecker family (Picidae) and *Nesocittes* is the largest and possibly least specialized of the piculets. It is thus conceivable that the ancestors of *Siphonorhis* and *Nesocittes* arrived in the Antilles some time in the mid-Tertiary.

We have already seen that the fossil woodcock of Puerto Rico must have reached the West Indies before the North American woodcock acquired its specializations of the wing, thus almost certainly before the Pleistocene.

Moving up the geologic time scale there are species that have obviously colonized the West Indies from North America during various stages of the Pleistocene. The Hispaniolan race of the White-winged Crossbill (*Loxia leucoptera megaplaga*) is an obvious example, probably having colonized the island during the last glaciation. Swales' Thrush (*Turdus swalesi*) evidently represents an earlier Pleistocene invasion of Hispaniola by North American robin stock (*Turdus migratorius*).

Further examples could be cited but at this time it should be sufficient to make the point that much of the Antillean fauna represents a collection of relict waifs from many geologic time periods that has accumulated over much of the Tertiary and Quaternary. Any analysis of the Antillean fauna should reflect this.

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ANNOTATED BIBLIOGRAPHY OF WEST INDIAN PALEORNITHOLOGY

I have tried to include here all of the literature pertaining to fossil or subfossil birds in the West Indies. I would be grateful to be informed of errors and omissions and to be sent copies of future papers on this subject for inclusion in revised versions of this list.

Arredondo, O. 1954. Toda una fauna extinguida hallada en las montañas de Pinar del Rio. *Bohemia* 46(35):46-48, 92 [not seen].

- . 1958. Aves gigantes de nuestro pasado prehistorico. *El Cartero Cubano* 17(7):10-12. [original description of *Ornimegalonyx oteroi* n. gen. et sp. (not seen)].
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- . 1971. El águila cubana de la prehistoria. *Bohemia* 63(6):94-97. [popular article (not seen)].
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