

Late Holocene Fossil Vertebrates  
from Burma Quarry, Antigua,  
Lesser Antilles

GREGORY K. PREGILL, DAVID W. STEADMAN,  
STORRS L. OLSON and FREDERICK V. GRADY

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## ABSTRACT

Pregill, Gregory K., David W. Steadman, Storrs L. Olson, and Frederick V. Grady. Late Holocene Fossil Vertebrates from Burma Quarry, Antigua, Lesser Antilles. *Smithsonian Contributions to Zoology*, number 463, 27 pages, 17 figures, 9 tables, 1988.—Vertebrate fossils collected from a limestone fissure filling at Burma Quarry on Antigua, Lesser Antilles, are associated with radiocarbon dates ranging from  $4300\pm 150$  to  $2560\pm 70$  years BP, contemporaneous with the earliest aboriginal human occupation of the island. Four Amerindian lithic artifacts (two blades and two flakes) were collected within the same sediments. Two taxa of invertebrates and ten of vertebrates from Burma Quarry are either completely extinct or have not been recorded previously from Antigua. These species, which represent more than one-third of the total number of species represented as fossils, include the land crabs *Cardisoma* and *Gecarcinus*, the lizard *Leiocephalus cuneus*, the snakes *Alsophis antillensis* and an uncertain genus, possibly Boidae, the birds *Puffinus lherminieri*, *Poliolimnas flaviventer*, and *Cinclocerthia ruficauda*, the bats *Pteronotus parnellii*, *Mormoops blainvillei*, and *Phyllonycteris major*, and a rodent (*Oryzomyini* sp.). The extinction of these vertebrates occurred well after any major climatic changes of the late Pleistocene and are best attributed to the environmental influences of man over the past several millennia. Such biotic alterations have affected patterns of distribution and species diversity throughout the West Indies and other island groups. The faunal distinctions between the Greater and Lesser Antilles have been exaggerated by late Holocene extinctions in the northern Lesser Antilles. Ecological and biogeographical studies in the West Indies that consider only the historically known fauna are likely to be based upon data that do not completely reflect natural events.

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*Gregory K. Pregill, David W. Steadman,  
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## Introduction

Human impact on insular environments is a topic that has become increasingly relevant to theoretical and empirical studies of islands. For many islands, the fossil record demonstrates the synchrony of human colonization and the extinction of vertebrates, as in Madagascar (Tattersall, 1982), New Zealand (Cassels, 1984), Hawaii (Olson and James, 1982a,b), and Galapagos (Steadman, 1986). Essentially all islands have been altered to some extent by man, regardless of their size, accessibility, or biotic complexity.

We found new evidence of man's impact in the Lesser Antilles in fossiliferous sediments that filled a limestone fissure at Burma Quarry, Antigua, that we excavated in 1980 and 1983. The fossils reviewed here document the late Holocene occurrence of many species of vertebrates that no longer occur on the island. The salient results and implications of our studies have been summarized elsewhere (Steadman, Pregill, and Olson, 1984). Herein we document our findings in much greater detail.

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*Review Chairman: Stanley H. Weitzman.*

## Site Description

### GEOGRAPHICAL AND GEOLOGICAL SETTING

Antigua is in the northern part of the Lesser Antilles, within the Leeward Island group, on the same bank as Barbuda (Figures 1, 2). Together, these two islands formed one much larger island during lowered sea levels of Quaternary glacial intervals. Whereas the bedrock of Barbuda is exclusively carbonate, that of Antigua consists of three distinctive types, which in turn represent three physiographic provinces known as the limestone district, the central plain, and the volcanic district (Harris, 1965, fig. 3). The volcanic district of southern Antigua consists of weathered late Tertiary volcanics that produce a hilly to mountainous terrain that rises to a height of 423 m at Bogy Peak. Five other peaks exceed 300 m in

elevation. In between the volcanic and limestone districts is the central plain, an area of late Tertiary sedimentary rocks derived from erosion of the volcanics to the south. These sedimentary rocks are secondarily eroded into a terrain of rolling hills with shallow valleys.

Northern and eastern Antigua consists of limestone that makes up part of the Antigua Formation, which by invertebrate fossils is late middle Oligocene to late Oligocene (Frost and Weiss, 1979), ca. 30 to 23 m.y.a.

The Burma Quarry fossil site developed in the carbonates of the Antigua Formation and is located in St. George Parish of north-central Antigua, between the Antigua International Airport and a shallow embayment known as Winthropes Foot Creek (Figure 3). The elevation of the site is about 10 m above sea level. Burma Quarry itself (Figure 4) is an active limestone quarry that produces crushed stone for construction. The

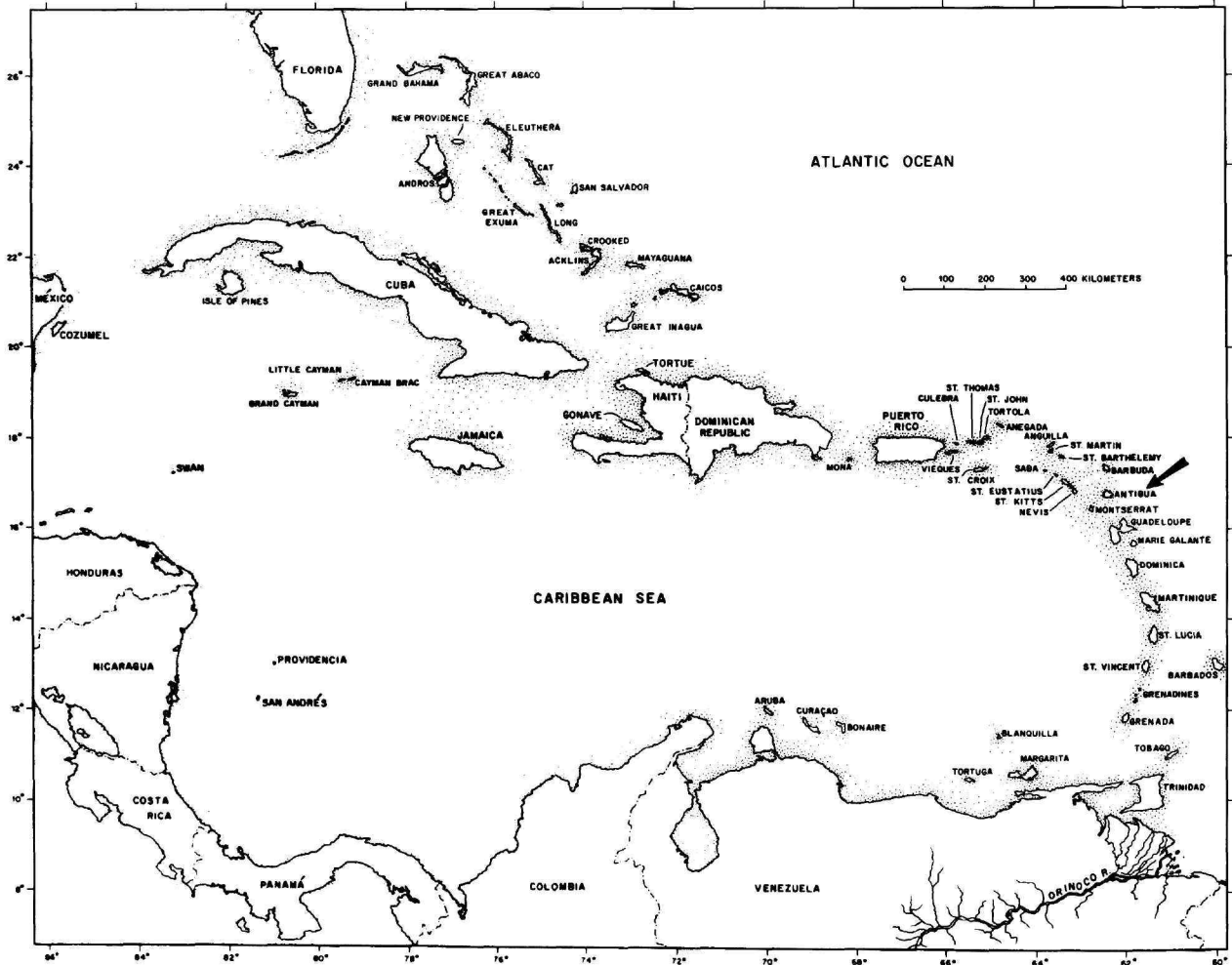


FIGURE 1.—Map of the West Indies showing location of Antigua (arrow).



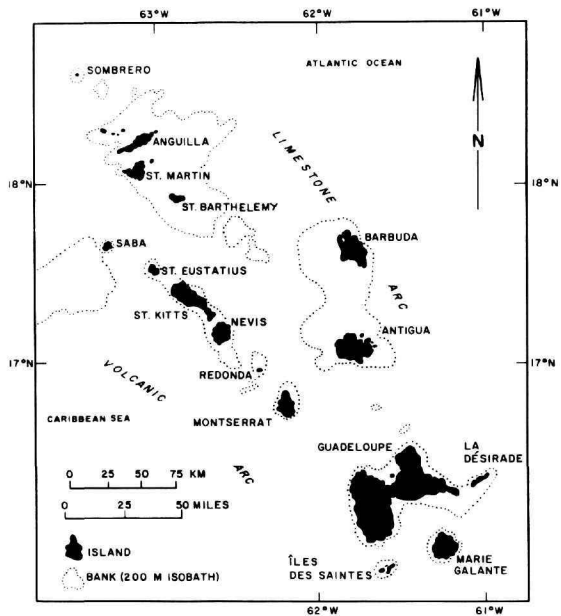


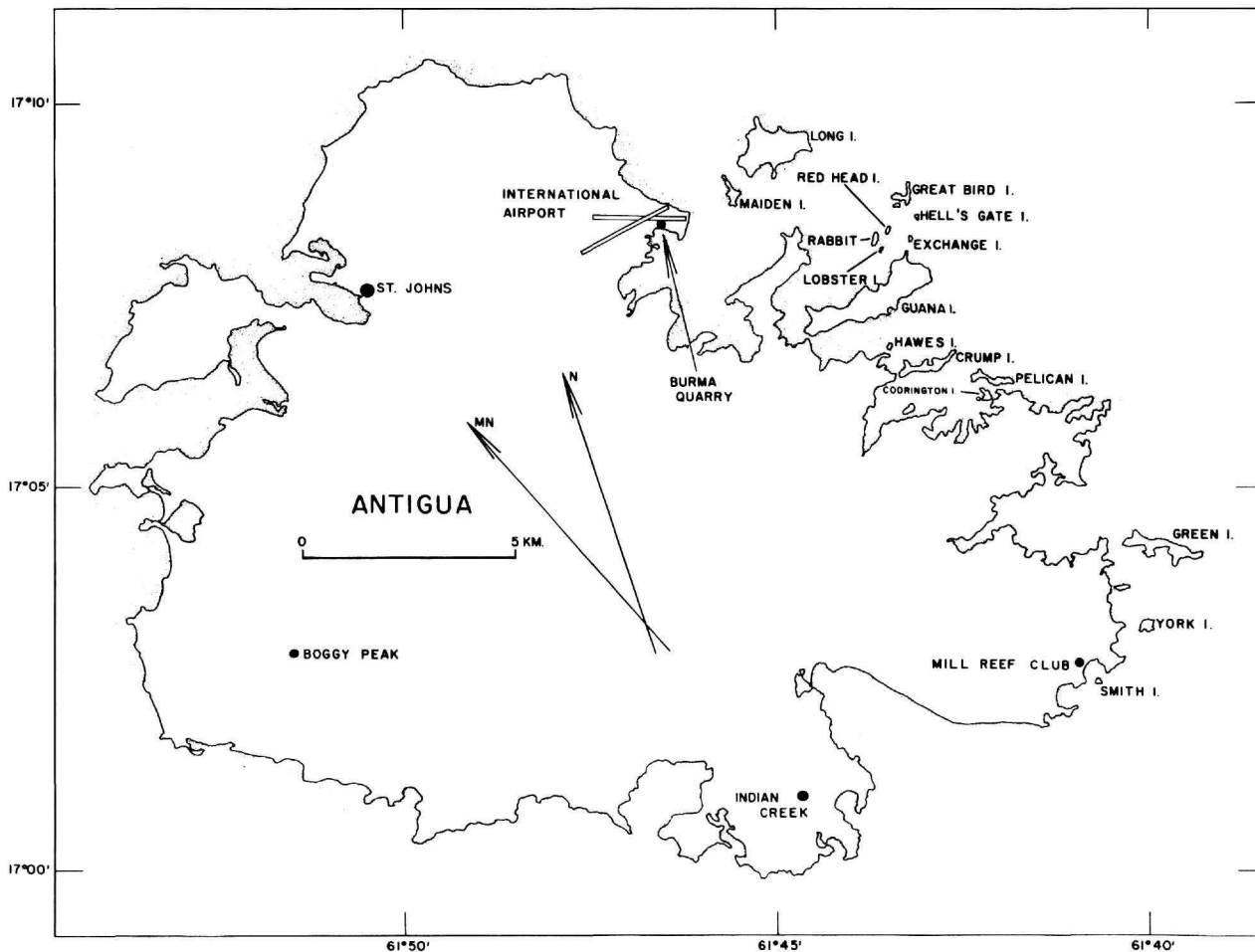
FIGURE 2.—Antigua and the Leeward Islands of the northern Lesser Antilles, showing the extent of submarine banks.

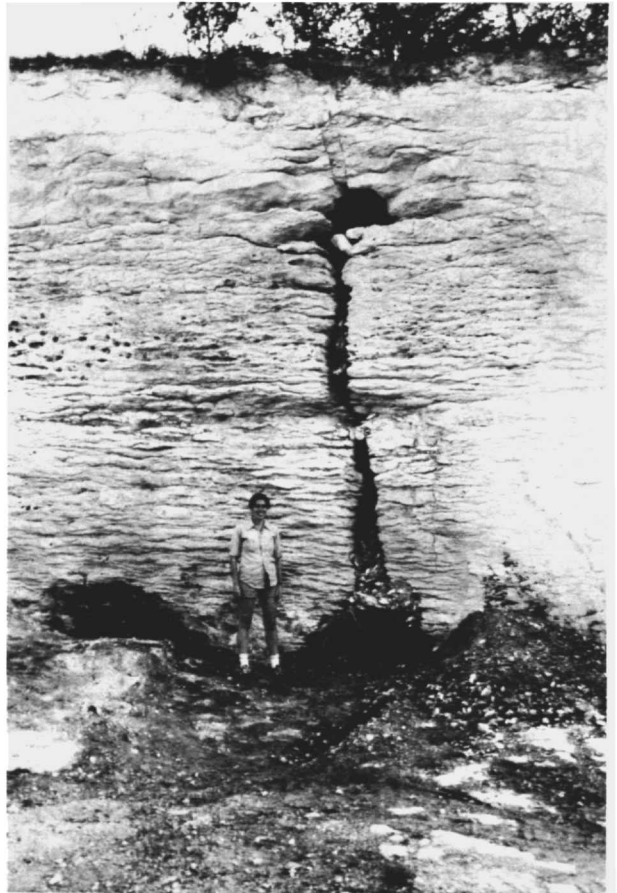
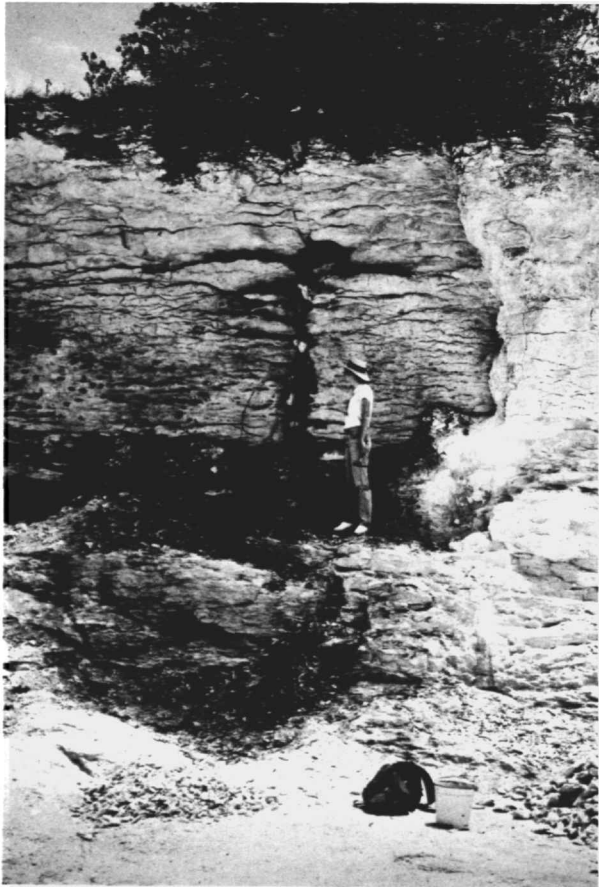
fossiliferous fissure at Burma Quarry probably formed within the past several million years.

STRATIGRAPHY AND CHRONOLOGY

The Burma Quarry fossil deposit (Figures 4–8) is an unconsolidated, unlaminated, poorly sorted accumulation of sediment that filled a fissure in the limestone of the Antigua Formation. Other, small, similar fissures were noted in Burma Quarry, although none of these had filled with sediment. The fossil-bearing fissure is cross-shaped, with a vertical component that leads to a small surface opening, and a horizontal component that crosses the vertical fissure about 5 m below the surface of the ground. This fissure formed from solution along joints in the limestone. The original dimensions cannot be determined because quarrying operations have destroyed an unknown portion of the fissure.

FIGURE 3.—Antigua and its satellite islands. Burma Quarry is located at the northeast corner of the island near the international airport.





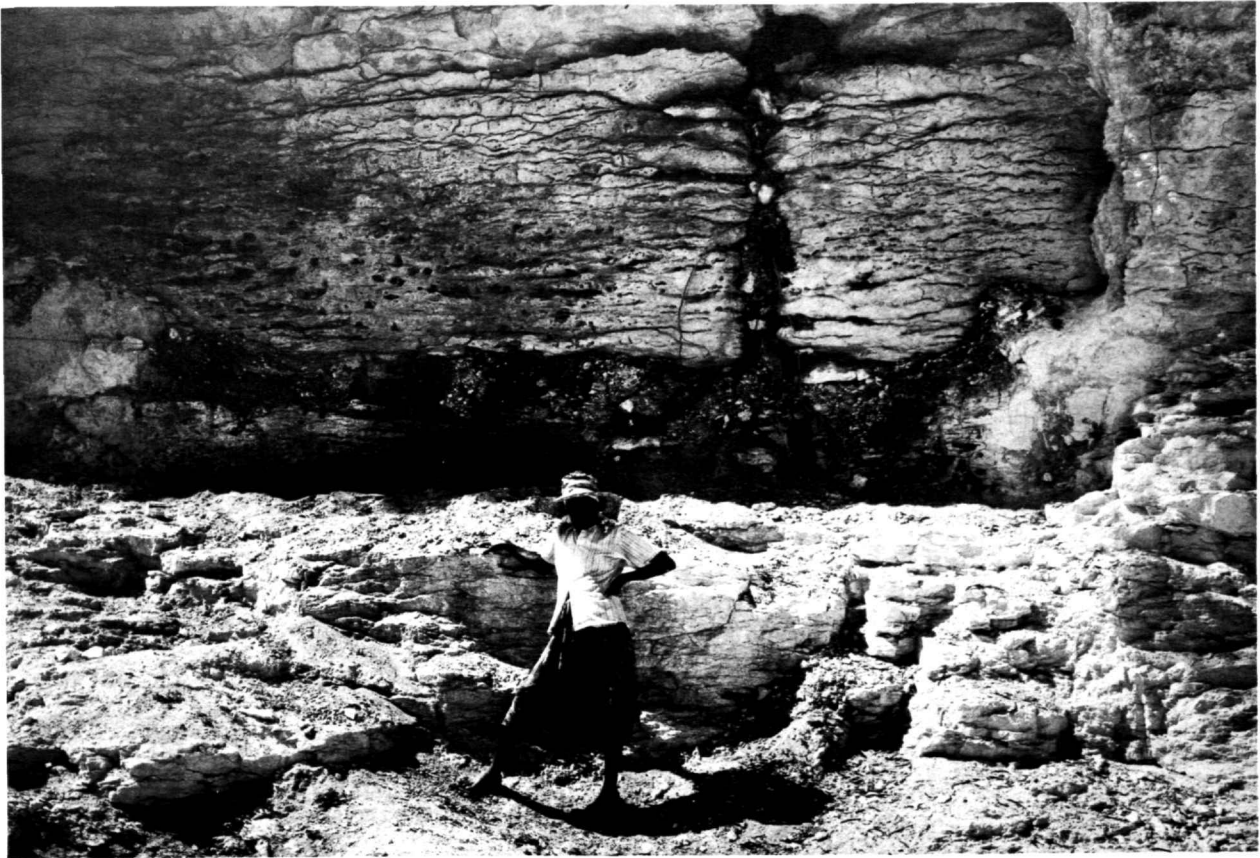


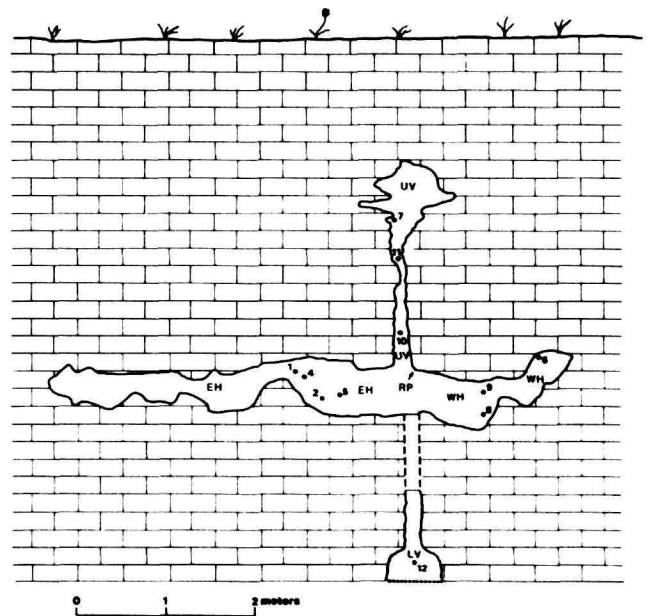
FIGURE 4 (opposite, top).—Burma Quarry, looking southwest, August 1980. The fossil site is indicated by an arrow.

FIGURE 5 (opposite, left).—The Burma Quarry fissure filling, on an active, working face of the limestone quarry. Helen James inspects the upper vertical and horizontal units of the fissure, still filled with sediment, just before our excavations began, August 1980.

FIGURE 6 (opposite, right).—The Burma Quarry site, January 1983. Sediments of the lower vertical units, exposed by Dorsett's labors of the previous two and a half years, are seen just to the right of Jean Sammon. The sediments of the horizontal and upper vertical units had been removed by us in 1980.

FIGURE 7 (above).—Alberta Dorsett, quarry worker who exposed the Burma Quarry sediments, August 1980. Note that the tailings below the cast horizontal unit, evident in Figure 5, have been removed.

FIGURE 8 (right).—Stratigraphic profile of the Burma Quarry fissure fill. UV = upper vertical units; LV = lower vertical units; EH = east horizontal units; WH = west horizontal units; RP = reference point from which all measurements were made. The numbered dots indicate the radiocarbon samples listed in Table 1. The area enclosed by dashed lines was destroyed by quarrying operations.



The sediments filled the fissure from above. Although both wind and water probably were involved in the infilling, there is no catchment basin today other than the surface opening itself. It is likely that another, larger opening existed during the time of deposition that was probably destroyed by quarrying operations. The sediment within the fissure was a loose, somewhat organic silty sand with limestone cobbles, the latter undoubtedly derived from the walls of the fissure. Within each designated area (upper vertical, lower vertical, east horizontal, and west horizontal units), we designated arbitrary subunits that extended for 1 m in each direction from a central reference point. We found no significant change in sediment or fauna in any of the major units or subunits. "Tailings" refers to the fossiliferous sediments that were not collected in situ, but that had been displaced by quarrying operations. Most of the sediments classified as "tailings" were probably derived from the two horizontal units. In the field, sediment was screened through 8.0 mm and 1.5 mm mesh; the concentrate was hand-picked in the laboratory with the aid of magnification.

The five radiocarbon age determinations from Burma Quarry (Table 1, Figure 8) are stratigraphically concordant, as one would expect in a sediment infilling within a very narrowly confined chamber. Vertical mixing of sediments would be minimal under these circumstances, as opposed to a wide vertical column where a debris cone would cause significant diagonal displacement of incoming sediment.

Most of the vertebrate fossils in Burma Quarry undoubtedly accumulated as prey remains of owls. The sheer volume of bones of *Anolis* alone would favor this argument. The burrowing owl (*Athene cunicularia*), the most commonly occurring bird in the fossil deposits, is a predator that feeds on a variety of small vertebrate as well as invertebrate species (Schlatter et al., 1980). Although its presence could account for the concentration of small frogs and lizards in the deposit, the rodents and probably the giant anoles would have been too large for this species to capture; most likely their remains can be credited to a much larger predator such as a barn owl (*Tyto* spp.). Although no fossils of barn owls were found in the Burma Quarry deposit, bones of two undescribed species are known from Barbuda (Steadman and Hilgartner, in litt.). In all likelihood the same or related species occupied Antigua as well. In other West Indian fossil deposits, for example on Puerto Rico, *Athene* itself was a preferred food item of *Tyto* (Pregill, 1981:57; Olson, 1982a), although remains of *Tyto* were rarely deposited.

Bones of bats (e.g., *Natalus stramineus*) may have come from individuals that roosted in or near the fissure. Many of the gastropod shells (Table 2) could have been transported to the site by hermit crabs (*Coenobita* sp.), and of the Crustacea recovered (Table 2) all are terrestrial forms that may have become entrapped naturally.

Because we did find Amerindian artifacts in the Burma Quarry sediments (see "Cultural Materials"), it is also possible that many of the invertebrates (see "Nonvertebrate Remains")

TABLE 1.—Radiocarbon ages from Burma Quarry, Antigua arranged stratigraphically (SI = Smithsonian Institution Radiation Biology Laboratory; A = University of Arizona Laboratory of Isotope Geochronology. EH = east horizontal unit; LV = lower vertical unit; UV = upper vertical unit; WH = west horizontal unit. See Figure 8 for locations of charcoal samples within the sediments).

Laboratory number	Age (years BP)	Strata (m)	Charcoal sample no.
SI-4621	2560±70	UV: 0-1, 1-1.7, 2-2.8	7, 10, 11
SI-4618	3515±60	EH: 0-1	2, 5
SI-4619	3330±50	EH: 1-2, 3-3.8	1, 4, unnumbered
SI-4624	3695±100	WH: 0-1, 1-2	6, 8, 9*
A-3282	4300±150	LV: 0-1	12

\*Sample was small and diluted.

and some of the other Burma Quarry fossils derived from middens. The size and shape of the existing fissure would have been unsuitable for human habitation; therefore, it is more reasonable to assume that there were camps or settlements nearby from which artifacts and food remains washed into the deposit.

#### CULTURAL MATERIALS

Four pre-Columbian lithic artifacts were recovered from the Burma Quarry sediments. In the tailings we found a long, slender, roughly triangular blade (Figure 9A-C) and two small chert flakes. In the east horizontal unit, 0-1 m subunit, we collected a much stouter, triangular blade or core (Figure 9D-F). The blades appear similar to some depicted by Davis (1982, fig. 3c,e) that were obtained from the archaic Amerindian site at Jolly Beach, Antigua, radiocarbon dated at 3725±90 years BP. The blades from Burma Quarry were submitted to William W. Fitzhugh for analysis, whose report of November 1981 we quote here.

#### Description

##### 1. Quarry tailing specimen [Figure 9A-c]

This piece is a small bladelet, or microblade, of fine-grained mottled brown chert, 42 mm long with a nearly equilateral cross-section whose sides each measure about 6 mm in width. Blade thickness is about 5 mm. The specimen has a single dorsal ridge and a modified striking platform on its proximal end. Neither the dorsal ridge nor the lateral sides of the microblade bear secondary removals or signs of scarring or usage. However, the distal end of the piece has either been modified for use as a tool or has had secondary removals resulting from use-damage along its 5 mm edge. One corner of the distal edge has been largely removed by extensive step-flaking from a heavier form of use than evident on the adjacent transverse section. While the piece is fairly irregular in form, it has the distinctive features of a true prismatic blade, indicating that it was produced by people possessing knowledge of this specialized form of technology. There is no doubt that the piece has been used as a tool for cutting, scraping or piercing functions.



TABLE 2.—Distribution of plants, mollusks, and crustaceans from Burma Quarry, by arbitrary levels (in m) (x indicates present; dash indicates absent; no specimens were identified from the lower vertical unit; see Figures 5–8 for the relative positions of these units).

Taxon	Upper Vertical Unit			East Horizontal Unit				West Horizontal Unit		Tailings
	1.7–2.8	1–1.7	0–1	3–3.8	2–3	1–2	0–1	0–1	1–2	
	Ulmaceae									
<i>Celtis [Trema] micrantha</i>	x	–	–	x	–	–	x	–	–	–
Unidentified seed	–	–	–	–	–	–	–	–	x	–
Prosobranchia										
ANNULARIIDAE										
<i>Adamsiella antiguensis</i>	x	–	x	x	x	x	x	x	x	x
BULIMULIDAE										
<i>Bulimulus</i> sp.	x	–	x	x	x	x	x	x	x	x
<i>Drymaeus</i>	–	–	–	–	–	–	–	–	–	x
cf. CAMAENIDAE										
(fragment)	–	–	–	–	–	–	–	–	–	x
CHONDRINIDAE										
<i>Gastrocopta</i> sp.	–	–	–	–	–	–	x	–	x	x
POLYGYRIDAE										
<i>Polygyra</i> sp.	x	–	x	x	–	–	x	x	x	x
PUPILLIDAE										
<i>Pupoides</i> sp.	x	–	x	x	–	–	x	–	–	x
SUCCINEIDAE										
<i>Succinea</i> sp.	x	–	–	x	–	–	x	x	–	x
TROCHIDAE										
<i>Cittarium pica</i>	–	x	–	–	–	–	–	–	–	–
(fragment)										
TURBENIDAE										
(fragment)	x	–	–	–	–	–	–	–	–	–
UROCOPTIDAE										
<i>Microceramus</i> sp.	x	–	–	–	–	–	–	–	–	x
<i>Pseudopineria schrammi</i>	x	–	x	x	–	–	x	x	x	x
Bivalvia										
LUCINIDAE										
<i>Linga pensylvanica</i>	–	–	–	–	x	–	–	–	–	–
MYTILIDAE										
<i>Brachidontes modiolus</i>	–	–	–	–	–	–	–	–	–	x
OSTREIDAE										
cf. <i>Crassostrea</i>	–	–	–	–	–	–	–	–	–	x
PTERIIDAE										
<i>Pinctada imbricata</i>	x	–	–	–	–	–	–	–	–	x
Crustacea (Decapoda)										
COENOBITTIDAE										
<i>Coenobita</i> sp.	–	–	–	x	–	–	x	x	–	x
GECARCINIDAE										
<i>Cardisoma</i> sp.	–	–	–	–	–	–	x	–	–	x
<i>Gecarcinus</i> sp.	–	–	–	x	–	–	x	x	x	x

## 2. West side 0–1 meter specimen [Figure 9D–F]

This piece, measuring 33 mm in length, has a tapered triangular cross-section decreasing from 14 to 6 mm and a thickness decreasing from 11 to 6 mm as measured from its proximal end. A clear bulb of percussion is present on the ventral face of the thick proximal end. The adjacent striking platform bears three parallel blade removal scars originating from a step-fractured and scarred

earlier striking platform at the top of the right dorsal side of the microblade. It appears that this piece was originally part of a larger microblade core that has been cannibalized or rotated for the removal of subsequent microblades, including this one. The blade's lateral sides are pristine and have no edge removals or evidence of use-scarring. However, the dorsal ridge, which is also the most acute edge on the piece, has microscopic scarring of the sort that

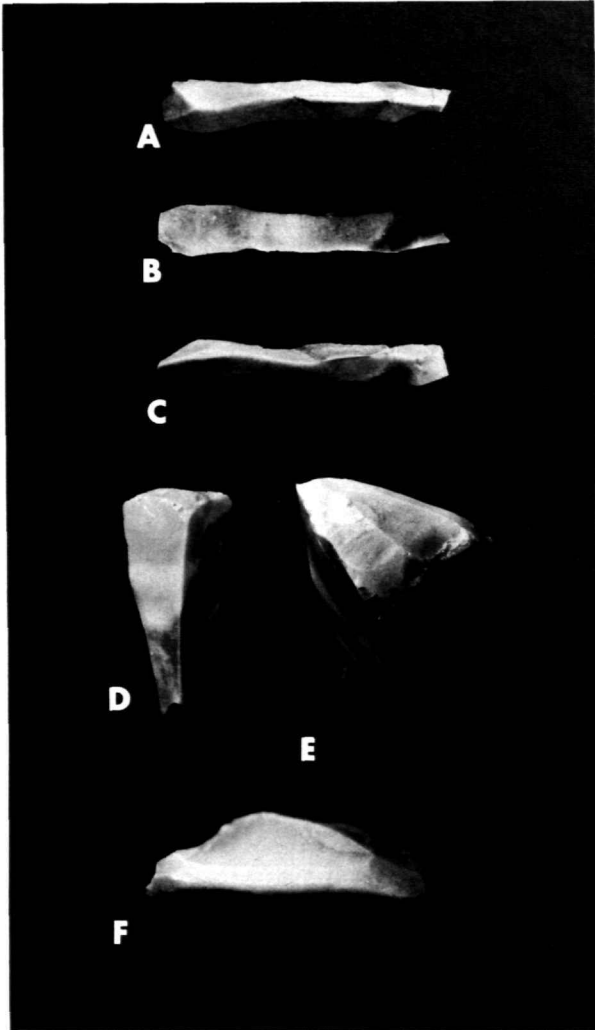


FIGURE 9.—Chert artifacts from Burma Quarry. A-C, blade from tailings. D-F, blade or core from east horizontal unit, 0-1 m east of reference point. See text for detailed descriptions. Natural size.

typically occurs when an unmodified edge is used as a cutting tool. As in the preceding specimen, this piece is most heavily modified at its distal end where a concave surface is found about 8 mm long. Modification is in the form of step-fractures and minute removals originating from one side of the edge only. The distal corners also show evidence of use. The specimen is of the same mottled brown chert as the former piece. Again, there can be no doubt as to its cultural origin.

#### Discussion

The occurrence of pristine, unmodified lateral and dorsal ridges together with the localized distal edge modification rule out natural origins for both specimens. Microblades are rarely found under natural circumstances, and if this had been the case small bits of flint materials and randomly shaped flakes would have been found at the site. The form of the specimens strongly suggests

they have been produced from specially prepared microblade cores even though their shape is somewhat irregular, indicating poor control of the technique or desirability of thick blades. The latter feature might be selected, for instance, if a projectile point function were the desired end-product. It would appear that the microblade industry from which these pieces came produced thick, irregularly shaped blades and that core rotation was a common practice. These features may serve to distinguish this technique from other microblade industries when the chronology of these techniques is refined in future research.

The function of the two specimens is difficult to determine. Evidence of cutting, scraping, and piercing is present. There is no suggestion of their having been hafted on the end of a shaft. They may have been used as miniature scrapers and knives. Alternatively, their morphology would also be consistent with use as projectile tips, perhaps on arrows or darts. Comparison with large numbers of pieces from archeological sites might assist in this determination.

As a result of a general dearth of archeological investigations, Antigua's prehistory is poorly known at present. Nevertheless, recent work suggests clues as to the age and cultural relationship of the people who produced the chert tools from Burma Quarry. Specifically, the Jolly Beach site south of St. John's (Davis, 1974) and Blackman's Point near Parham Harbor (Nicholson, 1976a, 1976b) contain similar types of microblades in pre-ceramic Archaic cultural contexts. The Jolly Beach site is one of the few from the Island with a radiocarbon date, in this case  $1775 \pm 90$  bc (I-7687; Nicholson, 1976a:260). Elsewhere in the Lesser Antilles the Archaic period seems to date ca. 2000-1 bc (Veloz Maggiolo, 1976:27). While the termination of microblade use in Antigua has not to my knowledge been determined, it is reasonable to expect the Burma Quarry tools to date somewhere in the period 2000 bc-AD 500.

The presence of these pieces at the quarry raises questions about how they became incorporated in the site's deposits. Given the absence of chert flakes or other archeological materials, one cannot consider the location to have been used at some point as an archeological site. However, there may be such a site in the vicinity from which the blades could have been transported by erosion or been accidentally dropped.

#### NONVERTEBRATE REMAINS

**PLANTAE.**—Apart from charcoal and a single unidentified seed, the only plant macrofossils recovered from the Burma Quarry deposits were seeds of *Celtis* [= *Trema*] *micrantha*. This Neotropical species is found from Florida, the West Indies, and Mexico, south through Central America to much of tropical and subtropical South America. It grows as a large shrub or small tree in forests and at forest edges. For Antigua, Harris (1965:44) lists this species as a member of the "mixed evergreen-deciduous forest," which today occurs only in the volcanic southwestern district of Antigua. Harris (1965:42) describes this type of forest as "taller, more luxuriant, and more complex—both structurally and floristically—than evergreen woodland [the type of forest that exists today in northern Antigua]." The rather common occurrence of *Celtis* in the fossil deposits (Table 2) reflects the durability of its seeds, which are commonly found as fossils under many conditions, and indicates that a more forested condition existed at the site at the time of deposition, whereas today there is very little or no native upland vegetation near the site.

**MOLLUSCA.**—All of the mollusks (Table 2) are marine forms and must have been transported to the site by some external agent. Hermit crabs (*Coenobita* sp.), which also occur in the deposits and are still present on the island, are the most likely source of the gastropod shells, although some, such as *Cittarium* in particular, may have been items of human food.

A human origin is almost certainly the case for all of the bivalves in the fauna. As with the artifacts, we assume that these probably washed into the site from overlying midden deposits.

CRUSTACEA.—Three different genera of terrestrial crustacea were found in the Burma Quarry deposits (Table 2): hermit crab, *Coenobita* sp. (doubtless *C. clypeata*, the only species of the genus recorded from the West Indies and still found on Antigua) and two large land crabs, *Cardisoma* sp. and *Gecarcinus* sp. Any of these would have been likely to fall into a crevice and become entrapped naturally, although the two larger species are commonly used as human food and might also have come from midden deposits, as postulated for the artifacts and bivalves.

As neither of the large land crabs has been recorded from Antigua (Chace and Hobbs, 1969), they must be considered extinct there. As summarized by Chace and Hobbs (1969:195–202), the distributions of the species of *Cardisoma* and *Gecarcinus* are very irregular in the West Indies. *Cardisoma gualanhumii* occurs from Bermuda, southern Florida, and Texas, through the West Indies to São Paulo, Brazil, although in the Lesser Antilles it has been recorded only from Montserrat, Dominica, and Barbados. *Gecarcinus lateralis* and *G. ruricola* are mainly West Indian in distribution but are also scattered. In the Lesser Antilles the former is known from Montserrat, Guadeloupe, Dominica, St. Lucia, and Barbados, and the latter from Saba, Montserrat, Dominica, and Barbados. With the discovery of *Cardisoma* and *Gecarcinus* in the Holocene deposits on Antigua, the scattered modern distributions of these crabs in the West Indies become highly suspect. It is likely that under natural conditions these crabs would have been distributed more or less uniformly throughout the Antilles. Once again, human interference is probably responsible for numerous recent extinctions of populations from individual islands. As food, these crabs, which are easily obtained, are a great delicacy. On Dominica, Chace and Hobbs (1969:199) reported that the species of *Gecarcinus* were “perhaps used to a greater extent as food than any other crustaceans on the Island.” Predation by man and introduced predators has probably had a severe negative impact on land crab populations throughout the human history of the West Indies.

### Systematic Accounts

#### AMPHIBIANS AND REPTILES

For the reptile and amphibian fossils from Burma Quarry, catalog numbers were assigned to individual bones or to lots consisting of a single taxon from a particular stratigraphic subunit. Thus, each number may represent one or more specimens. All of the material is housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Identifications of amphibians and reptiles were made by Pregill. The procedure for estimating snout-vent length (SVL)

has been explained fully in a previous paper (Pregill, 1981). Comparative skeletal material was obtained from the USNM collections of the National Museum of Natural History, Smithsonian Institution, Florida State Museum (FSM), Museum of Comparative Zoology, Harvard University (MCZ), San Diego Natural History Museum (SDSNH), and Gregory Pregill private collection (GKP).

The modern indigenous herpetofauna of Antigua and its satellites consists of one frog, *Eleutherodactylus johnstonei* (*E. martinicensis* may be an introduction, see below); two geckos, *Sphaerodactylus elegantulus* and *Thecadactylus rapicauda*; three iguanids, *Anolis bimaculatus leachi*, *A. w. watsi*, and *Iguana delicatissima*; one teiid, *Ameiva griswoldi*; and two snakes, *Alsophis antillensis* and *Typhlops monastus*. A single specimen of another blind snake, *Leptotyphlops albifrons*, was listed by Boulenger (1893); however, Thomas (1965) referred the specimen to *L. tenella* Klauber, known from Trinidad south to Brazil, and, more importantly, concluded that the Antigua record is most likely an error. In any case, only the frog, the anoles, *S. elegantulus*, and the blind snake *T. monastus* are common on Antigua today. The toad *Bufo marinus*, tortoise *Geochelone carbonaria*, and gecko *Hemidactylus mabouia* are thought to have been introduced, although the latter species probably occurs there naturally (Kluge, 1969:44). All of the indigenous taxa were represented in the Burma Quarry deposits except *Sphaerodactylus elegantulus* and *Iguana delicatissima*, whose absence may be due to very small and very large size, respectively.

### Order ANURA

#### Family LEPTODACTYLIDAE

##### *Eleutherodactylus johnstonei* Barbour

*Eleutherodactylus johnstonei* Barbour, 1914:249.  
*Hyla barbudensis* Auffenberg, 1958:251.

MATERIAL.—1 sphenethmoid, 37 ilia, 1 tarsus, 4 vertebrae (USNM 3401811). MNI = 19.

REMARKS.—The fossils probably came from one, remotely both, species of *Eleutherodactylus* currently inhabiting Antigua: *E. johnstonei* Barbour and *E. martinicensis* Tschudi. These two frogs are very similar to one another externally, but supposedly are distinguishable on size, hindlimb proportions, and to a lesser extent color and pattern (Schwartz, 1967:41). The fossil ilia, although badly worn, exhibit most of the generic features of West Indian *Eleutherodactylus*: the ilial prominence, dorsal protuberance, ventral acetabular expansion and the ridge on the distal aspect of the shaft. Beyond that, nothing about the fossils will distinguish them from any other small Antillean species of the genus.

Schwartz (1967:41) described *E. johnstonei* as being smaller than *E. martinicensis*, especially among females. His sample of 37 frogs from Antigua included females of *E. martinicensis* with snout-vent lengths up to 46 mm, whereas the largest of

*E. johnstonei* were 30 mm. Males of these two species obtain snout-vent lengths of 26 and 24 mm, respectively. All of the fossils from Burma Quarry came from small frogs having estimated snout-vent lengths of no more than 30 mm. By itself, the absence of larger frogs does not mean that *E. martinicensis* was not on Antigua at the time the Burma Quarry fossils were deposited. However, *E. martinicensis* does not occur anywhere in the Leeward Islands, except, according to Schwartz (1967:43), Antigua. It is supposedly native to Guadeloupe and its satellites, and to Dominica, and Martinique. We suspect that the species is a modern introduction to Antigua, if in fact it exists there at all. We never encountered the species on the island. *Eleutherodactylus johnstonei* inhabits most of the Leeward Islands, and all but Dominica in the southern Lesser Antilles; it occurs as an introduction on Jamaica and Bermuda.

The remains of *Eleutherodactylus* also bear directly on the supposedly extinct species *E. barbudensis* that was based on fossil ilia collected on Barbuda and originally described as *Hyla barbudensis* by Auffenberg (1958:251). Lynch (1966) redescribed the holotype (UF 2752) and referred material and showed that these bones were referable to *Eleutherodactylus*, but he stopped short of synonymizing the species *E. barbudensis*, as it then became. He concluded (1966:529) that "*E. barbudensis* is possibly extinct, but it is possible that the species is identical with the Recent form inhabiting Barbuda," i.e., *E. johnstonei*. In his comparisons between the Barbudan fossils and other skeletons of Recent *Eleutherodactylus*, Lynch suggested that the peculiarities of the Barbudan fossils were likely due to erosion, plus ontogenetic and individual variation. We examined this fossil material and concur with his assessment. The emergent land bridge between Barbuda and Antigua that existed during lowered late Pleistocene sea levels would have assured that these islands shared the same anuran fauna, as they do today. Yet there are no fossils from Burma Quarry indicating an extinct species of *Eleutherodactylus*. We therefore place *E. barbudensis* in the synonymy of *E. johnstonei*.

#### Order SQUAMATA

#### Family GEKKONIDAE

#### *Thecadactylus rapicauda* Houttuyn

**MATERIAL.**—52 dentaries and fragments, 32 maxillae, 3 premaxillae, 12 frontals, 2 pelves, 31 vertebrae (USNM 340166–340170, 340192). MNI = 35.

**REMARKS.**—Remains of this large gecko are indistinguishable from modern skeletons of *T. rapicauda*. The straighter, less pointed teeth distinguish this species from the other large, Greater Antillean geckos *Tarentola americana* and *Aristelliger* spp. (Etheridge, 1964; Pregill, 1982). The largest fossil dentary measured 19.1 mm along the tooth row and came from an individual with an estimated snout-vent length of 125 mm, the approximate maximum size attained by living forms. *Thecadactylus rapicauda* is the only large gecko occurring on

Antigua and elsewhere in the Lesser Antilles; the species extends north in the West Indies as far as Necker Island in the British Virgin Islands. Etheridge (1964:46) reported it as a fossil from Barbuda.

#### Family IGUANIDAE

#### *Anolis bimaculatus leachi* Duméril and Bibron and *Anolis* spp.

**MATERIAL.**—586 complete and 205 fragmentary dentaries, 22 coronoids, 32 articular + surangulars, 225 complete and 170 fragmentary maxillae, 17 premaxillae, 134 frontals, 7 prefrontals, 13 postorbitals, 32 jugals, 3 squamosals, 10 parietals, 20 quadrates, 5 basales, 16 basioccipitals, 41 pterygoids, 12 ectopterygoids, 10 scapulae, 14 interclavicles, 66 pelves, several hundred vertebrae (USNM 340120–340156, 340193–340195). MNI = 395.

**REMARKS.**—The hundreds of elements here referred to *Anolis* are only a fraction of the number of bones of these lizards that were removed from the Burma Quarry site, most of which were too fragmentary to be of use taxonomically and were left uncataloged. Bones of *Anolis* account for approximately 75%–80% of the total minimum number of individuals of amphibians and reptiles in the Burma Quarry herpetofauna.

Many of the fossils clearly belong to *A. bimaculatus leachi*, a large, arboreal species currently inhabiting Antigua. The only other anole on the island today is *A. watsi watsi* Boulenger, a much smaller lizard whose remains are almost certainly among the Burma Quarry fossils also. Unfortunately, except for the largest fossils, the majority cannot be assigned to either species with much confidence. Dentaries from lizards with a snout-vent length of 50–60 mm, for example, could represent small individuals of *A. b. leachi* or adults of *A. w. watsi*. The only fossils that can be identified with certainty are the large sculptured dentaries of adult male *A. b. leachi*. Where it occurs among *Anolis*, sculpturing is strictly a characteristic of males and is manifested fairly late in ontogeny (Etheridge, 1964:61). Shallow, longitudinal grooves first appear in individuals of about 80 mm snout-vent length (tooth row approximately 14 mm). At near maximum size, approximately 110 mm snout-vent length (tooth row of 16 mm), the ventrolabial face of the dentary is swollen into large, irregular bumps and furrows. Many of the fossil dentaries have tooth rows 18–20 mm in length, and the sculpturing in these has achieved massive proportions (Figure 10).

In his analysis of the fossil anoles from Barbuda, Etheridge (1964:5) recognized three species based on distinct size classes of pelves, basales, and parietals. Bones from individuals with an estimated snout-vent length over 89 mm were referred to *A. b. leachi*, the largest of which were over 120 mm snout-vent length and supposedly exceeded in size any known modern specimens by at least 25%. The medium-size species had an estimated snout-vent length of 61 to 72 mm, the smallest species 42 to 48 mm. Etheridge assumed that the other Recent



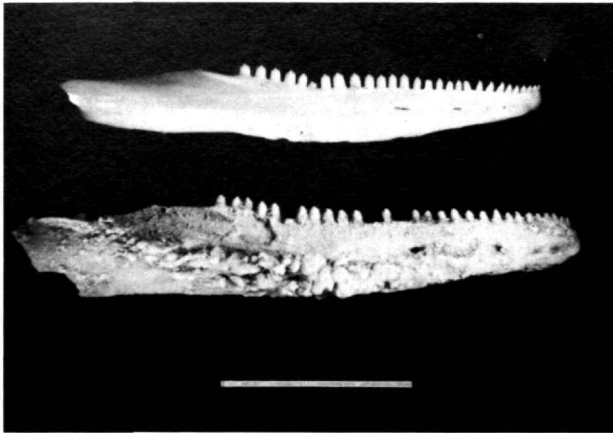


FIGURE 10.—Dentaries of *Anolis bimaculatus leachi* from Antigua, labial view. The bone at top (GKP 344) is from a modern, large adult male of approximately 115 mm SVL. The much larger bone below (USNM 340120) is from a typical adult male of the fossil population preserved in the Burma Quarry fauna. Also notice the heavy sculpturing on the ventrolabial surface, a feature of males that becomes elaborate with increasing age. Scale = 10 mm.

Barbudan anole, *A. watsii forrestii* Barbour, could be assigned to either the medium or small size class and that the remaining size class probably represented an extinct species. Subsequently, Lazell (1972:53) argued that the smallest size class described by Etheridge (1964:57) indeed represented *A. w. forrestii*, but that the other two size classes represented females and males of *A. b. leachi* rather than different species. Lazell noted that *A. b. leachi* is distinctly bimodal in body size, with females attaining a maximum snout-vent length of 75 to 80 mm (e.g. USNM 218325: 79 mm), and males actually exceeding 120 mm, contra Etheridge (1964). He cited one specimen from Barbuda (MCZ 75779) at 123 mm, as marked in his field notes (Lazell, 1972:53). Thus, Lazell concluded that the fossil anoles from Barbuda were nothing more than the two modern species currently inhabiting the island, and that none of the individuals of *A. b. leachi* were giants relative to recent specimens.

The fossils from Burma Quarry do not fall into three discrete size classes and thus support Lazell's (1972) argument. However, on Antigua *A. b. leachi* did in fact attain snout-vent lengths considerably in excess of any recent forms known (Figure 10). The range of estimated snout-vent lengths from the following number of fossil elements are: 14 dentaries, 121–140 mm (mean = 133); 7 maxillae, 123–147 mm (mean = 135); 2 frontals, 150, 153 mm; 2 basicrania, 172, 177 mm. Most of these individuals easily exceeded any of those known historically from the Antigua Bank.

We compared the largest fossil dentaries, maxillae, basicrania, frontals, and limb bones from Burma Quarry with the largest skeletal specimens known from Antigua (USNM 218327; GKP 344), and with another 13 skeletons (USNM 224021–224033) collected by Olson in 1981 from the

introduced population of *A. b. leachi* on Bermuda (Wingate, 1965). None of the recent specimens from either island is as large as the fossils. Yet the adults from Bermuda are appreciably larger than any individual from Antigua, being more or less intermediate between the fossil and recent Antiguan populations (Pregill, 1986). Adult males from Bermuda also show a higher degree of fusion among cranial elements, such as those of the brain case and palate, a phenomenon that accompanies growth and age in lizards. Table 3 shows this trend in size change by comparing measurements of the largest individuals available from each population.

"Gigantism" is also known among late Pleistocene anoles (and other lizards) of the Greater Antilles, and among lizard species from several other archipelagos around the world. Smaller adult size in modern lizards appears to be a phenotypic and genotypic adjustment by a population in which large body size has been eliminated because of human-introduced predators and loss of suitable habitat (Pregill, 1986).

#### *Leiocephalus cuneus* Etheridge

MATERIAL.—13 complete and 4 fragmentary dentaries, 3 complete and 5 fragmentary maxillae, 3 premaxillae, 5 frontals,

TABLE 3.—Measurements (mm) of selected bones of the largest individuals (mean, range, sample size) from three populations of *Anolis bimaculatus leachi* (from Pregill, 1986).

Character	Antigua (modern)	Bermuda (modern)	Burma Quarry
Length of tooth row (dentary)	14.8 14.1–15.8 (8)	17.2 16.0–18.5 (10)	19.0 17.8–19.8 (10)
Length of tooth row (maxilla)	14.1 12.5–15.2 (8)	15.6 14.6–17.2 (10)	17.4 16.0–19.1 (7)
Width of frontal <sup>1</sup>	10.3 9.1–11.4 (5)	11.1 10.2–12.2 (10)	12.9 12.8–13.0 (2)
Width of basale <sup>2</sup>	11.2 9.7–12.0 (5)	12.2 10.8–12.7 (10)	18.2 18.2 (1)
Height of skull <sup>3</sup>	7.2 6.5–7.7 (5)	7.6 7.3–8.2 (10)	—
Length of humerus	14.6 13.5–15.4 (10)	16.1 15.2–17.0 (10)	19.3 17.9–20.7 (7)

<sup>1</sup>Measured across parietal border.

<sup>2</sup>Measured across paraoccipital process.

<sup>3</sup>Measured from posterior angle of jugal to top of orbit.



FIGURE 11.—Fifth metatarsal in plantar view (USNM 340160) of the extinct lizard *Leiocephalus cuneus*. This bone came from an individual probably exceeding 200 mm SVL. Scale = 5 mm.

3 parietals, 2 pterygoids, 1 fifth metatarsal (USNM 340157–340164, 340196). MNI = 8.

REMARKS.—*Leiocephalus cuneus* is an extinct lizard described by Etheridge (1964) from fossils collected on Barbuda, where it was subsequently reported from the Indiantown Trail archeological site (Watters et al., 1984:401). The fossils from Antigua differ in no significant way from the type material and there is but one new skeletal element that was not already known, a fifth metatarsal (Figure 11). There are fewer bones of *L. cuneus* from Burma Quarry, and these are not as well preserved as those from Barbuda.

The holotype of *L. cuneus* (FSM 8226) is a left dentary measuring 15.6 mm along the tooth row. The largest nearly complete dentary from Burma Quarry has a tooth row length of 16.2 mm and came from an individual with an estimated snout-vent length of over 140 mm. The tooth row of the largest and most complete maxilla is 17.8 mm. The largest frontal bone is 12.5 mm across the parietal border, and 13.2 mm in midsagittal length. These bones came from individuals approximately 145 mm and 150 mm, respectively. Etheridge (1964) estimated that *L. cuneus* may have attained a snout-vent length of nearly 200 mm, making it the largest species of the genus known, fossil or living. The fifth metatarsal from Burma Quarry (Figure 11) must have come from an individual at least this length. This bone, easily recognized as that of *Leiocephalus* when compared with those of other West Indian lizards and mainland iguanids, is 4.7 mm at its widest proximal extent and 8.1 mm in a straight line taken from the proximal border to the tip of the angled, distal process.

The discovery of fossils of *Leiocephalus cuneus* on Antigua is not unexpected considering that Antigua and Barbuda were coalesced during lowered sea level of the Wisconsinian glacial period. None of the fossil material from Barbuda was radiocarbon dated, but Etheridge (1964:43) speculated that

“fossils from the loose floors of Caves I, II, and V are at least pre-Columbian in age but not older than post-mid-Wisconsin. Fossils from breccia and consolidated cave earth on the walls of caves III and IV are somewhat older but probably not older than late Pleistocene.” Given the age of the specimens from Burma Quarry, it is likely that *L. cuneus* survived into post-Columbian time but became extinct before the arrival of scientific collectors. *Leiocephalus herminieri* Duméril and Bibron nearly escaped detection before becoming extinct on the southern Lesser Antillean island of Martinique, as it is known only from four specimens collected prior to 1885 (Boulenger, 1885:166). Early this century, Barbour (1914) declared the species extinct.

Other extinct, late Pleistocene/Holocene species of *Leiocephalus* are known in the West Indies from Hispaniola (Etheridge, 1965; Pregill, 1984a), Jamaica (Etheridge, 1966), Puerto Rico (Pregill, 1981), Anguilla and Guadeloupe (Pregill, personal observation). The last two almost certainly persisted into historical time as evidenced by their association with bones of *Rattus*. Today, no species of *Leiocephalus* occur south of Hispaniola.

#### Family TEIIDAE

##### *Ameiva griswoldi* Barbour

MATERIAL.—3 complete and 9 fragmentary dentaries, 1 frontal (USNM 340164–340165, 340197). MNI = 5.

REMARKS.—West Indian *Ameiva* are easily distinguished from all other Antillean lizards by many cranial and postcranial characteristics (Pregill, 1981:44). The fragmentary jaws and frontal bones from Burma Quarry are nearly identical to the same elements of modern skeletons of *A. griswoldi*. The largest fossil individual was approximately 105 mm from snout to vent, the smallest about 60 mm.

As revealed in a series of nine skeletons from Great Bird Island, Antigua (USNM 218347–56), the central and posterior teeth on the jaws of both fossil and modern individuals of *A. griswoldi* undergo ontogenetic changes in morphology (Figure 12), although not as pronounced as that of some other Lesser Antillean species, such as *A. fuscata* (Pregill, personal observation). In all individuals the anterior 6 or 7 teeth show the same morphology: simple, pointed, and slightly recurved. In those less than 65 mm, the central 5 to 7 teeth are usually recurved and bicuspid in typical teiid fashion, i.e., having a small anterior cusp and a large posterior cusp; the posteriormost 3 or 4 teeth are tricuspid in this size class. In individuals 80 to 90 mm, the central and posterior teeth are taller and larger than the anterior sequence, rather blunt, not so recurved, and the anterior cusp is weakly differentiated; the penultimate and ultimate teeth are tricuspid. In specimens over 100 mm (to 107 mm), the central and posterior teeth are large, blunt, and show only a trace of an anterior cusp; tricuspid teeth are absent from the posteriormost teeth, although the last one or two may be faintly bicuspid. There is no significant increase in the number

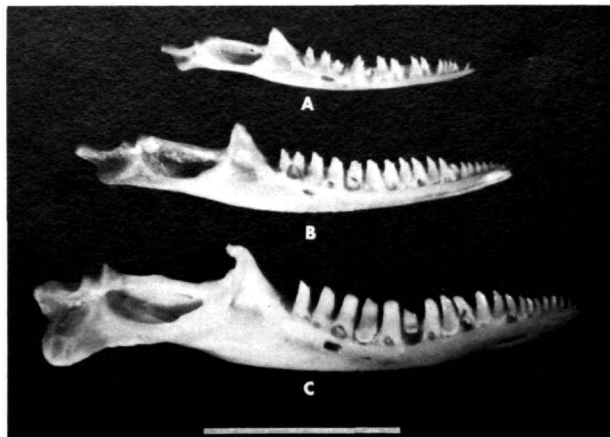


FIGURE 12.—The ontogenetic change in tooth crown morphology of *Ameiva griswoldi* proceeds from a short tricuspid condition in juveniles (A, USNM 218354, SVL = 61 mm) to a more acutely bicuspid type in subadults (B, USNM 218354, SVL = 86 mm), and finally to a blunt, truncated crown in the largest individuals (C, USNM 218349, SVL = 107 mm). Scale = 10 mm.

of teeth with growth, even though the mandible lengthens; the teeth simply become larger. The nine skeletons examined above have an average of 18.5 teeth on the dentary, the mode 19, the range 17 to 20.

An ontogenetic increase in the size of central and posterior teeth has been observed in a number of lizards (Estes and Williams, 1984), especially teiids, and is presumed to be associated with eating hard foods; but there has been little information published that documents a corresponding change in diet as the animals mature. Our current studies on species of Antillean *Ameiva* reveal that molariform dentition is not uncommon among them, and although snails do constitute a portion of the diet, enlarged posterior teeth actually seem to be an adaptation for omnivory (Pregill, 1984b).

*Ameiva griswoldi*, endemic to the Antigua Bank, is now all but extinct on Antigua proper (we saw only one individual in over a month of field work there), but it is common on nearby Great Bird Island where it lives among the scrub and sea grape leaves, free from predation. It also persists on Barbuda.

#### Family COLUBRIDAE

##### *Alsophis* cf. *A. antillensis* Schlegel

**MATERIAL.**—1 dentary, 1 pterygoid, 2 palatines, 715 vertebrae (USNM 340173–340180, 340198–340199). No meaningful estimate of MNI possible.

**REMARKS.**—These fossils are identified as *Alsophis* cf. *A. antillensis* because of their similarity to modern skeletons of that species from Montserrat (FSM 11369, 29785, 61072), Les Saints (FSM 61073), and Dominica (FSM 22261, 23118, 57816, 60805), and the fact that *A. antillensis antillensis* is the only colubrid snake known from Antigua. The single left pterygoid from Burma Quarry is missing the portion posterior

to the ectopterygoid process, but it is otherwise complete and is larger than any pterygoid examined in a modern skeleton of Lesser Antillean *Alsophis*. The length of the fossil is 9.4 mm. There are alveoli for 15 teeth, of which 2, 4, 6, 10, 11, and 13 are present. The base of the teeth have a proportionately greater circumference, and distally are less sharply recurved than those of the recent *A. antillensis* examined. In addition, the anterior edge of the ectopterygoid process meets at a more acute angle with the lateral edge of the bone, it being almost 90°. In the modern examples available, the angle is more obtuse and the entire bone anterior to the process is more rounded and deflected laterally.

The right palatine from Burma Quarry is complete, 9.0 mm in total length, and bears the anteriormost two teeth. The anterior portion of the left dentary is 0.5 mm long, and has two teeth in the middle of what remains of the tooth row. Neither of these fossils is appreciably larger than in the comparative skeletons. However, like the pterygoid, the teeth are more robust about their bases and less recurved.

The hundreds of fossil vertebrae are from all sections of the vertebral column and come from very small juveniles as well as large adults. The largest fossil vertebra has a centrum length of 5.3 mm, including condyle, and measures 10.5 mm across the tips of the prezygapophyses. By contrast, the smallest is a mere 2.4 mm across the prezygapophyses and has a centrum 1.2 mm in length. Nearly all of the fossil vertebrae fall into one or the other of these two discrete size classes, with approximately 15% being somewhere intermediate.

The vertebrae of very small *A. antillensis* have proportionately narrower and thinner neural spines than those of the adults, and the vertebral canal is nearly twice as large as the circumference of the centrum cotyle. The neural canal and cotyle of adults are nearly equal in size. In juveniles, the accessory processes are weakly developed, and overall there is less intra-vertebral variation in size and proportions.

*Alsophis antillensis* has had an erratic nomenclatural history. The name was first applied to certain populations of snakes from the Puerto Rican Bank islands of Vieques, St. Thomas, and St. John, as well as to forms from Martinique, Dominica, and Guadeloupe. Those from Puerto Rico are now regarded as subspecies of *A. portoricensis* (Schwartz, 1966). Schwartz (1966:183) credited Brongersma (1937) with restricting the name *A. antillensis* to the Lesser Antillean snakes, and in designating a specimen from Guadeloupe as the lectotype. However, a few years prior to Brongersma (1937), Parker (1933) described the only two known colubrid snakes (both juvenile females) from Antigua as *A. leucomelas antiguae*. Subsequently, he (Parker, 1936) provided additional information on the Antigua population from 24 additional specimens in the British Museum. Because of several characters of scutellation, notably the narrow frontal and low number of subcaudals, Parker (1936) then regarded the population as a full species, *A. antiguae*, and believed that its affinities were with the snakes immediately to the north on the islands of the Anguilla Bank (*Alsophis rijersmai*) and the St. Kitts Bank (*A.*

*rufiventris*). Brongersma (1937), however, made no mention of the Antiguan populations, nor of Parker's nomenclature, and he restricted his analysis of Lesser Antillean *Alsophis* to three specimens in the Leiden Museum that were originally described by Schlegel from Guadeloupe, Martinique and St. Thomas. In his review of Greater Puerto Rican *Alsophis*, Schwartz (1966:216) made mention of Parker's (1936) scale counts, and implied that Parker had regarded the snakes from Antigua as a race of *A. antillensis* (which had replaced the name *leucomelas*), whereas he actually had ranked them as full species. In either case, since Schwartz's review the snake from Antigua has been called *A. antillensis antiquae* (Schwartz and Thomas, 1975).

Parker's (1936) assessment of the affinities of the Antiguan snake with *A. rijersmai* and *A. rufiventris* to the north, rather than with other subspecies of *antillensis*, such as *A. a. manselli* of Montserrat or *A. a. sibonius* of Dominica, has merit because there are also some osteological similarities not shared with the southern forms. Both *A. a. antiquae* and the two northern forms have a pterygoid with a straighter medial border, and the teeth are more robust at the bases and less radically recurved, particularly in smaller individuals. Whether these are shared derived features or simply a consequence of size and individual variation is unclear. A systematic review of these taxa is certainly warranted.

*Alsophis antillensis antiquae* is known historically only from Antigua and its satellite Great Bird Island. Recently collected fossils also demonstrate that the species once occurred on Barbuda (Pregill, personal observation). Almost certainly the snake is extinct on Antigua, which was presumed over 50 years ago by Parker (1933). It may still exist on Great Bird Island; it was last collected there in the mid-1960s by Richard Thomas and J. D. Lazell (Lazell, 1967). We spent a day on this small, uninhabited cay during August 1980, and although no evidence of the snake was found, local residents on the adjacent mainland informed us that they had seen it there in recent years. Undoubtedly, the mongoose and feral cats have been instrumental in the elimination of the Antiguan population; these predators infest Antigua but are absent from Great Bird Island.

#### Family TYPHLOPIDAE

##### *Typhlops monastus* Thomas

MATERIAL.—5 vertebrae (USNM 340172). MNI = 3.

REMARKS.—Fossil vertebrae of West Indian typhlopoid snakes are identified by their very small size, depressed neural arches, and flattened centra. The specimens at hand are referred to *T. monastus* because of their similarity to modern skeletons, and the fact that the subspecies *T. m. geotomus* Thomas currently inhabits Antigua. The fossil vertebrae are all from the midbody and vary in size. The largest is 1.6 mm across the tips of the prezygapophyses, the smallest 0.9 mm. Two of the five specimens have a pair of median, subcentral foramina.

*Typhlops monastus* is a moderate-size blind snake attaining a maximum total length of 260 mm (Thomas, 1966). We collected this subspecies in scattered mesic and xeric localities on Antigua and its satellite, Great Bird Island. *Typhlops m. monastus* Thomas is restricted to Montserrat, whereas *T. m. geotomus* occurs both on the St. Kitts Bank and Antigua Bank.

#### Family cf. BOIDAE

##### Genus and Species Indeterminate

MATERIAL.—1 vertebra (USNM 340200).

REMARKS.—This curious small fossil vertebra consists of most of the neural arch and neural spine (Figure 13). Nothing remains of the centrum, nor of the arch laminae. On the arch itself the right posterior corner that includes the postzygapophysis and zygantrum is missing. Anteriorly, the zygosphenal arch is present but the prezygapophyses below are absent. The zygosphenal facets are directed ventrolaterally, 3.1 mm apart from one another. The bone is 3.1 mm wide, as measured from the front of the zygosphere to the posterior margin of the neural arch above the postzygapophysis. The neural arch is vaulted and fans out posteriorly to an estimated width of 6–8 mm, right corner broken. This vertebra is distinctly compressed anteroposteriorly. The left zygantrum is a deep, well-excavated socket occupying about half the length of the neural canal. From the horizontal facet of the postzygapophysis to the top of the neural spine the bone is 3.8 mm. The neural spine is 1.9 mm high and rises vertically from the neural arch. The dorsal midline of the neural arch is only 1.7 mm, and the thick base of the spine occupies practically all of this width. The spine is expanded dorsally, whence a faint cleft on the anterior and posterior surface divides it into a slightly bilobed cap.

We refer this fossil to the Boidae mostly by default. It has no features diagnostic of colubrids, and it certainly shares no

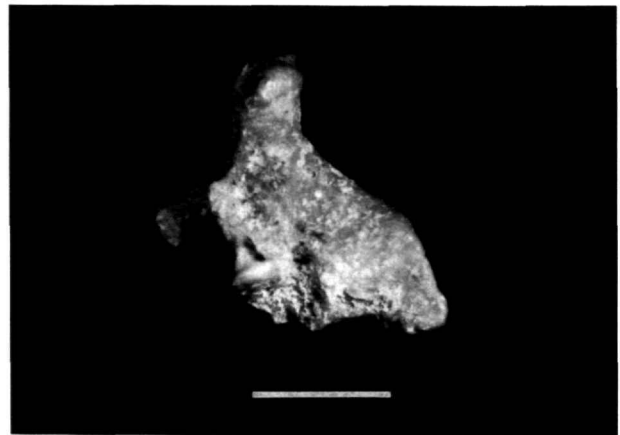


FIGURE 13.—Partial vertebra (USNM 340200) of an unidentified snake (cf. Boidae) in anterolateral aspect. Scale = 2 mm.



characters with West Indian xenodontines. The thick neural spine, expanded distally into a bilobed cap (slightly worn in the fossil), appears in a few scattered South American colubrids, *Nothopsis* for example (Bogert, 1964:521). This condition is more typical of the Boidae (Holman, 1967, 1979), yet the vertebra is not at all similar to either of the Antillean boids *Tropidophis* or *Epicrates* whose neural spines are broader and not as columnar. That of *Tropidophis* is hardly expanded and the capped spine of *Epicrates* is oblong. The neural spine of *Boa constrictor* is narrow and proportionately very tall.

The vertebra's small size and broad, horseshoe-shape zygosphenal arch suggests that it was from a juvenile. In most adult Henophidia and Caenophidia, the zygosphenes approximate each other on a flat, cantilevered shelf above the neural canal. The narrow profile of the fossil is also more typical of boids, although the cervical and anterior vertebrae of many snakes tend to be proportionately shorter than their width, further inhibiting identification. It was certainly frustrating to find that among the hundreds of snake vertebrae in the Burma Quarry deposits there was none other like this.

No boid snakes occur today in the Leeward Islands, although *Boa constrictor* has been found at the Indian Creek archeological site on Antigua (Table 9, and Steadman et al., 1984). In the West Indies *Epicrates* and *Tropidophis* are confined to the Greater Antilles; north of Grenada, *Boa constrictor* occurs only on Dominica and St. Lucia.

## BIRDS

Identifications of birds are by Steadman and Olson, based upon comparative material in the Division of Birds, National Museum of Natural History, Smithsonian Institution. Unless stated otherwise, we follow Holland and Williams (1978) and Steadman et al. (ms) for the modern distribution of birds on Antigua. Other important distributional references for Antigua birds are Cory (1891), Riley (1904), Danforth (1934), Bond (1956 and supplements, 1980a,b), and Hilditch et al. (1973).

### Order PROCELLARIIFORMES

#### Family PROCELLARIIDAE

##### *Puffinus lherminieri* Lesson

(Audubon's Shearwater)

MATERIAL.—Tarsometatarsus (USNM 338481). MINI = 1.

REMARKS.—The outer trochlea of the tarsometatarsus in *Puffinus lherminieri* is distinguished from that in other resident and formerly resident West Indian procellariids (*Pterodroma hasitata*, *P. caribbaea*, *P. cahow*) by its smaller size and its lack of a flange on the outer, plantar articulating surface. (No skeletons were available for *P. caribbaea*, which presumably would resemble *P. hasitata* in this regard, the two species frequently being regarded as conspecific.) Small size alone

distinguishes *Puffinus lherminieri* from the several other species of *Puffinus* that are known as rare, nonbreeding visitors in the West Indies.

We find no modern records of *P. lherminieri* from Antigua or any of its offshore islands, nor have we observed it there in life. Elsewhere in the West Indies, it nests on scattered islands from the Grenadines north to the Virgin Islands, and in the Bahamas. The scattered nature of its distribution in the West Indies suggests that the species probably had a more continuous range that has been fragmented in historic or prehistoric times. Bond (1980a:18) notes that this species nests "in burrows or in rock crevices," so it may be that it once nested in or near the Burma Quarry fissure itself. If not, it is likely that *P. lherminieri* once nested on the small islands adjacent to Antigua, such as Great Bird Island or Hell's Gate Island, where there seems to be plenty of suitable habitat.

*Puffinus lherminieri* has been reported from many paleontological and archeological sites in the West Indies, including the Mill Reef site (Wing et al., 1968) and Indian Creek site (Steadman, personal observation) on Antigua. These records, along with those from Barbuda (Brodkorb, 1963:246; Watters et al., 1984:403), suggest that *P. lherminieri* was widespread and perhaps common on the Antigua Bank during prehistoric times. Predation on nesting or roosting birds by humans and introduced rats may account for its apparent extirpation.

### Order RALLIFORMES

#### Family RALLIDAE

##### *Poliolimnas flaviventer* (Boddaert)

(Yellow-breasted Crake)

MATERIAL.—Tarsometatarsus (USNM 338479). Figure 14.

REMARKS.—We follow Olson (1970) in assigning the species *flaviventer* to *Poliolimnas* rather than *Porzana*. This tiny rail is in a size group that includes, among New World species, only *Laterallus jamaicensis*, *L. exilis*, *Micropygia schomburgkii*, *Coturnicops noveboracensis*, and *C. notata*. Of these species, only *L. jamaicensis* and *P. flaviventer* have been recorded anywhere in the West Indies. Tarsometatarsi were not available for *M. schomburgkii* (known from Costa Rica and tropical South America) or *C. notata* (tropical South America). These two poorly known species, unrecorded on any islands, have a tarsal size (Blake, 1977:508–509) that is similar to that of *P. flaviventer*. The Burma Quarry specimen resembles *P. flaviventer* in having a circular distal foramen in dorsal aspect (oblong in *L. jamaicensis*) and in being shorter (based on the hypotarsal ridge) than in *L. jamaicensis* or *L. exilis*. In addition, the trochleae and shaft are more robust in *L. exilis* and *C. noveboracensis* than in the Burma Quarry specimen or in modern skeletons of *P. flaviventer* and *L. jamaicensis* (Table 4).

*Poliolimnas flaviventer* is known today from the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) and the

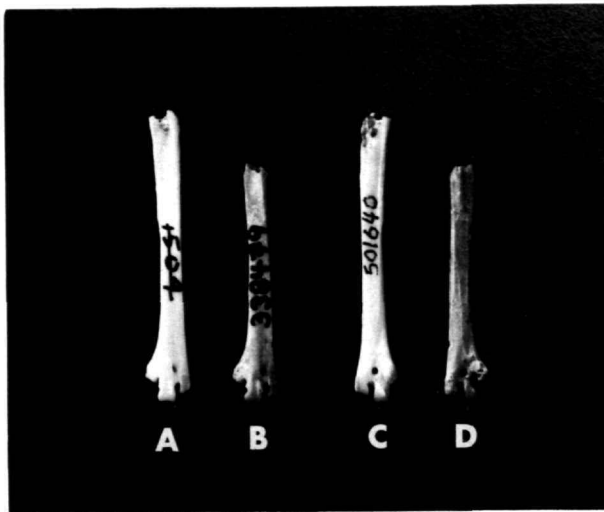


FIGURE 14.—Incomplete tarsometatarsi of *Poliolimnas flaviventer* in cranial (A,B) and caudal (C,D) aspects: A,C, modern specimen from Veracruz, Mexico (USNM 501640); B,D, fossil from Burma Quarry (USNM 338479).  $\times 2$ .

tropical lowlands of mainland Central and South America. Its occurrence in Antigua approximately 4300 years ago suggests that its distribution in mid-Holocene times included at least some of the Lesser Antilles. The Yellow-breasted Crake lives mainly in freshwater swamps, but little detail is known of its habits or habitat. The following account by Barbour (1923:55) is interesting in suggesting that this species, at least in Cuba, requires extensive swampy tracts.

The little Yellow Rails simply swarm in lake Ariguanabo and in the ponds of the Cienaga, although they always have been considered really rare and few birds have been less well represented in collections.

I owe my fine series to having learned by chance that they live far from shore in the extensive bonnet-beds. When frightened, they hop into one of the

TABLE 4.—Measurements (mm) of the tarsometatarsus of several small species of New World rails.

Specimen	Distal width	Least width of shaft
<i>Poliolimnas flaviventer</i>		
USNM 338479 (Burma Quarry fossil)	3.3	1.5
USNM 501640 (female, Veracruz)	3.2	1.6
<i>Laterallus jamaicensis</i>		
USNM 502495 (male, Florida)	3.2	1.6
USNM 492195 (male, Maryland)	3.2	1.7
<i>Laterallus exilis</i>		
USNM 511205 (male, Brazil)	3.5	1.8
<i>Coturnicops noveboracensis</i>		
USNM 343642 (male, Michigan)	3.5	1.7
USNM 343447 (sex?, North Carolina)	3.8	1.7
USNM 431601 (sex?, Louisiana)	3.4	1.7

big rolled-up bonnet leaves and stay there quietly until convinced that danger has passed. I have thus caught them in my hands. . . . I never have seen a single individual except where there were bonnet-beds, and I believe that they only frequent terra firma to build their nests and lay.

## Order CHARADRIIFORMES

### Family SCOLOPACIDAE

#### *Calidris* species

(indeterminate small sandpiper(s))

MATERIAL.—Carpometacarpus, tibiotarsus, sternum (USNM 330665, 338480). MNI = 3.

REMARKS.—These fossils, too fragmentary for species-level identification, probably represent two small species of *Calidris*. The sternum and carpometacarpus are closest in size to those of *C. mauri*, but may possibly represent a large individual of *C. pusilla*. The tibiotarsus is from a smaller bird, approximately the size of *C. minutilla* or a very small individual of *C. pusilla*. Each of these species occurs today in Antigua as migrants or winter residents. This is the first fossil record for *Calidris* in the West Indies.

## Order COLUMBIFORMES

### Family COLUMBIDAE

#### *Zenaida aurita* (Temminck)

(Zenaida Dove)

MATERIAL.—Femur, 2 tibiotarsi (USNM 330667). MNI = 1.

REMARKS.—*Zenaida aurita* may be distinguished from other Antiguan columbids by its size, being larger than *Columbina passerina* and smaller than *Columba squamosa*, *C. leucocephala*, *Geotrygon mystacea*, or *G. montana*. *Zenaida aurita* is very common and widespread on Antigua today. It has been reported from many paleontological and archeological sites throughout the West Indies, including the Mill Reef site (Wing et al., 1968) and the Indian Creek site (Steadman, personal observation) on Antigua.

#### *Columbina passerina* Linnaeus

(Common Ground Dove)

MATERIAL.—1 sternum, 10 coracoids, 1 scapula, 2 humeri, 4 ulnae, 7 carpometacarpi, 2 alar phalanges, 2 femora, 5 tibiotarsi, 3 tarsometatarsi (USNM 330653–330658, 338482). MNI = 11.

REMARKS.—*Columbina passerina* is readily identified by being much smaller than any other West Indian columbid. It is common today on Antigua in open or semi-open habitats whether these are natural or created by human activity. *C. passerina* has been reported from a number of paleontological and archeological sites in the Greater Antilles (Brodkorb, 1971:198). The only other fossil records for the Lesser Antilles

are from the Trant's site, Montserrat (Steadman et al., 1984) and the Indian Creek site, Antigua (Steadman, personal observation).

### Order STRIGIFORMES

#### Family STRIGIDAE

##### *Athene cucularia* (Molina)

(Burrowing Owl)

**MATERIAL.**—1 mandibular symphysis, 1 mandibular ramus, 1 sternum, 6 coracoids, 3 scapulae, 1 humerus, 6 ulnae, 2 ulnares, 2 carpometacarpi, 2 alar phalanges, 2 femora, 1 tibiotarsus, 2 fibulae, 10 tarsometatarsi, 20 pedal phalanges, 4 unguis phalanges (USNM 330646–330652, 338484, 338485). MNI = 13.

**REMARKS.**—The burrowing owl is the only owl recorded from Antigua. The only other small owl found anywhere near Antigua is *Otus nudipes* of Puerto Rico. Osteological distinctions between *Athene* and *Otus* have been outlined by Olson and Hilgartner (1982). In reviewing the past and present distribution of *A. cucularia* in the West Indies, Olson and Hilgartner (1982) note fossils from Jamaica, Barbuda, Mona, and Cayman Brac, four islands where the species no longer occurs. Wing et al. (1968) recorded *A. cucularia* from the Mill Reef site in southeastern Antigua.

The burrowing owls of Antigua belong to the recently extinct subspecies *A. c. amaaura*, also known from Nevis and St. Kitts. The only complete elements are a coracoid (length 24.4 mm) and two tarsometatarsi (length, 30.8, 41.8 mm; proximal width, 6.6, 6.3 mm; shaft width, 2.5, 2.7 mm; distal width, 7.0, 6.7 mm).

These owls became extinct on Antigua during the early part of this century, the last specimens having been collected by Cyrus S. Winch in 1890 (Cory, 1891). H.G. Selwyn Branch did not obtain any during several months of collecting birds on Antigua in 1903 (Riley, 1904). Danforth (1934:362) regarded the burrowing owl to be extinct on Antigua, noting the following.

It is said to have become extinct soon after the introduction of the mongoose, and only the old-timers among the residents can remember it. Mr. W. G. Heath gives me his recollections regarding it in the following words: 'As a boy I used to see the small Owls living in burrows in a road cutting of marl .... It appeared only at dusk. It was never very plentiful as far as I know.'

Holland and Williams (1978) imply incorrectly that Danforth recorded *A. cucularia* from Antigua. They go on to say (p. 1105): "Some local residents state they have seen owls [possibly barn owls (*Tyto alba*)?] up through the late 1950s, but there are no recent sightings."

*Athene cucularia* is the most abundant bird in the Burma Quarry fauna. Certain smaller taxa in the fauna may represent the prey remains of burrowing owls that lived in or near the crevice during the time of sediment infilling (see "Stratigraphy and Chronology"). In turn, the remains of burrowing owls at

Burma Quarry could have been deposited as the prey remains of barn owls (*Tyto*).

### Order TROCHILIFORMES

#### Family TROCHILIDAE

##### *Orthorhynchus cristatus* (Linnaeus)

(Antillean Crested Hummingbird)

**MATERIAL.**—Coracoid (USNM 330666). MNI = 1.

**REMARKS.**—*Orthorhynchus cristatus* is distinguished from the other two species of hummingbirds on Antigua by its much smaller size. The species is common and widespread on Antigua today. This is only the fourth published record of fossil hummingbirds, each from a late Quaternary cave deposit: Olson and Hilgartner (1982) reported *Chlorostilbon ricordii* and another indeterminate genus and species from New Providence, Bahamas; Bernstein (1965) reported *Anthracothorax dominicus* from the Dominican Republic; and Winge (1888) reported an indeterminate trochilid from Brazil. The *Chlorostilbon* from New Providence was later suggested as being referable to the historically extinct endemic species *C. bracei* (Graves and Olson, 1987).

### Order PASSERIFORMES

#### Family TYRANNIDAE

##### *Tyrannus cf. T. dominicensis* (Gmelin)

(Grey Kingbird)

**MATERIAL.**—Coracoid (USNM 330668). MNI = 1.

**REMARKS.**—Large size distinguishes the coracoid of *T. dominicensis* from that of all other Lesser Antillean tyrannids, including that of *T. caudifasciatus*, which occurs in the Greater Antilles east to Vieques. The fragmentary specimen from Burma Quarry, however, is not adequate for an unequivocal identification.

The Grey Kingbird is common on Antigua today. It has been reported from fossil sites only in Puerto Rico (Wetmore, 1922).

#### Family MIMIDAE

##### *Margarops fuscatus* (Vieillot)

(Pearly-eyed Thrasher)

**MATERIAL.**—1 furcula, 2 coracoids, 1 scapula, 1 humerus, 1 ulna, 3 radii, 1 ulnare, 2 carpometacarpi, 1 synsacrum, 1 pelvis, 1 tibiotarsus, 3 tarsometatarsi, 3 unguis phalanges (USNM 330659–330662, 338486, 338487). MNI = 2.

**REMARKS.**—The skeletal elements of *M. fuscatus* are consistently larger than those of other Antillean mimids. *Margarops fuscatus* is very restricted in its range on Antigua today, being confined to forested hills in the volcanic southwestern part of the island. The fossils show that *M.*

*fuscatus* probably occurred throughout Antigua before the limestone forest of the lowlands was destroyed. Danforth (1934) observed this species at English Harbour, near the south-central coast, where it probably does not occur today. Thus a small portion of the range contraction of *M. fuscatus* on Antigua has occurred during this century, although most of it doubtless occurred during the extensive clearing of the lowlands for sugar cane in the 18th and 19th centuries.

Elsewhere in the West Indies, *M. fuscatus* has been reported from paleontological sites in Puerto Rico (Wetmore, 1922 [this record may be erroneous, however, Olson, pers. obs.]) and the Trant's archeological site in Montserrat (Steadman et al., 1984). The supposed Pleistocene record of *M. fuscatus* from Great Exuma Island, Bahamas (Wetmore, 1937), has been corrected by Olson and Hilgartner (1982), who refer these specimens to the Icteridae, probably *Sturnella* sp.

*Cincloertheria ruficauda* (Gould)

(Trembler)

**MATERIAL.**—Combined tailings: 1 quadrate, 3 mandibles, 1 tibiotarsus (USNM 330664). MNI = 1. Figure 15.

**REMARKS.**—We compared these specimens to those of other resident and migrant West Indian turdids and mimids except *Mimus magnirostris*, *Ramphocinclus brachyurus*, *Turdus fumigatus*, *T. swalesi*, and *T. ravidus*, of which only *R. brachyurus* of Martinique and St. Lucia occurs anywhere near Antigua. The fossils agree with the quadrate, mandible, and tibiotarsus of the monotypic genus *Cincloertheria* in being much larger than those in *Dumetella carolinensis*, *Catharus ustulatus*, *C. minimus*, *C. fuscescens*, *Sialia sialis*, *Myadestes elizabeth*, or *M. genibarbus*. In *Margarops fuscatus* and *Cichlherminia therminieri* these elements are larger than in the fossils. Further distinctions for each fossil element are as follows. Quadrate: smaller than in *Margarops fuscus* or *Turdus plumbeus*; main body of quadrate more gracile than in any species of *Turdus*; and distal end of orbital process more expanded than in any species of *Mimus*. Mandible: larger than in *Mimus polyglottos*, *M. gilvus*, *Margarops fuscus*, *Turdus migratorius*, *T. nudigenis*, *T. jamaicensis*, or *T. aurantius*; in lateral aspect, postarticular process aligned more in the plane of the ramus (less perpendicular to the ramus) than in all species of *Mimus* or *Turdus*. Tibiotarsus: shorter shaft than in *Mimus gundlachii*, *Margarops fuscus*, *Turdus migratorius*, *T. plumbeus*, or *T. aurantius*; stouter than in *Mimus polyglottos*, *M. gilvus*, *Turdus nudigenis*, or *T. jamaicensis*.

This is the first authentic record of *C. ruficauda* from Antigua. Although Holland and Williams (1978) reported a sight record of a Trembler from the Wallings Reservoir region of southwestern Antigua, Bond (1980b:13) regarded this and many other of their observations to be "highly questionable." We concur, and would also note that the similarly sized *Margarops fuscus*, which is common in forested parts of Antigua, often shakes or "trembles" its wings and tail in a

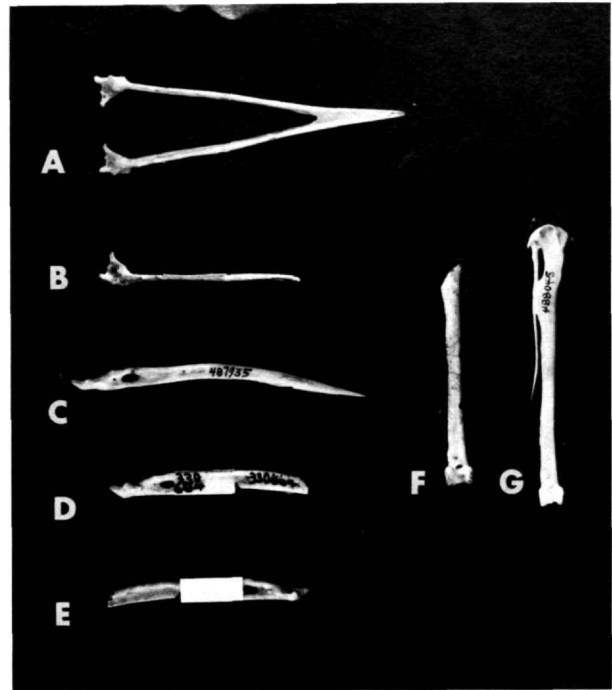


FIGURE 15.—Mandibles (left) and tibiotarsi (right) of *Cincloertheria ruficauda*: A,C, modern specimen from Dominica (USNM 487935) in dorsal and lateral aspects; B,D,E, fossil from Burma Quarry (USNM 330664) in dorsal, lateral, and medial aspects; F, fossil from Burma Quarry (USNM 330664) in cranial aspect; G, modern specimen from Dominica (USNM 488045) in cranial aspect. Natural size.

manner reminiscent of, although not identical to, that of the Trembler. If Tremblers had been resident on Antigua for the past 100 years, it is likely that one would have been collected.

The Trembler is endemic to the Lesser Antilles, ranging from Saba, St. Eustatius, St. Kitts, Nevis, Montserrat, and Guadeloupe south through St. Vincent. It is not known to have occurred on the Anguilla Bank (Anguilla, St. Martin, St. Bartholomew) or, until this report, on the Antigua Bank (Antigua, Barbuda). The species shows adaptations for arboreal feeding and is most abundant in "optimal rain forest" (Zusi, 1969:162), although Bond (1980a:170) states that it may also be "found sparingly in secondary growth and drier woodland." Our own field experience with Tremblers is confined to St. Kitts and Montserrat, where it seems to be found strictly in, or at the edge of, wet forests, regardless of elevation. The record of *C. ruficauda* from Burma Quarry indicates the probable presence of a well-structured, canopied forest in northern Antigua at the time of fossil deposition. No such forest occurs today anywhere in the lowlands of Antigua, except perhaps for small, isolated patches at Santa Maria Hill and at Ayres Creek just north of Gaynors Mill. Remains of the Trembler may well be expected in other paleontological or archeological sites on the Antigua or the Anguilla Banks.

The only other prehistoric record of *C. ruficauda* is from the Trant's archeological site, Montserrat (Steadman et al., 1984).

#### Family FRINGILLIDAE

##### *Loxigilla noctis* (Linnaeus)

(Lesser Antillean Bullfinch)

**MATERIAL.**—1 mandibular symphysis (USNM 330663). MNI = 1.

**REMARKS.**—The mandible of *L. noctis* is easily distinguished from that of the only other emberizine of the region, *Tiaris bicolor*, by its greater size. Likewise, it is much smaller than that of *L. grandis* of nearby St. Kitts. Bullfinches are of little use in paleoenvironmental interpretations, for they are very common today on Antigua in a variety of natural and disturbed habitats.

This is the first fossil record for *L. noctis*, a species that occurs essentially throughout the Lesser Antilles.

#### Order PASSERIFORMES, Species Indeterminate

**MATERIAL.**—27 specimens (USNM 338488–338490). MNI is indeterminate.

**REMARKS.**—Postcranial elements of small passerines, particularly many of the New World 9-primaried oscines, may be impossible to distinguish at even the familial level (Olson and Hilgartner, 1982:51; Steadman, 1982). Among the 27 specimens noted above, 9 are from birds larger than *Loxigilla noctis*, 14 are equal to that species in size, and 4 are from a smaller species that must represent a taxon otherwise unrecognized from Burma Quarry, such as *Coereba flaveola*, *Tiaris bicolor*, or a variety of paruline warblers.

#### Indeterminate Bird

**MATERIAL.**—72 specimens. MNI is indeterminate.

**REMARKS.**—These often fragmentary specimens consist mainly of vertebrae, ribs, and pedal phalanges.

#### MAMMALS

The rodents were studied by Steadman, and the bats by Grady, with assistance from Linda K. Gordon, Karl F. Koopman, Gary S. Morgan, and Steadman. We used the comparative skulls and skeletons in the Division of Mammals, National Museum of Natural History, Smithsonian Institution, supplemented by fossils and/or skeletons from the Florida State Museum and American Museum of Natural History. Modern and fossil distributions of bats are from Varona (1974), Baker and Genoways (1978), and Silva Taboada (1979).

At least four of the species of bats in the Burma Quarry fauna (*Brachyphylla cavernarum*, *Natalus stramineus*, *Tadarida brasiliensis*, *Molossus molossus*, and probably *Monophyllus*)

still live on Antigua. These species account for 97% of the individuals in the deposit. Three other species, previously known only from the Greater Antilles, are now extinct on Antigua. These are *Pteronotus parnellii*, *Mormoops blainvillei*, and *Phyllonycteris* cf. *P. major*. All of the bats recorded from Burma Quarry are known or suspected cave dwellers.

#### Order CHIROPTERA

##### Family MORMOOPIDAE

##### *Pteronotus parnellii* (Gray)

**MATERIAL.**—1 mandible, 1 humerus, 1 radius (USNM 338534). MNI = 1.

**REMARKS.**—The mandible was identified on the basis of overall shape, the tooth count, and the very small P3 (Figure 16A). The distal end of the humerus has a very rounded medial condyle and a large, pointed ectepicondylar process. *Pteronotus parnellii* is confined today to the Greater Antilles. This is the first record, fossil or modern, from the Lesser Antilles. The nearest modern record of *P. parnellii* is from Puerto Rico. The species is also known from the late Pleistocene of the Bahamas (Olson and Pregill, 1982).

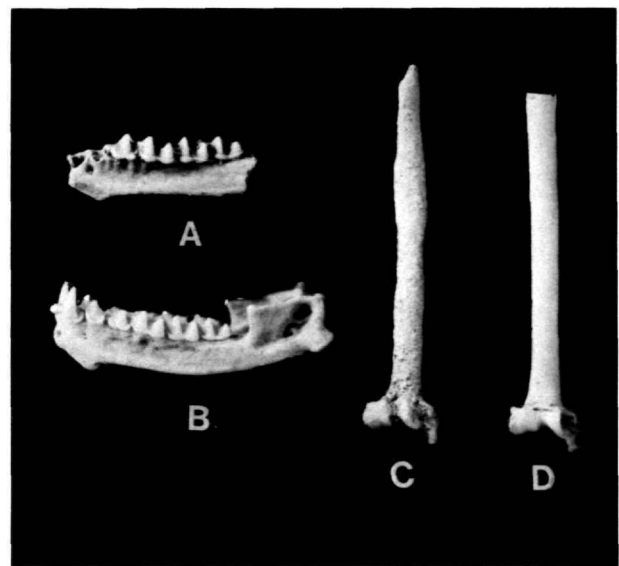


FIGURE 16.—A, Fossil mandibular fragment (USNM 338534) of *Pteronotus parnellii* from Antigua; B, modern mandible (USNM 535249) of *P. parnellii* from Hispaniola; C, fossil humerus (USNM 338535) of *Mormoops blainvillei* from Antigua; D, modern humerus (USNM 545146) of *M. blainvillei* from Jamaica.  $\times 2$ .



***Mormoops blainvillei* Leach**

MATERIAL.—2 humeri (USNM 338535). MNI = 2.

REMARKS.—The distal end of the humerus in *Mormoops* is very distinctive in its "hourglass" shape and the very long, pointed ectepicondylar process (Figure 16c). Small size refers the specimens to *M. blainvillei*, a species that has never before been reported from Antigua, or anywhere else in the Lesser Antilles. We also found unstudied fossils of *M. blainvillei* from fossil sites on Barbuda collected by the Florida State Museum. As with *Pteronotus parnellii*, the nearest modern occurrence of *M. blainvillei* is in Puerto Rico.

**Family PHYLLOSTOMATIDAE****?*Monophyllus* species**

MATERIAL.—2 mandibles, 1 questionably referred humerus (USNM 338536, 338537). MNI = 2.

REMARKS.—The shape of the mandibles, and the number and spacing of the alveoli, refer this material to *Glossophaga* or *Monophyllus*. The depth of the mandibles behind M3 is 2.4 mm, which is greater than in any specimens of either genus, although approached by some specimens of *Glossophaga longirostris* from Grenada. *Monophyllus plethodon* is known from Antigua, whereas *Glossophaga longirostris* is recorded only from several of the southern Lesser Antilles. Another species of *Glossophaga*, *G. soricina*, is known from Jamaica and the Bahamas. In addition, a large extinct subspecies of *Monophyllus*, *M. redmani frater*, has been described from Quaternary fossils from Puerto Rico (Anthony, 1917).

***Brachyphylla cavernarum* Gray**

MATERIAL.—20 mandibles, numerous isolated teeth and fragmentary postcranial elements (USNM 338520–338530). MNI = 13.

REMARKS.—The mandibles and teeth resemble 14 modern specimens of *B. cavernarum* from Antigua. The six humeri from Burma Quarry are inseparable from a modern specimen from St. Vincent (USNM 106082). *B. cavernarum* inhabits Puerto Rico and most of the Lesser Antilles, including Antigua.

***Phyllonycteris* cf. *P. major* Anthony**

MATERIAL.—3 mandibles, 4 humeri (USNM 338531–338533). MNI = 4.

REMARKS.—The mandible and humerus of *Phyllonycteris* are easily distinguished from those of other West Indian bats (Figure 17). The mandibles are identified by the following suite of characters: overall slenderness, coronoid process set at approximately 45° to ramus of jaw, distinct diastema between last molar and coronoid, and M2–M3 lacking distinct cusps (Koopman and Williams, 1951; Hall, 1981:171–172). The humerus of *Phyllonycteris* has a cylindrical distal end with a

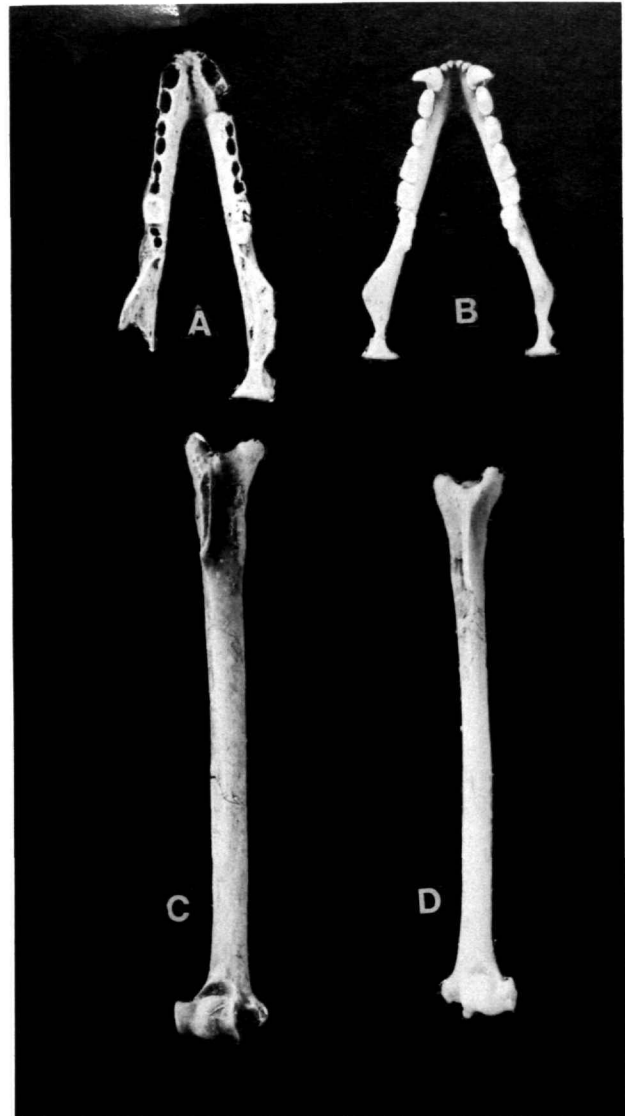


FIGURE 17.—A,C, mandible and humerus (USNM 338531) of the extinct bat *Phyllonycteris major* from Antigua (previously known only from fossil deposits on Puerto Rico); B,D, mandible and humerus (USNM 538349) of the extant species *P. poeyi* from Hispaniola.  $\times 2$ .

rounded medial condyle that runs parallel to the shaft. The ectepicondylar process is a blunt knob. Based upon size alone, these specimens resemble *P. major* most closely, although no measurements are available for *P. aphylla*, a Jamaican endemic. The Burma Quarry specimens are larger than *P. poeyi* or *P. obtusa* in mandibular as well as humeral dimensions (Tables 5, 6).

*Phyllonycteris* is confined today to the Greater Antilles, with endemic species on Cuba (*P. poeyi*), Jamaica (*P. aphylla*), and Hispaniola (*P. obtusa*). *Phyllonycteris major* is known only from Quaternary fossils from Puerto Rico, and apparently was

TABLE 5.—Measurements (mm) of mandibles of *Phyllonycteris* (? = unknown; CA = canine alveolus; dash = measurement not obtainable).

Catalog number	Sex	Total length	CA to M3
<i>Phyllonycteris poeyi</i> (Cuba)			
USNM 103583	F	15.6	8.7
USNM 103582	F	15.0	8.6
USNM 103581	M	15.0	8.9
USNM 103580	F	15.9	8.9
USNM 103579	M	16.4	9.1
USNM 103578	?	15.9	8.8
USNM 103577	?	15.6	8.6
USNM 103576	?	16.2	—
<i>Phyllonycteris obtusa</i> (Dominican Republic)			
USNM 538349	F	15.3	8.6
USNM 535324	F	15.5	8.6
USNM 535319	F	15.7	8.6
USNM 535325	M	15.9	8.6
USNM 535320	F	15.4	8.2
USNM 535293	M	15.8	8.7
<i>Phyllonycteris major</i> (Puerto Rico)			
KU <sup>1</sup>	?	17.6–18.6	—
AMNH 40933 <sup>2</sup>	?	18.1	—
AMNH 40934	?	17.6	—
<i>Phyllonycteris cf. major</i> (Antigua)			
USNM 338531	?	17.8	9.8
USNM 338531	?	—	9.3

<sup>1</sup>University of Kansas; Choate and Birney (1968), no catalog numbers given.

<sup>2</sup>Anthony, 1925.

a smaller species than *P. aphylla* (Anthony, 1917, 1918, 1923; Choate and Birney, 1968; Koopman and Williams, 1951).

#### Family NATALIDAE

#### *Natalus stramineus* Gray

MATERIAL.—264 mandibles, numerous other cranial and postcranial elements (USNM 338491–338510, 338547). MNI = 138.

REMARKS.—This small, insectivorous bat is by far the most abundant chiropteran in the Burma Quarry fauna. The only vertebrate to occur in greater numbers is the lizard *Anolis bimaculatus leachi*. The Burma Quarry fossils of *N. stramineus* are inseparable from modern specimens from Dominica and are smaller than in *N. major* from Dominican Republic.

TABLE 6.—Measurements (mm) of humeri of *Phyllonycteris* (? = unknown; PW = proximal width; DW = distal width; dash = measurement not obtainable).

Catalog number	Sex	Length	PW	DW
<i>Phyllonycteris poeyi</i> (Cuba)				
USNM 535219	F	29.2	3.6	4.3
USNM 538349	F	28.2	3.7	4.0
<i>Phyllonycteris obtusa</i> (Dominican Republic)				
USNM 49565	F	27.7	3.8	4.1
USNM 49568	F	27.7	3.9	4.4
USNM 103445	?	28.7	3.9	4.4
<i>Phyllonycteris cf. major</i> (Antigua)				
USNM 338531a	?	30.6	3.9	4.6
USNM 338531b	?	—	3.9	—
USNM 338532	?	—	—	4.2
USNM 338533	?	—	—	4.2

TABLE 7.—Measurements (mm) of humeri of *Natalus stramineus* (? = unknown; numbers in parentheses indicate number of individuals in a series with the same catalog number).

Catalog number	Sex	Length
Dominica		
USNM 113604	?	20.6
USNM 362100	F	20.9
USNM 362101	F	21.3
USNM 362102	F	21.9
USNM 362103	M	21.1
USNM 362104	M	20.4
Antigua		
USNM 338509(1)	?	22.2
USNM 338509(2)	?	22.4
USNM 338509(3)	?	21.8
USNM 338509(4)	?	21.7
USNM 338509(5)	?	21.8
USNM 338509(6)	?	21.2
USNM 338509(7)	?	21.5

Although the fossil humeri average slightly larger than in modern specimens (Table 7), only one of the fossils exceeds the range of the modern sample.

*Natalus stramineus* occurs today on Antigua, as well as Anguilla, Saba, Montserrat, and Dominica. The closely related *N. major* is known only from the Greater Antilles.

**Family TADARIDAE**

***Tadarida brasiliensis* (I. Geoffroy)**

**MATERIAL.**—4 mandibles, 3 humeri (USNM 338511–338513). **MNI** = 6.

**REMARKS.**—The mandibles of *T. brasiliensis* are readily distinguished from those of the closely related *Molossus molossus* in being more slender and having a larger mental foramen. The medial condyle of the humerus in *T. brasiliensis* protrudes more distinctly from the shaft than in the closely related *Molossus molossus*.

*Tadarida brasiliensis* occurs today on Antigua and most other Lesser Antillean islands.

**Family MOLOSSIDAE**

***Molossus molossus* (Pallas)**

**MATERIAL.**—5 mandibles, 2 maxillae, 9 humeri (USNM 338514–338519). **MNI** = 6.

**REMARKS.**—The Burma Quarry fossils of *M. molossus* do not differ from modern specimens. The only nearly complete fossil mandible measures 11.0 mm in length, compared to 10.5–11.9 mm for specimens from Antigua and Barbados (**N** = 8).

*Molossus molossus* occurs throughout the Antilles.

**Order CHIROPTERA, Species Indeterminate**

**MATERIAL.**—Approximately 170 specimens (USNM 338538–338546). **MNI** is indeterminate.

**REMARKS.**—Although lacking diagnostic features, most of these fragmentary specimens represent a small bat, such as *Natalus stramineus*.

**Order RODENTIA**

**Family MURIDAE**

**Subfamily CRICETINAE**

**Tribe ORYZOMYINI species**

(undescribed rice rat)

**MATERIAL.**—42 cranial fragments, 8 maxillae, 12 mandibles, 88 molars, 121 incisors, 590 postcranial bones (USNM 330602–330618, 330621–330624, 330626, 330626, 330628–330645, 338548, 338549). **MNI** = 47.

**REMARKS.**—This undescribed species of large oryzomyine rodent is known from archeological and paleontological sites on Barbuda, Antigua, Montserrat, Guadeloupe, and Marie Galante (Wing et al., 1968; Wing, 1973; Steadman et al., 1984; Watters et al., 1984). It is the species reported as “undescribed species B” from Montserrat and Barbuda by Steadman et al. (1984) and Watters et al. (1984). Nearly all of the rodent bones from Burma Quarry appear to represent this species; however,

three distinct sizes of femora are present in the assemblage. The largest of these agree with “undescribed species B.” Thus one or two smaller species of rodents also may have occurred on Antigua. On Montserrat, Steadman et al. (1984) reported a smaller species (“undescribed species A”) in addition to the present species. Limited material from Montserrat suggests the presence of two other rodents, one larger than either species A or B, and the other smaller.

The radiation of cricetine rodents in the Lesser Antilles remains poorly documented. Pending a comprehensive study of the entire radiation, the taxonomy and systematic relationships of the species from Burma Quarry cannot be treated in further detail.

**Discussion**

Much of the historic impact by humans on the flora and fauna of Antigua has been reviewed by Harris (1965). Our work extends the faunal record into prehistoric times and adds numerous species that have been lost from the island. The Burma Quarry sediments contain nine species of vertebrates that were not recorded in the historic period on Antigua; these make up 33% of the total number of vertebrate species in the fossil fauna (Tables 8 and 9). To these may be added the apparent local extinction of two land crabs, *Cardisoma* and *Gecarcinus*.

Additional extinct vertebrates have been recorded from archeological sites on Antigua (Table 9) at Indian Creek and Mill Reef, two large ceramic cultural sites (Figure 3). The former ranges in age from 1915±80 years BP to 845±80 years BP (Rouse and Allaire, 1978), and the latter from approximately 1450 to 800 years BP (Wing et al., 1968). Bones from these sites include species such as the agouti (*Dasyprocta agouti*) that were certainly brought to Antigua from South America by Amerindians, and others, such as the boa (*Boa constrictor*) and parrot (*Amazona* sp.), that may also have been brought by man from there or from other islands in the Antilles. The bones of manatee (*Trichechus manatus*) and flamingo (*Phoenicopterus ruber*) suggest resident populations, although neither has been recorded from Antigua, even as a vagrant, in historic times.

Some species are known to have become extinct on Antigua during the historic period. The burrowing owl (*Athene cunicularia*), as mentioned above, disappeared in the late 1800s; the lizard *Ameiva griseoides* and snake *Alsophis antillensis* have been effectively eliminated from Antigua in this century and now persist only on outlying islets. An endemic subspecies of butterfly, *Papilio polydamas antiquus*, is known only from a painting made in 1770, according to Rothschild and Jordan (1906:517). They also commented (1906:517) that “on the continents and the Greater Antilles the species is very common in open ground, while it is decidedly rare on the Lesser Antilles, having perhaps become rare in consequence of extensive cultivation of the soil.”

It is difficult to distinguish the relative importance of

TABLE 8.—Distribution of vertebrates in the Burma Quarry site, by arbitrary levels (in m) (numbers are minimum number of individuals (MNI) based on an assumption that there is no overlap in individuals between the arbitrary levels; + indicates present, although MNI was not calculated for lack of paired elements, not included in totals; dash indicates absent. See Figure 8 for the relative positions of the units).

Taxon	Upper Vertical Unit			East Horizontal Unit				West Horizontal Unit		Lower Vertical Unit		Tailings	Total
	1.7-2.8	1-1.7	0-1	3-3.8	2-3	1-2	0-1	0-1	1-2	0-0.7	0.7-1		
	<b>AMPHIBIANS</b>												
<i>Eleutherodactylus johnstonei</i>	-	-	-	2	-	3	3	1	4	-	-	12	23
<b>REPTILES</b>													
<i>Thecadactylus rapicauda</i>	-	-	1	1	-	2	3	1	5	2	2	18	35
<i>Anolis</i> spp.	-	1	6	16	3	15	32	8	34	45	55	198	413
<i>Leiocephalus cuneus</i>	-	-	-	-	-	1	1	1	1	1	1	7	13
<i>Ameiva griswoldi</i>	-	-	-	-	-	1	-	-	1	1	1	4	8
<i>Alsophis</i> cf. <i>A. antillensis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Typhlops monastus</i>	-	-	-	-	-	-	1	-	1	-	-	1	3
cf. <i>Boidae</i>	-	-	-	-	-	-	-	-	-	1	-	-	1
<b>BIRDS</b>													
<i>Puffinus lherminieri</i>	-	-	-	-	-	-	-	-	-	1	-	-	1
<i>Poliolimnas flaviventer</i>	-	-	-	-	-	-	-	-	-	1	-	-	1
<i>Calidris</i> sp.	-	-	-	-	-	-	-	-	-	1	-	2	3
<i>Zenaida aurita</i>	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Columbina passerina</i>	-	-	-	1	-	1	1	-	-	1	1	6	11
<i>Athene cucularia</i>	-	1	-	1	1	1	1	-	1	2	1	4	13
<i>Orthorhynchus cristatus</i>	-	-	-	-	-	-	-	-	-	-	-	1	1
cf. <i>Tyrannus dominicensis</i>	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Margarops fuscatus</i>	-	-	-	1	1	-	1	-	-	1	1	1	6
<i>Cincloerthia ruficauda</i>	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Loxigilla noctis</i>	-	-	-	-	-	-	-	-	-	-	-	1	1
<b>MAMMALS</b>													
<i>Pteronotus parnellii</i>	-	-	-	-	-	-	-	-	-	1	-	-	1
<i>Mormoops blainvillei</i>	-	-	-	-	-	-	-	-	-	1	-	-	1
<i>Glossophaga/Monophyllus</i>	-	-	-	-	-	-	-	-	-	-	-	2	2
<i>Brachyphylla cavernarum</i>	-	-	-	-	-	1	1	2	1	1	1	18	25
<i>Phyllonycteris</i> cf. <i>P. major</i>	-	-	-	-	-	-	1	-	-	1	-	2	4
<i>Natalus stramineus</i>	2	1	1	7	2	7	7	9	24	9	10	59	138
<i>Tadarida brasiliensis</i>	-	-	-	-	-	-	-	-	-	4	1	1	6
<i>Molossus molossus</i>	-	-	-	-	1	-	1	-	-	1	1	5	9
<i>Oryzomyini</i> sp.	3	2	3	3	1	2	3	2	2	4	2	20	47
<b>TOTAL</b>	<b>5</b>	<b>5</b>	<b>11</b>	<b>32</b>	<b>9</b>	<b>34</b>	<b>54</b>	<b>24</b>	<b>74</b>	<b>79</b>	<b>77</b>	<b>365</b>	<b>769</b>

prehistoric versus historic events in extinctions on Antigua. The degree of habitat modification by prehistoric peoples is poorly known, and the fossil record for the past several thousand years is incomplete. The occurrence of fossils of an extinct species in the Burma Quarry deposits does not mean that that species did not persist into the historic period even though no historic records of it exist. As noted above, species of the iguanid lizard *Leiocephalus* persisted into post-Columbian time on several Lesser Antillean islands, but only one of these species was collected before becoming extinct.

As we emphasized in our initial report on Burma Quarry

(Steadman, Pregill and Olson, 1984), it is likely that many more islands in the West Indies and elsewhere in the world will be shown to have suffered appreciable habitat degradation and faunal extinction as a result of human settlement. For ecological modeling, biogeography, and conservation, this likelihood confounds the ability to make meaningful generalizations about processes of insular evolution.

Deposits such as those at Burma Quarry are an overlooked source of both faunal and archeological data. Traditional vertebrate paleontology probably would have dismissed such a site as being of little importance because of its geologically

TABLE 9.—Extinct vertebrates on the main island of Antigua (identifications from Burma Quarry and Indian Creek are our own; those from Mill Reef are from Wing et al., 1968; \* totally extinct species; x present; dash absent).

Taxon	Burma Quarry	Indian Creek	Mill Reef	Historic Record or Specimen
<b>REPTILES</b>				
<i>Leiocephalus cuneus</i> (curly-tailed lizard)*	x	—	—	—
<i>Alsophis</i> cf. <i>A. antillensis</i> (ground snake)	x	—	x	x
cf. <i>Boa constrictor</i> (boa constrictor)	—	x	—	—
cf. Boidae (unknown boid snake)*	x	—	—	—
<b>BIRDS</b>				
<i>Puffinus lherminieri</i> (Audubon's Shearwater)	x	x	x	—
<i>Poliolimnas flaviventer</i> (Yellow-breasted Crane)	x	—	—	—
<i>Porphyryla martinica</i> (Purple Gallinule)	—	x	x	—
<i>Phoenicopterus ruber</i> (Greater Flamingo)	—	—	x	—
<i>Amazona</i> sp. (parrot)*(?)	—	x	x	—
<i>Athene cunicularia</i> (Burrowing Owl)	x	—	—	x
<i>Cinlocerthia ruficauda</i> (Trembler)	x	—	—	—
<b>MAMMALS</b>				
<i>Pteronotus parnellii</i> (bat)	x	—	—	—
<i>Mormoops blainvillei</i> (bat)	x	—	—	—
<i>Phyllonycteris</i> cf. <i>major</i> (bat)*	x	—	—	—
<i>Oryzomyini</i> sp. (rice bat)*	x	x	x	—
<i>Trichechus manatus</i> (manatee)	—	—	x <sup>1</sup>	—

<sup>1</sup>Identified from the Hawkes Bill Bay site rather than the Mill Reef site (Wing et al., 1968).

recent age. Yet, as we have seen, even late Holocene sediments may be repositories of fossils documenting undescribed species, range extensions, extinctions, and paleoecological conditions. Equally, traditional archeology might disdain such a deposit because it contains too little cultural material to be of interest (Olson, 1982). However, it should not be forgotten that even a few traces of human presence in a controlled, datable stratigraphic context can provide positive evidence for at least the minimum age of human colonization of an island. In the case of Burma Quarry, this evidence corroborates that from prior archeological excavations on the island, whereas in other instances such evidence might well provide the only available information. There continues to be a great need to apply a paleontological approach to studies of both biogeography and anthropology on islands.



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