Fossil Vertebrates
from the Bahamas

Introduction to the Paleontology
of Bahaman Vertebrates

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In relation to their accessibility and their biological interest, the Bahamas have been relatively poorly studied. The present collection of papers attempts to bring together all that is as yet known of one aspect of the natural history of the archipelago, namely, vertebrate paleontology. This is largely an outgrowth of the more extensive and detailed collection of fossils obtained by Smithsonian personnel in 1978 from the only truly productive vertebrate fossil locality yet discovered in the Bahamas—a sinkhole on the island of New Providence. In addition to analyzing this collection, we have reviewed the literature on Bahaman fossil vertebrates and, with the exception of mammals, we have re-examined and re-evaluated all of the previously reported fossil specimens. Particularly in the case of birds, this has resulted in a number of taxonomic and nomenclatural changes. Furthermore, we have attempted to interpret our findings in the context of the more general picture of Pleistocene biogeography and paleoecology that has emerged from our recent studies in the Antilles. Yet this does not alter the fact that the fossil vertebrates of the Bahamas are still poorly known. What we hope to provide is an updated baseline, a consolidated starting point, from which our knowledge can be expanded by future exploration. We would like to think that we have shown that the little details of anatomy, systematics, geology, and distribution that are the building blocks of studies such as those included here, eventually lead to significant generalizations of wider application. We will have succeeded if this volume stimulates additional research of this nature.

The Bahamas form an extensive archipelago of low (maximum elevation 67 m), limestone islands and cays that are spread out over a distance of nearly 1000 km. The larger islands are almost all in the northern part of the archipelago, where the predominant vegetation type is pine forest (*Pinus caribaea*). Rainfall (data from Buden, 1979; Young and Cant, 1977) is greatest at the northern end of the archipelago, averaging 1300 to 1550 mm per annum on Grand Bahama and Great Abaco, respectively. On the islands of the Great Bahama Bank, rainfall ranges from 1295 mm per annum on New Providence, in the north, to 920 mm per annum on Long Island, in the south. The southern islands are quite dry (860 mm per annum on Mayaguana; 738 per annum on Great Inagua) and vegetation here consists mainly of xeric

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broadleaf scrub. This rainfall gradient has important zoogeographical ramifications (see other papers in this volume).

The most important factor in any consideration of the faunal history of the Bahamas is the effect that eustatic fluctuations in sea level in the Pleistocene would have had on the archipelago. Although there is not full agreement on the extent of Pleistocene changes in sea levels, a maximum lowering of 120 m during the height of the Wisconsinan glaciation, 17,000 years ago, is a reasonable estimate (Gascoyne et al., 1979). This would have consolidated the 29 islands and 661 cays of the present-day Bahamas into five major islands and several smaller ones (Figure 1). In addition, a large island would have been created from the Cay Sal Bank, where there is now almost no dry land, and several islands would have formed from the Mouchoir, Silver, and Navidad banks southeast of Turks and Caicos, where there is no land at all. Land area in the Bahamas was increased by more than an order of magnitude, from 11,406 km^2 at present, to about 124,716 km^2 in the Wisconsinan (Buden, 1979). What is now the Great Bahama Bank constituted the bulk of the land area and was separated from the Cuban mainland by the 15-km-wide Old Bahama Channel (Buden, 1979), thus presumably greatly facilitating the dispersal of organisms from Cuba. At the close of the Wisconsinan glaciation, 12,000 to 13,000 years ago, sea levels began rising and much land was submerged, fragmenting the formerly continuous large islands into many smaller ones. Today, most of the Great Bahama Bank is under 3 to 30 m of water.

During the Wisconsinan glaciation, average temperatures in the Bahamas would have been cooler than at present by about 4° C (Lynts and Judd, 1971), and the fossil record provides evidence that climate and vegetation in general were altered as well (see discussions on pp. 18, 52). This evidence corroborates that from other is-
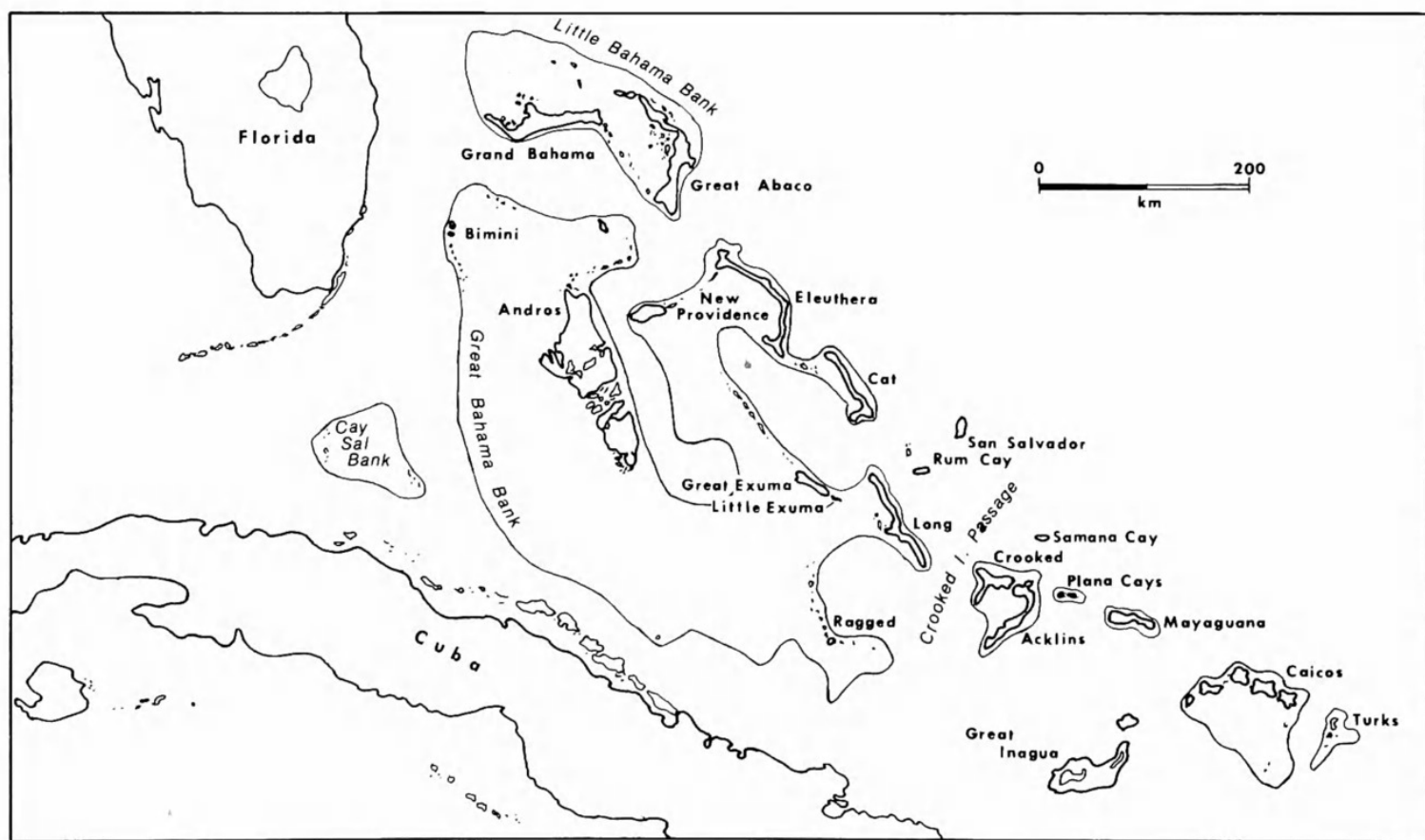

FIGURE 1.—Map of the Bahamas showing the extent of the present banks and thus the approximate configuration of the islands during the last glaciation.

lands, showing that in Wisconsinan times, the West Indies as a whole were more arid, and open savanna and scrubland habitats were much more prevalent than today (Pregill and Olson, 1981).

Although the Bahamas are riddled with sinkholes and caves, such as usually provide ideal sites for the accumulation of fossil vertebrates, the islands have been relatively little explored paleontologically. Barbour (in Lawrence, 1934) and Hecht (1955) lamented that many deposits of cave earth have been obliterated for use as fertilizer, but there must still be many unexploited sources of fossils awaiting discovery on the various islands of the Bahamas.

Among the first fossil or subfossil vertebrates collected in the Bahamas were those obtained by Froelich Rainey in 1933–34 for Yale University. He obtained bones from Great Abaco, Eleuthera, Long, and Crooked islands. The material from Crooked Island came from one of the Gordon Hill caves along the northeast shore, where bones were obtained from a hard stratum under a layer of sand associated with charcoal, food remains, and artifacts indicating human occupancy. The specimens were "considered pre-Columbian though there is no definite criterion to establish the actual age" (Wetmore, 1938:51). Apart from introduced mammals, only the rodent *Geocapromys ingrahami* and remains of birds were recorded from this site (Lawrence, 1934; Wetmore, 1938). Only *Geocapromys* was reported from Great Abaco (Imperial Lighthouse Cave, Hole in the Wall), Eleuthera, and Long Island (no precise localities given). Although Lawrence's (1934) account implies that these specimens were all derived from archeological deposits, Barbour's comments (in Lawrence, 1934) imply that Rainey may have been sampling genuine fossil deposits as well.

Shortly after Rainey's discoveries, vertebrate fossils were forwarded to the Museum of Comparative Zoology at Harvard University, supposedly from Great Exuma. Glover Allen (1937) discussed the remains of *Geocapromys* from this collection and Wetmore (1937b) identified the birds, among which were three species of raptors that he described as new. Bones of "reptiles, and

frogs" were also included in this sample (G. M. Allen, 1937:370), but these were never studied and they cannot now be located in the MCZ collections (Ernest Williams, pers. comm.). This may have been the "mass of small miscellaneous bones" from which Williams forwarded specimens to Koopman (1951), who identified two mandibles of bats, one of which belonged to a species (*Mormoops blainvillii*) that no longer occurs in the Bahamas.

Very little was originally recorded about the Exuma site other than that fossils "were sorted out by Mrs. Vivienne Knowles from cave earth excavated for use as fertilizer . . . during the early part of 1937" (Wetmore, 1937b;427). Although Wetmore referred to the fossils as having come from Great Exuma, G. Allen (1937) made reference only to "Exuma Island." It was later determined that these fossils were actually taken on Little Exuma, from a cave known as "Upper Pasture Cave" located "about fifty feet above sea level facing the western side of Little Exuma" (Hecht, 1955:134). Hecht and party found in 1953 that this and all similar sites in the vicinity "had been completely cleared of the fossiliferous cave soils." The presence of extinct species, such as the gigantic hawk *Titanohierax*, combined with the heavy mineralization of the specimens from the Little Exuma deposits, probably indicates a Pleistocene age, but as with most Antillean cave deposits, there is little direct evidence for dating.

Hecht and Koopman's expedition to the Exumas in 1953 resulted in the collection of a few additional fossils (Hecht, 1955; Koopman et al., 1957). Remains of *Geocapromys ingrahami* were reported from "a small cave on the west side of Pigeon Cay just off Mosstown, Great Exuma" and in "Robertson cave near Williamstown, Little Exuma" (Hecht, 1955:134–135). Koopman et al. (1957) reported five bones of four species of bats from a cave near Forest Settlement, Great Exuma, and a mandible of an additional species from the cave near Williamstown, Little Exuma.

For the sake of completeness, we shall mention two other papers that are of minimal paleontological interest. The first of these is a study of

vertebrates from an Amerindian midden on San Salvador (Watling's) Island, which contained, in addition to fish and introduced mammals, the remains of a large iguanid lizard (*Cyclura*), a booby (*Sula*), and "a few individuals" of *Geocapromys ingrahami* (Wing, 1969:26). Conklin (1971) reported 19 modern species of birds from a "Post-Columbian" cave deposit from "Abaco" containing the bones of *Rattus*, as well as birds. It is probably misleading to refer to these specimens as fossils and the identifications of some of the specimens, particularly of small passerines, are very much in doubt in any case (p. 22).

The most important fossil vertebrate locality in the Bahamas, and the only one yielding a true faunal assemblage, is Banana Hole, situated on the west end of New Providence Island. The entire fossil herpetofauna thus far known from the Bahamas, as well as the vast majority of specimens of fossil birds, were obtained from this site. New Providence is a low limestone island with an area of about 150 km^2 that lies in the northwest central part of the Bahamas and is separated from the adjacent, much larger island of Andros by a deep trench, the Tongue of the Ocean.

Although called Banana Hole by the original collectors for a "large banana tree growing in the sink" (Brodkorb, 1959:351), this designation is nowise distinctive. It is common practice in the arid, rocky Bahamas to cultivate banana trees in the rich, moist earth of sinkholes, and large sinks are therefore generally referred to as "banana holes." *The* Banana Hole, is a limestone sink about 6 m deep, with an opening nearly 12 m across. The hole is undercut on the western and northern sides for approximately another 12 m and it was in this sheltered portion that fossils occurred. Bones were first collected here in 1958 for the Florida State Museum by J. C. Dickinson, Jr., and Walter Auffenberg, who evidently sampled but a small portion of what was available. Brodkorb (1959) analyzed the fossil birds that they collected. The tortoise material and some of the fossil lizards from this sample were reported on by Auffenberg (1967) and Etheridge (1966),

respectively. Additional collections were made in 1959–1960 by William Hanon, the birds from which are in the collection of Pierce Brodkorb.

From 11 through 15 August 1978, Olson visited Banana Hole with Helen F. James, Frederick V. Grady, and Charles A. Meister, and collected still more material. At this time, a ladder was present that allowed easy access to the bottom of the sink. There were two large areas in the sheltered portion from which a layer of about 20 cm of soil had been removed, possibly for agricultural purposes, as the soil had not been dumped elsewhere in the sink. Olson's party was most successful in finding fossils by excavating pockets and crevices between large blocks of fallen rock, which were filled with loose, unstratified, powdery red soil. All soil was screened through 1/8 inch mesh and most of it through window screen as well. Large bones were removed on the spot. Later, the remaining concentrate was washed, dried, and sorted. The fossils are buff to dark brown in color, some having a leached appearance, and a few showing signs of permineralization.

The greatest number of vertebrate fossils were bones and teeth of *Geocapromys*. The concentrations of this relatively large mammal were almost certainly the result of predation by the giant extinct barn owl *Tyto pollens*. Smaller prey remains are presumably attributable in part to the modern Barn Owl, *Tyto alba*. Fossils of both these predators are represented.

The age of the Banana Hole deposits is gauged only by inference. Brodkorb (1959:368) reasoned that the "richer Pleistocene avifauna would seem to require a larger land mass" and therefore that the deposits must have been formed "during the early portion of the Wisconsin (fourth) glacial stage and preceding the mid-Wisconsin (Pamlico) temporary rise in sea level." The avifauna contains a number of species characteristic of arid or savanna-type habitats, such as no longer exist in the Bahamas. Evidence from fossil reptiles (Pregill, 1981) and birds (Pregill and Olson, 1981) indicate that similar conditions prevailed in the late Pleistocene of Puerto Rico. One of the older Puerto Rican fossil sites, that containing the most

species of xerophilic vertebrates, has been tentatively radiocarbon dated at about 18,000 to 20,000 years before present (Pregill, 1981), which is at or just before the maximum extent of the Wisconsinan glaciation. While the fossil avifauna from Banana Hole indicates a more open, arid environment than at present, the herpetofauna suggests that extinction of the more xerophilous elements may already have taken place (p. 20), thus implying that the deposits formed after the Wisconsinan glacial maximum but before the close of the Pleistocene.

By comparison with the reptiles and birds, the mammalian fauna of the Bahamas is quite depauperate. Because we do not otherwise deal with the fossil mammals, we shall use this opportunity to evaluate the status of the few taxa thus far known.

Raccoons (*Procyon lotor elucus*) are known to have been introduced to Grand Bahama from Florida around 1932 or 1933 (Sherman, 1954), but a population found on New Providence was described from a single specimen as an endemic species, *Procyon maynardi* Bangs (1898). In his revision of *Procyon*, Goldman (1950) retained *P. maynardi* as a full species on the basis of three specimens, but noted that it was most similar to *Procyon lotor incautus* of the extreme southern Florida keys. With seven additional specimens, Koopman et al. (1957:164) found that the cranial and dental characters alleged by Goldman did not hold and they considered "*maynardi* as at best no more than a subspecies of *P. lotor*." Presumably the only distinction that can now be ascribed to *maynardi* is Goldman's assertion that it is darker than *incautus*. The fact that *P. l. maynardi* occurs only on the most densely populated island in the Bahamas but nowhere else on the Great Bahama Bank, and the fact that there are no fossils of *Procyon* in the rich material from Banana Hole, makes it very unlikely that *Procyon* can be regarded as occurring naturally in the Bahamas. Until there is evidence to the contrary, we shall regard it as having been introduced.

Thus, discounting *Procyon* and excepting bats, there is only one species of native land mammal known in the Bahamas, the endemic rodent *Geocapromys ingrahami* J. A. Allen (1891). The genus *Geocapromys* is otherwise known only from the Cayman Islands (Patton, 1966; Morgan, 1977), Jamaica, Little Swan Island, and Cuba, whence the ancestors of *G. ingrahami* doubtlessly originated. The nominate subspecies, *G. i. ingrahami*, is known only from tiny, arid East Plana Cay (near Acklins Island but not on the Crooked-Acklins Bank), where it survives today and is relatively abundant (Clough, 1972).

On the basis of midden material from Crooked Island, Lawrence (1934) named a new subspecies, *Geocapromys ingrahami irrectus*, to which she referred specimens from Eleuthera and Long islands, although as we have mentioned, it is not certain whether these came from midden or fossil deposits. G. M. Allen (1937) and Koopman et al. (1957) referred fossil specimens from Great and Little Exuma to *G. i. irrectus*. Remains far in excess of 500 individuals of *Geocapromys* were collected from Banana Hole on New Providence, and Morgan (1977) mentions specimens at Florida State Museum from Andros and Cat islands. Presumably these would be referable to the same taxon as the specimens from other islands on the Great Bahama Bank. The specimens of *G. ingrahami* reported by Wing (1969) from midden deposits on San Salvador were not identified to subspecies and were subsequently lost (G. S. Morgan, pers. comm.). San Salvador was never part of a larger island and was isolated from the island formed by the Great Bahama Bank during the Wisconsinan glaciation. Furthermore, Crooked Island, the type-locality of *G. i. irrectus*, is likewise part of a separate island system—the Crooked-Acklins Bank. A few specimens from Great Abaco, on the Little Bahama Bank, were designated by Lawrence (1934) as a third subspecies, *Geocapromys ingrahami abaconis*, but again it is not certain whether these were derived from midden or fossil deposits. The extent to which Amerindians transported *Geocapromys* from one island to another is not known, so that in the absence of series of genuine fossils from each bank system, it would be difficult to evaluate the taxonomic status and

natural distribution of the various populations of *G. ingrahami*, even if consistent morphological differences could be demonstrated between populations on different banks.

What caused *G. ingrahami* to become extinct everywhere in the Bahamas except on East Plana Cay? To what extent was it affected by the late Pleistocene changes in habitats that caused the extinction of many other vertebrates in the Bahamas, and to what extent was it affected by human predation and human-wrought environmental changes? Again, the possibility of Amerindian transport obfuscates our knowledge of events in the history of *Geocapromys*, because Amerindians could have carried the animals to islands where they had become extinct naturally. The fact that remains of *Geocapromys* occur in middens on a particular island does not necessarily mean that the rodents occurred there naturally at the same time or were even liberated there, as they could well have been raised in captivity. For example, the rodent *Isolobodon portoricensis* is known as a fossil only from Hispaniola. Although it is abundant in middens on Puerto Rico, whence originally described, it does not occur there as a fossil, nor in any noncultural context (Olson, pers. observ.). Furthermore, the same species, along with the flightless rail *Nesotrochis debooyi*, which *is* known from fossils in Puerto Rico, is found in middens in the Virgin Islands, including St. Croix (Olson, 1974). Because St. Croix is not part of the Puerto Rican Bank, it is unlikely that it would have had the same species of flightless rail as found on Puerto Rico. Thus *N. debooyi* must have been brought there by Amerindians. Not only did Amerindians clearly transport native animals from place to place in the West Indies, but they also appear to have practiced some form of animal husbandry as well.

Why is there only a single native species of terrestrial mammal in the Bahamas? In Cuba, the most likely source of colonizers, there were several different genera and species of insectivores and edentates, as well as a considerable radiation of capromyid rodents (Varona, 1974). The fact that *Geocapromys* has differentiated at best only at

the subspecific level within the Bahamas is probably an indication of the relative recency of its arrival, but there is no apparent reason why it should have arrived alone.

A review of the extant and fossil bats of the Bahamas provides more useful information than the non-chiropterans. The fossil bats from Banana Hole, New Providence, have not yet been studied in detail, but Karl Koopman, to whom we continue to be indebted, has identified specimens representing three significant range extensions among this material.

Disregarding two living species that are known only from single accidental or mislabeled specimens, eleven species of bats are extant in the Bahamas (Koopman et al., 1957; Buden, 1975, 1977; Baker and Genoways, 1978). Four of these, *Monophyllus redmani*, *Artibeus jamaicensis*, *Lasiurus borealis*, and *Tadarida brasiliensis*, have not been reported as fossils in the Bahamas. *Macrotus waterhousii*, *Erophylla sezekorni*, *Eptesicus fuscus*, *Natalus lepidus*, and *N. tumidifrons* are known from fossils from the Exumas (Koopman et al., 1957). Of these, only *N. tumidifrons* does not occur in the Exumas today.

Two species of bats are known from the Bahamas only as fossils. *Mormoops blainvillii*, endemic to the Greater Antilles, was found in the Little Exuma deposits (Koopman, 1951) and in Banana Hole, New Providence (Koopman, pers. comm.). *Pteronotus parnelli*, which occurs in the Greater Antilles and much of Central and South America, but has not hitherto been recorded from the Bahamas, was also found in the Banana Hole deposits (Koopman, pers. comm.).

Monophyllus redmani and *Brachyphylla cavernarum* have only recently been taken in the Bahamas, and then only on islands south of the Crooked Island Passage (Buden, 1975, 1977). *B. cavernarum*, however, was found as a fossil in Banana Hole (Koopman, pers. comm.), suggesting that this species, and perhaps *Monophyllus redmani* as well, was once more widely distributed in the Bahamas and subsequently withdrew to the south.

Natalus tumidifrons is endemic to the Bahamas, where it is known only from San Salvador and

Great Abaco. It is absent from the islands of the Great Bahama Bank, where, however, it was found as a fossil on Great Exuma. Similarly, the present Bahaman distribution of the West Indian Red-bellied Woodpecker, *Melanerpes superciliaris*, includes only San Salvador, Great Abaco, and also Grand Bahama (where, however, it may now be extinct). It, too, is absent from islands of the Great Bahama Bank, but fossils of it are known from Little Exuma and New Providence. Its patchy distribution appears to have been caused by environmental changes (p. 45), and it is probable that the same is true of *Natalus tumidifrons*.

We doubt that competitive replacement by the smaller species *N. lepidus*, as suggested by Koopman et al. (1957), is a likely explanation. No such competitor exists for the woodpecker, yet its pattern of distribution is virtually the same as that of *N. tumidifrons*.

Although the published fossil record of bats in the Bahamas is scant, there is evidence of the same patterns of extinction and fragmentation of range that are so strongly manifested among the birds (p. 54), and also of contractions in range southward, as has apparently occurred with reptiles (p. 20) and to a lesser extent with birds.