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## Quaternary Mammal Localities and Heptaxodontid Rodents of Jamaica

R. D. E. MACPHEE<sup>1</sup>

### ABSTRACT

Harold E. Anthony (1920a, 1920b) identified five species of fossil rodents in material he collected from Jamaican caves during 1919–1920. *Clidomys osborni*, *C. parvus*, *Speoxenus cundalli*, and *Spirodontomys jamaicensis* were referred to the endemic Antillean caviomorph family Heptaxodontidae; *Alterodon major* was compared with members of Octodontidae *sensu stricto* but never actually placed as to family. No other West Indian island has a native octodontid or an equivalent abundance of heptaxodontids. These facts could be used to support hypotheses to the effect that Jamaica was the locus of a major adaptive radiation of caviomorphs, or that it was an important way-station for mammals penetrating farther into the Caribbean. Neither hypothesis is justified, however, because Anthony's species list is decidedly oversplit. Although cheek teeth of Jamaican heptaxodontids display some degree of variability, postcranial bones recovered from the same sites do not. Measurement of tali and calcanei, for example, demonstrates that there are only two size clusters in the available sample. These phenae could represent two species of the same genus, or they could be the sexes of a single, highly dimorphic species. Investigation of variation in a few other

caviomorphs, including the Puerto Rican heptaxodontid *Elasmodontomys*, indicates that the phenae are best interpreted as different species. The larger species is *Clidomys osborni* (now including *Speoxenus cundalli*) and the smaller is *C. parvus* (now including *Spirodontomys jamaicensis*). The putative octodontid *Alterodon major* is based on a broken tooth; it is almost certainly heptaxodontid, and probably belongs in *C. osborni*. The genus *Clidomys* is defined and the distribution of Antillean Heptaxodontidae is briefly considered in light of dispersionist and vicariist concept of Caribbean biogeography.

Although several expeditions have prospected in Jamaica for fossil mammals, for the most part the deposits yielding such remains have not been adequately described, and none has been radiometrically dated. Described here are locations, major features, and faunas of several localities, including Wallingford Roadside Cave, Wallingford Main Cave, Sheep Pen, and Long Mile Cave. A chelonian shell sample from Wallingford Roadside Cave has a minimum date of 33,250 BP; this is the oldest published date for a mammal-bearing fossil site in the Caribbean, and proves that the heptaxodontids from the same site are truly Pleis-

<sup>1</sup> Assistant Professor, Department of Anatomy, Duke University Medical Center, Durham, North Carolina 27710.

tocene animals. At Long Mile Cave, bones drawn from unit 2, the layer believed to have yielded the jaw of the enigmatic primate *Xenothrix*, produced a date of 2145 BP. In view of the distinc-

tiveness of this primate, so recent a date is astounding. Unfortunately, no additional bones referable to *Xenothrix* have been found at this or any other fossil locality.

## INTRODUCTION

This paper has two purposes. The first is to present a survey of fossil land mammal localities in Jamaica, with notes on their ages and contained faunas. The second is to provide a revision of the Jamaican extinct large-bodied caviomorph rodents, members of family Heptaxodontidae. This is the third in a series concerned with the extinct land mammals of the Greater Antilles and their phylogenetic and biogeographical history (MacPhee and Woods, 1982; MacPhee, Woods, and Morgan, 1983).

Koopman and Williams (1951; Williams and Koopman, 1952; Williams, 1952) are responsible for the only existing correlative studies on mammalian fossil localities in Jamaica. Their work remains valuable, but as a result of more recent investigations it needs extension and updating. Beyond this, there are several additional reasons for presenting a survey of known localities at this time. First, not a single site report containing the accepted minimum of correct map location, physical description and faunal list has been published for any Jamaican fossil site which has yielded extinct land mammals, and only one such locality is sufficiently well identified to warrant inclusion in the "reliably located" category of the Jamaican Cave Register (Fincham, 1977). As a direct result of this inattention to detail, the whereabouts of several important localities is presently indeterminate. Secondly, with the publication of the first radiometric dates for any Jamaican land mammal fauna (table 3), it is vital to have adequate descriptions of sites and the position of remains within sites. Thirdly, and most important, Jamaica is still prime prospecting territory. According to the existing fossil record, Jamaica appears to have had fewer mammalian colonists than the other Greater Antilles, which is odd in view of the island's proximity to Central America. Whether appearance reflects reality in this case is essentially untested, since so few paleontologists

have collected in Jamaica. All known fossil sites are situated on the mid-Cenozoic limestone plateau that covers the central part of the island. Exploration should now extend to the Cretaceous inliers that have been exposed by erosion in several parts of the island; the flanks of some of them may have been sub-aerial for large portions of the Cenozoic (Weyl, 1966) and are probably the only places where truly ancient mammals may be found.

## ABBREVIATIONS

### INSTITUTIONAL

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History  
FSM and UF, Florida State Museum and University of Florida  
NRCD, Natural Resource Conservation Department, Ministry of Mining, Government of Jamaica

### DENTAL ABBREVIATIONS (see also fig. 6)

b-l, buccolingual  
D, deciduous (used in combination with L/UP4 to designate deciduous premolar)  
L/UP4, lower/upper fourth premolar  
L/UM1-3, lower/upper first-third molar  
m-d, mesiodistal

### STATISTICAL SYMBOLS

CV, coefficient of variation (in %)  
 $S_{cv} (\pm)$ , estimate of standard error of CV  
SD, standard deviation  
 $\bar{X}$ , arithmetic mean

The letter "F," followed by a number, refers to the cave catalogued under that number in Fincham's (1977) registry.

## ACKNOWLEDGMENTS

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#### ANTILLEAN BIOGEOGRAPHY AND THE CONTRIBUTION OF H. E. ANTHONY

A historical review of vertebrate paleontology in the Caribbean was recently published by Olson (1978), and no useful purpose would be served by an additional treatment of the same subject here. I have limited myself to presenting those historical details which seem relevant either to site description or to the systematic issues considered later in this paper.

The history of fossil land mammal discovery in Jamaica begins with the 1919–1920 expedition of H. E. Anthony. Like several of his contemporaries—Matthew, Glover Allen, J. A. Allen, Miller, Barbour—Anthony had become fascinated by what is still the single most intractable problem of Antillean biogeography—how and when did terrestrial vertebrates migrate to the West Indies? Some authors favored the view that land-bound organisms must have traveled over now-foundered land bridges stretching to North and South America and between the islands themselves (e.g., Allen, 1911; Sharff, 1922; Rutten, 1935). Others assumed that the Caribbean was originally occupied by a continent which subsided in the late Cenozoic, leaving only isolated tracts of high ground—and isolated populations of animals—above water (Spencer, 1895; Barbour, 1916). Still others pointed to the complete lack of geological evidence for the two previous contentions and argued instead that the island faunas were built up by many independent events involving rafting, hurricane transport, or other exceptional means of dispersion. This last set of inferences was originally championed

by Matthew (1919) and later refined by Darlington (1938) and Simpson (1956). The dispersionist argument is still widely regarded as the soundest available (Pregill, 1981), although it has faced some recent challenges (Rosen, 1976, 1978).

Anthony (1918, 1926) favored dry passages: he was convinced that there had to have been trans-Antillean land bridges that connected the big islands to one another and to Central or South America (or both). At the same time, he recognized that the available biogeographical evidence gave no support to his views. This evidence has not altered much in the intervening decades and may be summarized as follows: (1) By any measure the known vertebrate fauna of the West Indies is depauperate. There is no record of native mammalian carnivores, ungulates, or marsupials, despite the fact that all three groups were superabundant in one or more of the Americas during the Cenozoic. (2) The known fauna of each island is highly endemized, suggesting little contact or interchange between circumjacent land masses except on the most infrequent basis. (3) As a whole, the Antillean fauna bears no resemblance to any past or present continental fauna—yet overland routes, had they existed, ought to have permitted the entry of a wide variety of species from adjacent mainlands.

If the absence of a continental fauna implied the absence of land bridge connections, then, Anthony reasoned, the converse should also apply. Evidence for an ancient, considerably more varied fauna could be regarded as an indication of ancient continental connections—or, at least, would place under considerable strain the notion that every terrestrial Antillean species owed its introduction to rafting. The key was to find the fossils of this hypothetical ancient fauna, and this Anthony attempted to do during several expeditions to the West Indies in the years preceding the end of World War I. Anthony hypothesized that one island had probably been the stepping-off place for emigration to the others; that island should therefore have the oldest fauna. By 1919 he had made prospecting trips to both Cuba and Puerto Rico, without, however, having found any evidence bearing on either the age of land mammals in the Antilles, or the route they used

to enter the West Indies in the first place. The collecting localities that he found, although rich in bone, were exclusively recent in age: many were clearly Amerindian kitchen middens, and no more than a few millennia older than the time of first European contact. If mammals did not enter the Antilles through the northern tier of islands, then in Anthony's mind the only other likely route was through Jamaica, just 700 km from the Central American coast and at that time completely unknown paleontologically.

Anthony's opportunity to assess the biogeographic role of Jamaica came in November 1919, when he was granted permission to make natural history collections in Jamaica under American Museum of Natural History auspices. He spent the next four months visiting all parts of the island and amassing a large collection of extant birds and mammals. His paleontological work was less rewarding: he found only three sites containing the fossils of extinct mammals. Although new to science, none of the fossils shed any important light on the age of land mammals in the Caribbean. Anthony never returned to Jamaica, having apparently reached the conclusion that the island had never supported the Cenozoic fauna he had tried so strenuously to find.

The fossils that Anthony discovered were of large caviomorph rodents, among the largest ever found. Caviomorphs were the dominant members of the extinct faunas of the other Greater Antilles, and consequently their discovery in Jamaica came as no surprise. What was unusual, however, was the number of species which Anthony (1920b) believed he could detect in his fossil sample. He named five species, four of which he regarded as closely related—*Clidomys osborni*, *C. parvus*, *Speoxenus cundalli*, and *Spirodontomys jamaicensis*. Anthony posited that these species might be primitive relatives of an endemic family of Antillean caviomorphs, Heptaxodontidae, but did not reach a firm conclusion on the matter. Classifications of Caviomorpha assembled since Anthony's report generally include his Jamaican forms in Heptaxodontidae, with or without a question mark.

Anthony regarded a fifth species, *Alterodon major*, as the representative of a quite different lineage, one not at all closely related to

*Clidomys* and its allies. He did not assign this form to a specific family, but leaned toward placing it in Octodontidae *sensu stricto*.

These uncertain allocations and the number and validity of Anthony's species have been repeatedly questioned by rodent specialists, although usually on an informal basis. Connected with these strictly systematic issues are two others of wider biogeographical significance. The first concerns the significance to be placed on the number of nominal heptaxodontid species recognized by Anthony. In naming four new heptaxodontids, Anthony doubled the number of species then regarded as heptaxodontid or heptaxodontid-like. This, combined with the supposed primitiveness of the Jamaican forms compared to the central genus *Elasmodontomys* (from Puerto Rico and nearby islands), could be taken as evidence for the thesis that Jamaica was the original home for at least this group of Antillean endemics. If Anthony's Jamaican forms were as diversified as his species list implies, then one could reasonably infer that the caviomorph occupation of Jamaica must have been of sufficient duration to accommodate a fairly extensive adaptive radiation. If, alternatively, these taxa are excessively split, then no positive evidence exists for either adaptive radiation or extensive tenure.

The second issue concerns whether or not the form *Alterodon* is evidence for the penetration of the Octodontidae into the West Indies. This family is otherwise restricted to the southern part of South America, and a record of far northern penetration like the one at hand should be regarded as suspect.

In this paper I show that "*Speoxenus cundalli*" is not significantly different from the morph which Anthony called *Clidomys osborni*, and that "*Spirodontomys jamaicensis*" is not distinguishable from the morph *C. parvus*. The only remaining question is whether these two morphs represent valid species, or are instead the sexes of a single, highly dimorphic species. This problem is pursued as far as it can be with existing evidence.

As to *Alterodon major*, MacPhee, Woods, and Morgan (1983) have shown that the type and only known specimen of this species—a broken cheektooth—cannot have belonged to an octodontid. It assuredly represents either

*Clidomys* or a closely related form. Parsimony favors the former alternative.

#### RECONNAISSANCE OF LAND MAMMAL FOSSIL LOCALITIES

Although parts of Jamaica were probably emergent during certain phases of the Cretaceous and early Cenozoic (Khudoley and Meyerhoff, 1971), during much of the latter period (early middle Eocene to lower Miocene) the Jamaican land mass was mostly below sea level (Robinson, Lewis, and Cant, 1977). Re-emergence, which first affected the north central periphery of the island in early middle Miocene times, was rapid and may have been instituted by the evolution of the Cayman Trough (Robinson, 1976). In any event, by the close of the middle Miocene some 15 m.y. ago, Jamaica in its present configuration was in existence save for the final definition of the southern coast and the addition of a few recently emergent Pliocene terraces (Weyl, 1966).

All the fossil land mammal localities described in this report occur in karst structures developed within rocks of the White Limestone group (middle Eocene to lower Miocene). As it happens, White Limestone rocks are largely concentrated in the Clarendon Block, the large structural unit making up the central portion of the island. The oldest dated rocks (which are no older than early Cretaceous) occur in the Blue Mountains of eastern Jamaica, but this part of the island is extremely difficult to explore and no cave sites have been identified therein.

In this section only those caves which have yielded fossils are described in detail (fig. 1). A number of other caves and karst features were visited by the author in 1981, but all proved either to be non-fossiliferous or to contain only the remains of extant mammals. A list of these caves has been deposited with the heptaxodontid collection made by the author for the NRCD.

#### WALLINGFORD ROADSIDE CAVE

The narrow mouth of Wallingford Roadside Cave is situated about 3 m above a sharp bend in the main road (Highway B6) between Oxford and Balaclava, on the moderately eroded fault scarp defining the westernmost

boundary of a large, fault-bounded interior valley (here called the Oxford depression). The better-known Wallingford Main Cave (F96), sometimes confused with the Roadside Cave, is also located above this road, but on the hillside diagonally opposite the one containing the latter (Peck and Kukal, 1975).

Roadside Cave (fig. 2) consists of a single, dry, deeply infilled chamber whose north-west-facing mouth was presumably created by the events that produced the Oxford depression. There is a small, choked aperture at the rear of the present cave that no doubt leads deeper into the hillside. Since Main Cave is at essentially the same elevation, the two caves may in fact represent truncated portions of the same system.

At present, neither cave appears to be linked to major drainage systems. However, prior to the downfaulting of the area to the east, the Wallingfords may have accommodated a substantial flow, assuming that drainage patterns have not altered radically. It is of considerable interest that the One Eye River, the major watercourse in the Oxford area today, currently empties into the headwaters of the Black River by passing *underneath* the Wallingford hills. About 40 m directly beneath the mouth of Wallingford Main Cave, the river enters a sink (Wallingford Sink, F95), to resurge about 1 km to the west at Mexico Cave (F91) at the top of Nassau Valley. This preferred direction of drainage was probably obtained before the Oxford depression was created, since it was probably controlled by the dip of the whole southern part of the island (cf. Arden, 1975). Prior to the downfaulting of the area to the west, Roadside and Main caves would have been on the right axis for receipt of substantial flood deposits. This is of some importance for the interpretation of the origin of the bone-bearing conglomerates in the Wallingford caves (see below).

In 1981, signs of disturbance within Roadside Cave included a large trench adjacent to the rear wall (fig. 2), hammer and chisel marks on the sloping rear wall, and a scattering of small pits in the cave fill. The trench is almost certainly the one begun by Charles Falkenbach, Anthony's field assistant (Anthony, MS); it may have been extended by later researchers, who were presumably also responsible for the smaller pits. The tool marks establish

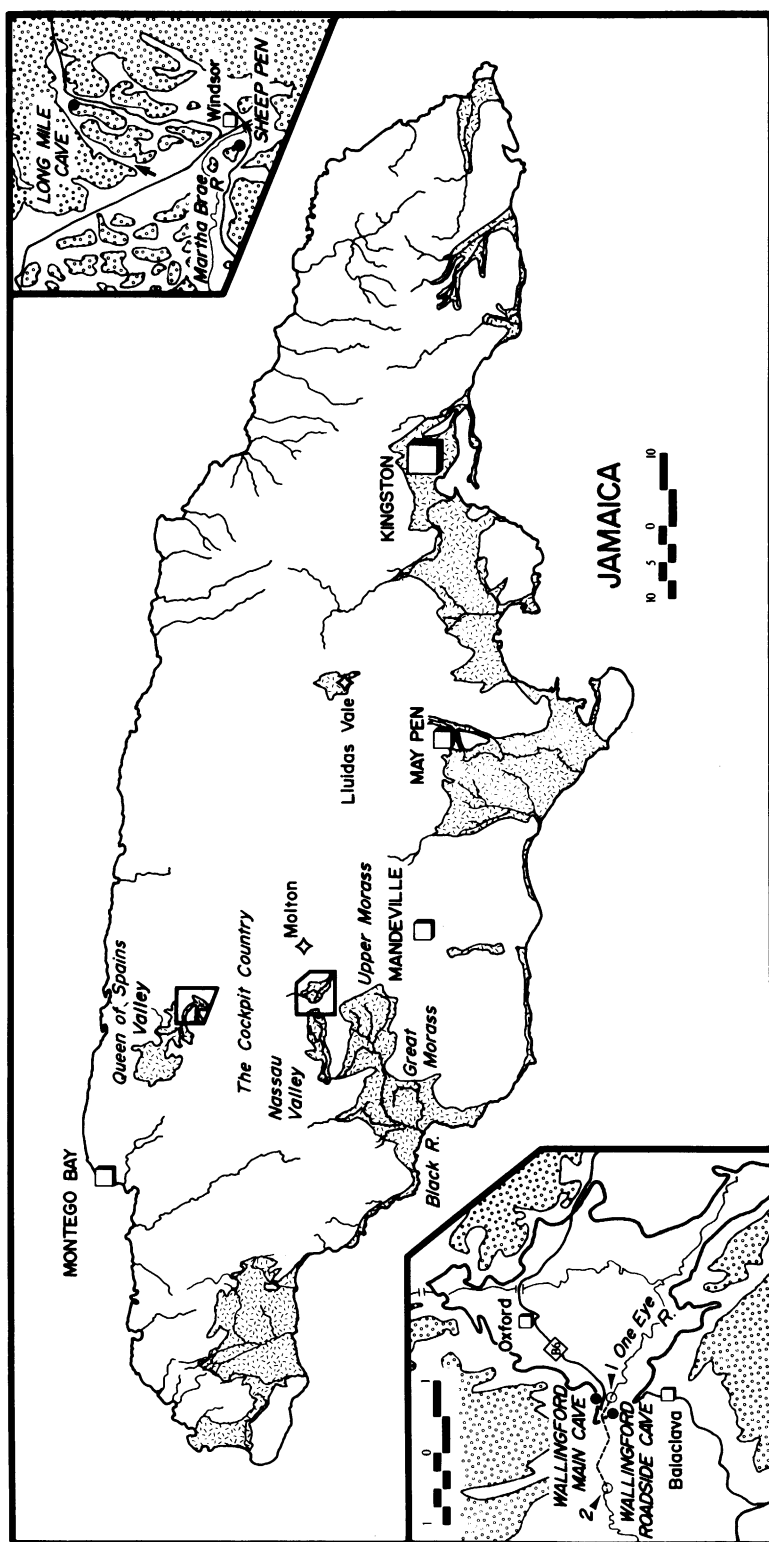
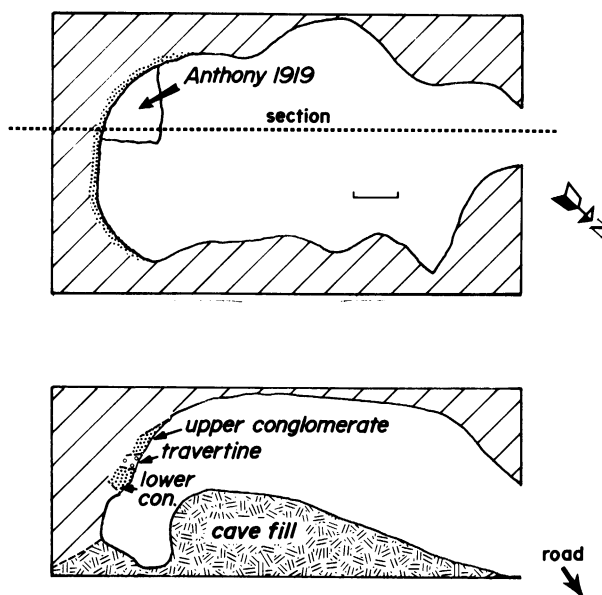


FIG. 1. Fossil land mammal localities in Jamaica. Irregular stipple on main map identifies Quaternary deposits situated in certain parts of the island (southern coastal plains and various interior valleys mentioned in text). Open-circle stipple identifies land over 1000 ft (305 m) in Oxford inset, and over 500 ft (152 m) in Windsor inset. Area bounded by thick line in Oxford inset is the Oxford depression (land under 750 ft [229 m]). Main map based on 1:250,000 scale geological map issued by Ministry of Mining and Natural Resources, Government of Jamaica (2nd proof version, 1977). Insets based on sheets C and D of 1:50,000 scale topological series (Ordnance Survey, reprinted 1978). Scales in kilometers; both insets to same scale.

Black circles identify locations of main localities discussed in text. Precise position of localities near communities of Molton and Lluídas Vale (stars) not known. Arrow in Windsor inset marks southern end of "Long Mile Piece." Dashed line in Wallingford inset connects swallet (1, Wallingford Sink [F95]) and resurgence (2, Mexico Cave [F91]) of One Eye River; exact route of underground river not known.



### WALLINGFORD ROADSIDE CAVE

FIG. 2. Schematic plans of Wallingford Roadside Cave. Scale = 1 m.

the general location of the bone-bearing "breccia" described by Anthony, some of which still remains in difficult to reach areas.

**PREVIOUS WORK:** On December 5, 1919, Anthony (MS) found the first specimen of the rodent that he later named *Clidomys* in the surface litter of Wallingford Roadside Cave. As he soon learned from further investigation, the true source of the rodent remains was not easily dug cave fill, but an extremely indurated conglomerate plastered over the rear wall of the cave. Nevertheless, sure that he had discovered mammals of Pleistocene age, he spent the following week hammering out large blocks of this conglomerate for later preparation in New York. Unfortunately, only a very small proportion of the material that he brought back was ever worked on or catalogued, and he discussed his own discoveries in print only twice (Anthony, 1920a, 1920b).

Thirty years later, in 1950, Roadside Cave was visited by Williams, Koopman, and their colleagues, who were then engaged in making a wide-ranging investigation of the living and recently extinct fauna of Jamaica (Koopman and Williams, 1951; Hecht, 1951; Williams and Koopman, 1952; Williams, 1952). At

Roadside Cave they concentrated on recovering remains from the unconsolidated cave fill and do not appear to have collected any new specimens from Anthony's breccia (cf. Williams, 1952). They did, however, evaluate the probable antiquity of the Roadside conglomerates in relation to other cave deposits, and concluded that the Wallingford "hard breccias" (Koopman and Williams, 1951) were among the oldest fossiliferous deposits then known from Jamaica.

The cave's next scientific visitor was T. H. Patton (then of the FSM), who in 1966 undertook a series of excavations at various cave sites in central Jamaica. Much material was removed, including several hundred pounds of consolidated and unconsolidated deposit from the Wallingfords. Patton's partly prepared faunal collection has never been described and his field journal and lab notes are not in the possession of the FSM (C. A. Woods, personal commun.).

Peck and Kukal (1975) searched for Anthony's Roadside Cave, but were unable to locate it.

**PRESENT INVESTIGATION:** When I visited Wallingford Roadside Cave in December 1981, very little was left of the bone-bearing

layers which Anthony (MS) described as lining much of the rear wall of the cave to a depth of 4 to 6 inches. However, in a few crevices some slabs of matrix remained *in situ*, permitting the account given here. In the best-preserved section three structural parts to the deposit could be distinguished—two brownish, bone-bearing layers separated by a thick band of white travertine lacking organic inclusions (fig. 2). The upper bone-bearing layer was more fossiliferous than the lower, but apart from that there was little to distinguish them. Both consisted almost exclusively of small, variably indurated lumps of cave earth separated by narrow seams of calcite crystals. These seams were randomly arranged and gave the typical hand sample a honeycombed appearance. The small volumes of entrapped cave earth varied greatly in their hardness: the softest of them could be easily converted to silty mud upon the application of water. In some areas the matrix seemed to exhibit lamellation, but on the whole its organization was chaotic. "Pebbles" were mentioned as frequent inclusions by Anthony (1920a), but in the matrix available for this investigation, water-worn gravels (if this is what Anthony meant to convey by "pebbles") were not in evidence. Angular limestone fragments, probably representing breakdown, were occasionally found. Next to indurated cave earth, the major constituent of this conglomerate was bone. The state of preservation of fossil specimens recovered from these layers varied widely. Most were badly broken or crushed and had the consistency of soft chalk. Elements in this condition usually could not be successfully freed from their matrix without disintegrating. Other bones appeared to have survived the fossilization process in better condition; some, against all odds, were even preserved in their original articulations (fig. 14). This variation strongly implies that the Roadside fauna was deposited under more than one taphonomic regime. Other than rodent and chelonian remains, the only fossils present in abundance were shells of various species of terrestrial gastropods.

Turtle shell fragments from the upper bone-bearing layer were submitted for radiocarbon dating. Only the apatite fraction proved datable, since too little collagen was left for a

reliable count. The single available date, roughly 33,250 BP (table 3) has a disturbingly large standard error and is close to the age limit achievable with routine  $^{14}\text{C}$  dating techniques. This age estimate should probably be considered a minimum. As far as I am aware Wallingford Roadside Cave is currently the oldest dated land-mammal locality in the Greater Antilles.

**DISCUSSION:** The faunal lists presented in table 1 indicate that there is broad agreement in species representation in the several faunal collections made at Roadside Cave. The fauna of Main Cave is similar but less extensive, and for practical purposes the two localities may be considered as a unit. (This is necessary in any event, since Roadside and Main Cave specimens appear to have been thoroughly commingled in the AMNH collection. Moreover, only a handful of specimens were ever accessioned or even provisionally labeled prior to being stored.) Anthony himself did not consistently distinguish between Roadside Cave and Main Cave; these sites are severally referred to as "Caves near Balclava," "Wallingford Cave," and even "Balclava Cave" on labels bearing his handwriting. (In his field journal, he noted that bones from Roadside Cave and Main Cave were respectively inscribed "J1" and "J2"; perhaps 10 specimens in the whole collection are so identified.) Patton's collection is more consistently labeled, but for obscure reasons he chose to identify the Wallingford caves not by their usual names but by the Roman numerals "I" and "II." Judging from the number of fossils assigned to each site, the richer "Wallingford I" must be Roadside Cave. The FSM collection is boxed according to a series of zone and level designations developed by Patton. Since there is no way of determining how these zones and levels relate to one another, they are simply ignored in evaluating the collections from the cave fill.

There are several features of the combined faunal list (table 1) which require comment.

It is difficult to reconstruct the conditions under which the organic contents of the bone-bearing layers were originally deposited. Williams (1952, p. 175) thought that a "pond turtle and a crocodile imply an aquatic character for the fauna and perhaps the rodents fit this picture also. It is probable that the



TABLE 1  
Wallingford Roadside Cave: Vertebrate Fauna<sup>a</sup>

	Anthony	Koopman/ Williams/ Hecht	Patton	Present Investigation
CONGLOMERATE				
<i>Clidomys osborni</i> <sup>b</sup>	X	X	X	X
<i>Clidomys parvus</i>	X	X	X	X
<i>Geocapromys brownii</i>	[X]	—	X	X
<i>Celestus</i> sp.	—	—	[X]	—
<i>Crocodylus</i> sp.	X	X	X	—
<i>Pseudemys floridana</i>	X	X	X	X
Unidentified "tortoise"	X	—	—	—
Unidentified fish	—	—	X	—
CAVE FILL				
<i>Geocapromys brownii</i>	X	—	X	X
<i>Oryzomys palustris</i> (=antillarum)	—	—	X	X
<i>Rattus</i> sp.	—	—	X	X
<i>Sus scrofa</i>	[X]	—	X	X
<i>Tonatia saurophila</i>	—	X	—	—
<i>Natalus major</i>	—	X	—	—
<i>Reithronycteris aphylla</i>	—	X	—	—
<i>Eptesicus</i> sp.	—	X	—	—
Other bats (?)	—	—	[X] <sup>c</sup>	—
<i>Celestus</i> sp.	—	X	—	X
Other lizards and snakes (?)	—	—	[X] <sup>c</sup>	—
Unidentified birds	—	—	X	—
Heptaxodontid fragments	X	—	X	—

<sup>a</sup> Species and final identifications made by the original authors. In some cases the specimens used for identification can no longer be located, and presence is therefore based only on notes in field journals or published papers. "[X]" indicates additional identifications made by present author in previous workers' samples.

<sup>b</sup> For synonymy of Anthony's other large Jamaican rodents, see page 30.

<sup>c</sup> In the Patton collection are vials marked "Wallingford I" which contain remains labeled *Mormoops blainvilli* and *Arитеus flavescens*. Neither species was recorded at Roadside Cave by Koopman and Williams (1951), who in fact used their absence as an indication that the deposit at Wallingford was older than the other important fossil bat locality in Jamaica, Dairy Cave. As these authors note, however, they had only small samples which were not necessarily representative. Among lizards and snakes Hecht (1952) notes only *Celestus*, but Patton recovered species of *Alsophis*, *Tropidophis*, and *Anolis*.

hard breccias of Wallingford [?Roadside] Cave . . . and the mixed breccias of Sheep Pen Cave . . . are flood deposits or reworked flood deposits." These opinions are possibly contradictory: if a deposit originated via the action of flood waters, it is clearly unsafe to infer that all of its contained fauna were aquatic because some were. Indeed, since the Roadside fauna is a death assemblage, the co-occurrence of turtle, crocodile, and rodent remains may not mean much as an indication of the fauna's aquatic character. More in need of explanation is the apparent absence of bats in these same deposits. Since it would be ludicrous to infer from present evidence that

there were no chiropterans in Jamaica 33,000 years ago, other hypotheses are required. Here Williams's flood deposit argument is appropriate. Absence of bat bones might be attributable to their lightness and ability to float; the bat-bone density fraction was deposited in a place different from the one consisting of heptaxodontid and chelonian remains. This interpretation can be buttressed by the observation that other small faunal remains are also absent, save for one *Celestus* dentary (extracted from a small piece of matrix allegedly from "Wallingford I" in the Patton collection).

The degree of comminution of many of the

large rodent and turtle remains certainly suggests the effects of transportation by turbulent water. Furthermore, the structural deterioration of these same bones suggests deposition in a wet environment, in which tiny bones would be unlikely to survive. The problem with these arguments is that they refer to conditions which are by no means unusual for Jamaican cave settings—yet many caves possess conglomerates of varying degrees of induration with bat and lizard remains preserved in profusion. The fact that some heptaxodontid remains were apparently deposited in Roadside Cave before all soft tissues had disappeared is possibly an indication that *Clidomys* denned in caves, although it is just possible that carcasses were washed down into the cave and settled on its floor. Considering the probable size of living *Clidomys*, it would have taken a fair-sized stream to do the job. However, Peck and Kukal (1975) found fresh piles of flood debris on ledges within Wallingford Sink, which is evidence that a river of the One Eye's size is large enough to produce significant accumulations.

The presence of *Pseudemys* and *Crocodylus* in the bone-bearing layers is interesting, although the only indication of an obligate aquatic form is a single unidentified fish tooth, UF 27424. This could be a secondary deposition. The *Pseudemys* from Roadside Cave is large and very thick-shelled compared with extant *P. floridana*; this may have led Anthony (1920a) to infer that another chelonian was represented in the Wallingford material (table 1). Crocodile remains were evidently few; Anthony (1920a) mentions only "fragments," Williams and Koopman (1951) mention only a single vertebra, and I found nothing that was certainly *Crocodylus*. *Pseudemys* was observed in the Wallingford area in 1981, but *Crocodylus* is not known to have inhabited the One Eye in recent times. However, crocodiles persist today in southern St. Elizabeth, in the large swamps (Great Morass, Upper Morass) on the lower Black River (fig. 1). This area, ringed by the Lacovia and Nassau mountains to the north and the northern Figueredo and Santa Cruz mountains to the east and south, constitutes a topographic low: substantial parts of it are below the 50 ft (15.3 m) contour line. A period

of much greater rainfall or marine transgression could have brought marshy or even lagoonal conditions far into northern St. Elizabeth, probably to within 5 or 10 km of Wallingford. Such habitats would have been eminently suited to *Crocodylus*.

Broad embayments of the Caribbean must have existed in Pleistocene time in southern Jamaica, because elements of the Mio-Pleistocene Coastal Group and even younger neritic sediments have been identified 15 km inland in southern Clarendon, not far from May Pen (Zans et al., 1962; Robinson, Lewis, and Cant, 1977). When these embayments existed is another (and, as it happens, a critical) matter. Pregill and Olson (1981) make the argument that the Caribbean was probably significantly drier in late Wisconsin time (using the range 14,000–17,000 BP) than it is today, and that the amount of water locked up in ice masses probably produced a sea level low of –120 m at ca. 17,000 BP. This figure is in accord with other data sets demonstrating consistent worldwide lowering of sea levels from about 125,000 BP to just before the beginning of the Holocene (e.g., Dodge, Fairbanks, Benninger, and Maurasse, 1983). These studies assume constant uplift, however, and local variations no doubt occurred where uplift was not constant (e.g., evidence for +8 to +10 m in Florida at ca. 65,000 BP [Alt and Brooks, 1965]). Other things being equal, at 30,000 BP sea level would have been on the order of –40 m; southern Jamaica would have extended a considerable distance toward Pedro Bank, leaving the present Wallingford area some 40 km inland. If conditions were also appreciably xeric at that time, it is hard to account for the presence of amphibious forms in the Wallingford fauna so far from the littoral or large bodies of water. As noted earlier, the radiometric age of this fauna may seriously underestimate its actual age. On faunal grounds it would be more consistent to assign the Wallingford assemblage to a period of higher sea levels (?125,000 BP or earlier), but there is at present no solid evidence which would warrant doing so.

Little comment is needed regarding the fauna drawn from the unconsolidated cave fill. In 1981 Anthony's original pit was taken down to a depth of approximately 1 m and



FIG. 3. Sheep Pen. Arrow points to one of several bone- and shell-laden conglomerates plastered onto the exposed face of the Pen.

all deposit removed from it was screened. Only a few vertebrate remains were recovered, with hutia bones and jaws comprising the majority of finds. Examination of available collections revealed no land mammals other than *Geocapromys*, *Oryzomys*, and some domesticants. Humans were probably also responsible for the single fish element recovered (table 1), a vertebra. Many fragmentary heptaxodontid remains were found on the surface by both Anthony and Patton (recorded in the Patton collection as finds from the "back surface" and "below cave entrance"). While all of these fossils probably eroded out of the conglomerate, it should be noted that a number have a "fresh" appearance due to the absence of crystalline efflorescence in medullary cavities and cancellous tissue. This may be evidence of significant temporal variation in the age of the remains from the conglomerate, although I doubt that any are as recent as the first human settlement in Jamaica.

#### SHEEP PEN

The locality provisionally identified as Anthony's Sheep Pen is an overhang on the northeast side of a low hill, which is in turn situated about 350 m west of the bridge cross-

ing the Martha Brae River near Windsor great house (fig. 2). To find it, cross the bridge and follow the dirt road running to the west; go to the house on the north side of the road, then walk due west through the banana grove until hillside is reached. Look for overhang and conglomerate shelves 2–3 m above-ground (fig. 3).

The precise location of Sheep Pen was not given by Anthony in his field journal, and the site does not appear to have been visited by any later expedition. During the days when Windsor was a private estate, a number of places in the surrounding hills were used as pens (i.e., small wood or stone enclosures for poultry or livestock, built against limestone outcrops). None of them is known to have been a "sheep" pen, but this is of little relevance in view of the fact that sheep have not been kept at Windsor for many years. The spot ultimately selected as the likeliest candidate for Anthony's site was an eroded limestone wall bearing shelves of a crumbly, reddish-to-white, bone-bearing conglomerate much scarred by hammer and chisel marks. The texture and color of the conglomerate cannot be regarded as diagnostic, although there are pieces of matrix in the Anthony collection at the AMNH which are similar to it. The tool marks are circumstantially

important, given that the local inhabitants would be unlikely to break down an indurated deposit having no conceivable practical use.

Anthony's (MS) description of Sheep Pen "Cave," where he worked January 22 to January 27, 1920, brings out certain details worthy of comment:

The cave is really an overhang of about 50 feet front and 30 feet high, running out at the right onto a hillside where the cliff ceases, and on the left continuing as a straight fronted cliff, no overhang and plain limestone face. The overhang gives shelter for about 10 feet out from the cliff, at its maximum. The breccia extends in a more or less continuous face, along this entire frontage of 50 feet, considerable pieces of it still cemented to the wall along the left half of the exposure, and here and there completely eroded away on the right half.

The breccia is cemented to the face of the cliff and is evidently the remnant of the former cave contents. About 10' to 12' above the present ground level may be seen several narrow shelves of breccia which were at one time the cave floor. Since then the whole front of the cave has evidently fallen down, letting in wind and rain and the former cave content has been eroded away, leaving only fragmentary remain [*sic*] cemented to the cliff . . . Bone may be found from the uppermost breccia clear to the bottom but is most abundant in the mid-section of 6–8 feet, more particularly localized in areas about a foot thick which may appear anywhere . . . Shells of several species are very abundant through the breccia. The *Capromys browni* [*sic*] (if it proves to be *browni*) is shown to have [been] contemporaneous with the large rodent for it has been found both above and below the new species.

The cave is . . . at the foot of a fairly high hill and the cave floor is flush with the level of the valley. No remains of the former cave roof are to be seen, evidently having completely disintegrated.

It is evident from Anthony's notes that he believed that Sheep Pen was very old. Not the least of his reasons for so concluding was his interpretation of the history of the "cave" as given above. If I am correct in my re-identification of this site, Sheep Pen was never a cave in the proper sense and ought not to be regarded as the last remnant of a long-vanished solution cavern. Frequently seen in White Limestone areas of Jamaica are isolated scarps, varying in height (2 to 20 m)

and lateral extent (tens to hundreds of meters), which rise straight up from valley floors. A characteristic feature of these scarps is the presence of a thick veneer of hard conglomerates containing shells of terrestrial mollusks and, more rarely, bone. These conglomerates could not possibly have originated above-ground. On the other hand, it is also unlikely that they formed at deep levels within the phreatic zone, where solution caverns originate, because the detritus they contain is unlikely to have been carried so far. I suspect that the scarp faces they cover were originally parts of major joints in rocks immediately beneath the thin, porous lateritic cover. Over time these joints were at first corrosively widened, then slowly choked in their superficial portions by detritus-laden fills after corrosion activities progressed to deeper levels. With aeration, these fills progressively hardened into conglomerates in this subsurface setting. Finally, these conglomerate-covered blocks were exposed by faulting, their lateral surfaces becoming "overhangs" like Sheep Pen. Although this sequence of events is conjectural, it does not require that a "cave"-like environment or unusual erosion process be interpolated in order to explain observed structures. Nor is it necessary to believe that such structures are very old. "Breccias," as indurated as any I encountered in true cave settings, plaster fault block walls in southern Lluidas Vale, but they contain only extant vertebrates. Degree of induration is not a good index of age in Jamaica.

Anthony also had a deep pit dug in the deposit beneath the overhang, on the theory that he might find the original cave floor and perhaps old remains as well. After reaching 8 ft (2.4 m) he abandoned the pit, having found nothing but a few hutia bones. No sign remained of this pit in 1981; it had presumably been filled in, by human or natural agency.

Anthony never accessioned any bones from Sheep Pen according to AMNH records, and the letter/number combination for the site (J.6 and J.6.1) was not found on any specimens or matrix blocks still in the AMNH collection. There were, however, a few bones and small lumps of conglomerate in open cigar boxes marked "Sheep Pen Cave." Among the former were remains of *Clidomys*. Both

the bones and the conglomerate lumps were whitish and chalky, and altogether different in texture from those recovered at the Wallingfords. Their assignment to Sheep Pen therefore appears to be correct, except for the fact that conglomerate of this color and consistency is not specifically mentioned by Anthony in his notes.

In their investigation of Anthony's collection of Sheep Pen "hard breccia," Koopman and Williams (1951) found no bats. This absence can be explained along the same lines as the interpretation offered for the Wallingford conglomerate (i.e., through water transportation and fractionation of bones of different densities). The absence of turtle and crocodile remains is in line with the fact that the northern periphery of Jamaica (save for coastal stretches) has probably been above sea level since the Miocene. Koopman and Williams's (1951, p. 6) hypothesis, that the *Clidomys*-bearing deposit may be reworked and therefore older than the surrounding *Geocapromys*-bearing layers, is unnecessary in view of the fact that heptaxodontid and capromyid remains are intermingled at Wallingford Roadside Cave.

The pieces of conglomerate in the AMNH collection allegedly from Sheep Pen are of little significance. Sampled blocks were filled with the fragmentary remains of small vertebrates (mainly of *Geocapromys* and lizards, some bats) in extremely poor condition. No extinct forms were found.

#### LLUIDAS VALE CAVE AND "FISSURE NEAR MOLTON"

Lluidas Vale (fig. 1) is another large interior valley in White Limestone rocks. As in the Oxford area, faulting and displacement have resulted in the exposure of several cave systems on the scarp faces that ring the Vale. Relief in surrounding hills exceeds 3000 ft (914 m) above sea level, but the Vale itself is below the 1250 ft (381 m) contour line.

Molton (or Malton, as it is spelled on some maps) is a community in Manchester, about 32 km by road from Mandeville and about 10 km ENE of Wallingford (fig. 1).

"Lluidas Vale Cave" and the "fissure near Molton" are localities known only from labels in the Patton collection. Both evidently

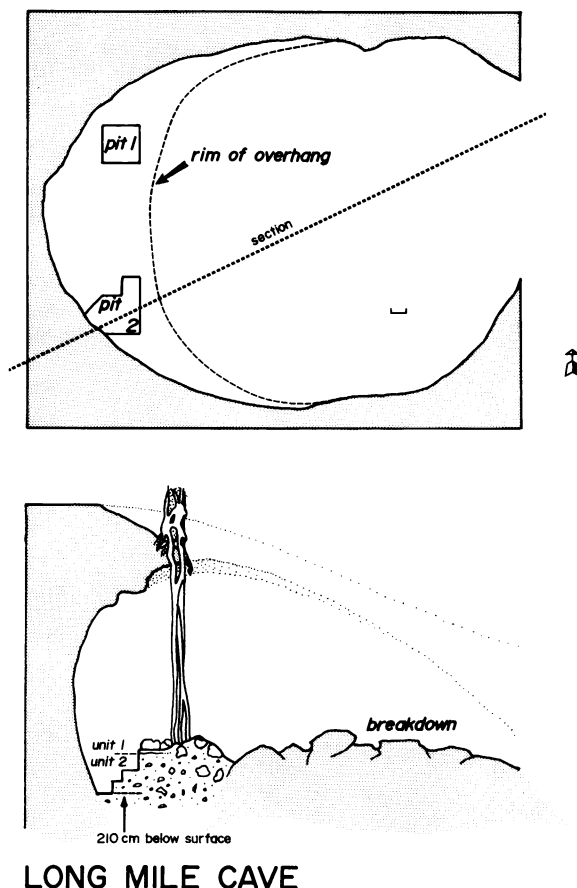
yielded *Clidomys* remains (UF 2840 from Lluidas Vale Cave and UF 27438 from Molton fissure, plus several unnumbered teeth); both proved to be unlocatable in the absence of any useful description. The Lluidas Vale and Molton regions were combed for additional fossiliferous localities, but with negative results. With the exception of the discovery of *Geocapromys*-bearing conglomerates in Lluidas Vale, where hutias are never found today, no new proveniences of land mammals were discovered.

#### LONG MILE CAVE

Anthony's "cave on the Long Mile piece," locally known as Pick'ny Mama Cave, is situated on the west side of the Coxheath-Sherwood road, about 2 km north of Windsor great house (fig. 1). At present the "cave" is only a simple overhang or rock shelter (fig. 4) but, unlike Sheep Pen, it is unquestionably a remnant of a once-extensive chamber. Evidence of collapse abounds: an 18 by 20 m elliptical area, bounded by rounded walls continuous with the shelter's roof, is filled with very large pieces of breakdown (some of which must weigh several tons) representing the ceiling of the original cave. Large blocks of breakdown are also found under the small (6 m) overhang, but most are at least partly covered by a mantle of dry, gray to yellow-brown deposit. In all of these respects, Pick'ny Mama accords with Anthony's brief notes on the physical features of Long Mile Cave, and I conclude that they are the same.

On entry in 1981, evidence of digging was noted under the southwest corner of the overhang, and charcoal, broken glass, and a prodigious number of gastropod shells littered the surface.

PREVIOUS WORK: Anthony (MS) records that he worked at Long Mile Cave for a few days in early 1920 (Jan. 16–17, 20–21). On entering the cave he moved some breakdown aside, found several unspecified bones, and began to dig a hole. In or immediately under the "dark and ash like" surface layer he encountered a kitchen midden, some human remains, and a number of pottery sherds. Pressing on "in the hopes of getting material antedating the Indian occupation," he passed into a layer he identified as "yellow limestone



### LONG MILE CAVE

FIG. 4. Schematic plans of Long Mile Cave. Roots of a large strangler fig (*Clusia rosea*) hide part of the mouth of the cave. Scale = 1 m; arrow points north.

detritus" or as "yellow soil." Hutia bones were the only mammalian remains found in the "detritus" on the sixteenth, but on the seventeenth he came upon what was, and still is, the only evidence for a non-human primate in Jamaica—the mandible of *Xenothrix mcgregori*. This find (which was accompanied by a femur, possibly associated) was not, however, regarded as significant by the discoverer: although the monkey was "deeper . . . than any of the human bones by at least 10"—1' [25.4–30.5 cm]," it was "not so far from them that the animal must not be strongly suspected as an introduced species." He concluded that he had to go deeper to find earlier material, and he records that he dug to a depth of "at least 5' [1.5 m]," where he came upon a nearly sterile horizon. His entry ends with a dissatisfied coda: "It looks as if

further work in this cave would be desirable but I do not expect to secure any truly Pleistocene material there." Pleistocene was what he wanted, after all; and having spent most of January 20–21 finding "nothing of importance" at Long Mile, he was more than ready to abandon this site for the breccias at Sheep Pen (q.v.) on the twenty-second.

Much but not all of the vertebrate bone from Long Mile was cleaned, shellacked, and numbered (with the identifier J5) after Anthony's return to the AMNH, and later stored in the Department of Mammalogy. This material was apparently not re-studied until Williams and Koopman began their investigations in the early 1950s.

Miller (1932) visited Windsor early in 1931. Although he reports that he investigated "a rock shelter" in which he found Indian pot-

tery, ashes, land snails, and pig bones, his description gives no clue regarding the shelter's form or whereabouts. However, I think it highly probable that Miller's rock shelter was Anthony's Long Mile Cave. Of the 10 caves Anthony explored during his two weeks at Windsor, Long Mile was the only one in which he found express signs of Indian occupation. Moreover, since Willie Hill, the school boy who guided Anthony to Long Mile Cave in 1920, is undoubtedly the William Donald-Hill who hosted Miller in 1931, one may assume that Miller was taken around to the most interesting sites in the area. If Miller did visit Long Mile, he must have limited his collecting activities to the surface and Anthony's backdirt, because there is no sign of pits additional to the one attributed to Anthony. Uncertainty about the identity of Miller's site will probably persist: he never published a full report on the mammals recovered from his Jamaican expedition. His uncatalogued collection, which is housed in the Division of Paleobiology at the USNM, contains no elements ascribable to *Xenothrix*.

The Williams-Koopman expedition visited Long Mile in 1950 (Koopman, personal commun.), but it appears that neither surface collecting nor excavation was undertaken. Williams (1952), in describing the origin of the fill in the cave, hypothesized that the deeper layers under the kitchen midden might be flood or fissure deposits. Judging from the number of angular fragments and lack of apparent stratification in these deeper layers, they are more likely to represent colluvium brought down from the hillside above the cave. Much of this deposit could have originated catastrophically if, for example, the collapse of the cave was caused by an earthquake. However, the occasional recovery of hutia bones at deep levels in 1981 suggests that slow accumulation via runoff is the more likely agent. Obviously, the original floor of Long Mile Cave is buried under tons of rock.

**PRESENT INVESTIGATION:** One of the prime objectives of the 1981 expedition was to find additional evidence of *Xenothrix*, and the period December 15–23 was spent in a fruitless effort to uncover more monkey remains at Long Mile Cave.

Controlled excavations, with screening of all backdirt, were undertaken in two areas

(figs. 4, 5). Pit 1 was dug on the north side of a particularly large ash concentration in the central part of the floor. Anthony's deep hole was included within pit 2, located under the southwest part of the overhang. Although there were differences in the character of the deposits encountered in the two pits, only two stratigraphic units are worth discriminating. Unit 1 is a gray silt containing a large number of angular limestone fragments, shells, ash, charcoal, and burnt cave earth. Its maximum depth was 20 cm below surface in pit 1. In addition to a range of cultural artifacts, found in both pits, pit 1 also contained human remains. Articulated limb bones from the left side, parts of the spine, and some cranial fragments were collected, suggesting that the skeleton was intact at the time of deposition. The right side of the skeleton lay beyond the confines of the pit and was not recovered. The skeleton appeared to be lying on top of the deeper layer (unit 2), and though relatively complete it may not represent an actual interment. Non-interment would be in keeping with the practices of Jamaican Indians, who frequently used caves and rock shelters as ossuaries (Howard, 1956).

The age of unit 1 is indeterminate, although it is surely fairly recent. Charcoal from a hearthlike feature in pit 1 was found to be too recent in origin for reliable dating (table 3), suggesting deposition in the last 100 years or so. The commingling of such objects as iron nails and pottery fragments of Amerindian manufacture (table 2) strongly implies that unit 1 is highly disturbed. The pottery is not likely to be very old, judging from the dates available for other Jamaican archaeological sites. The oldest reported site date is a scant  $1300 \pm 120$  years BP; and most other dates are considerably younger, in the period 800–400 BP (Rouse and Allaire, 1978). Situated more than 16 km from the coast, Long Mile is deeper inland than almost every other known Indian occupation, and this too may be an indication of comparative recency (cf. Howard, 1956).

Unit 2, equivalent to Anthony's "yellow limestone detritus," lacks artifacts and ash but shells remain abundant. Excavation of pit 2 to a depth of 2 m failed to attain the bottom of this layer. Anthony's subjective marker for the lower limit of unit 2 (a "loose

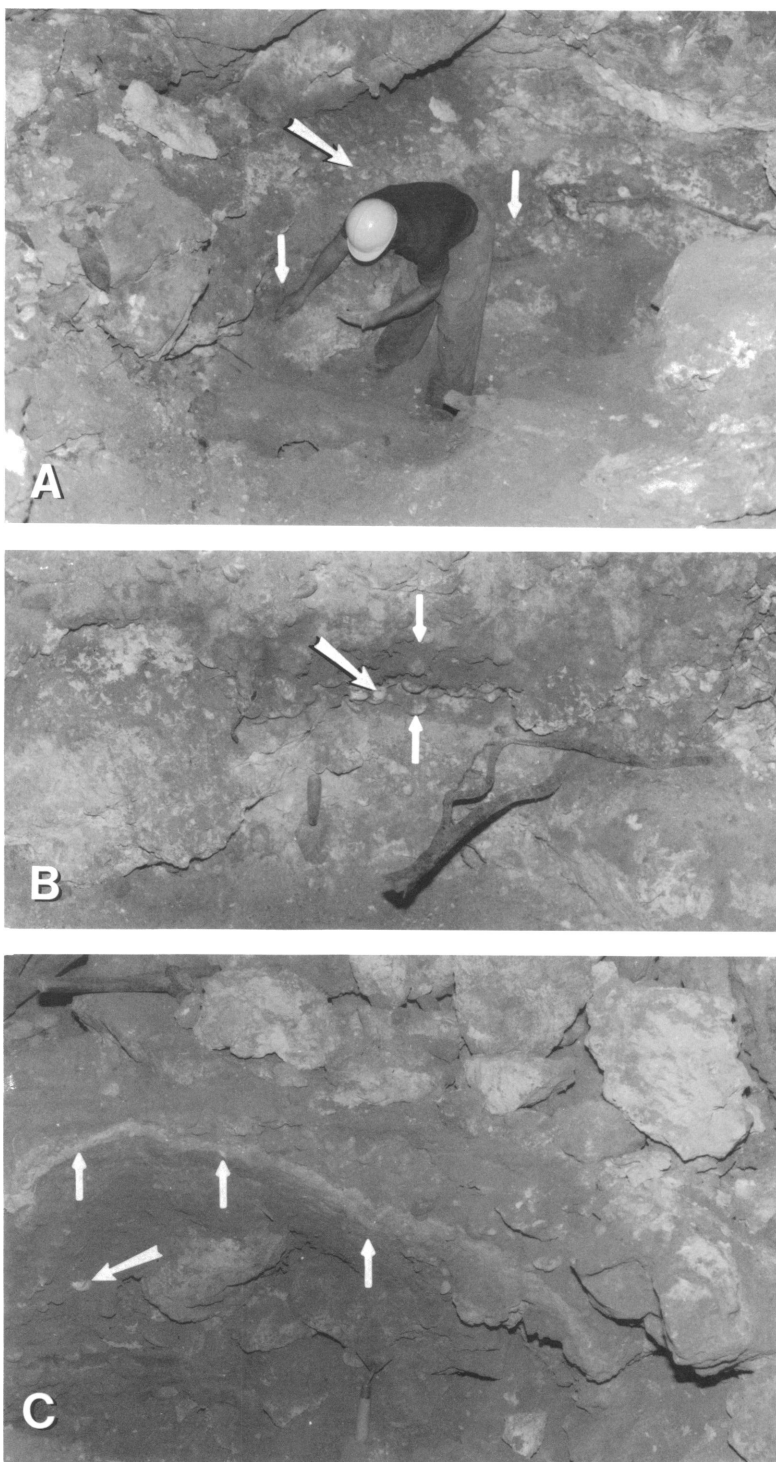


FIG. 5. Excavations at Long Mile Cave. (A), Pit 2, looking down from west rim of pit. This trench was dropped over previous excavation, attributed to Anthony; backdirt from earlier excavation can be seen piled above worker's head (large arrow). Level of actual cave floor (top of unit 1) marked by small



TABLE 2  
Long Mile Cave: Fauna and Artifacts<sup>a</sup>

	Anthony	Williams/ Koopman	Olson & Steadman	Present Investigation
<b>MAMMALIA</b>				
<i>Geocapromys brownii</i>	X	—	—	X
<i>Oryzomys palustris</i> (=antillarum)	—	—	—	X
<i>Rattus</i> sp.	—	—	—	X
<i>Herpestes auropunctatus</i>	—	—	—	X
<i>Sus scrofa</i>	[X]	X	—	X
<i>Homo sapiens</i>	X	—	—	X
<i>Canis familiaris</i>	[X]	—	—	—
<i>Bos taurus</i> (?) <sup>b</sup>	—	—	—	X
<i>Xenothrix mcgregori</i> <sup>c</sup>	X	X	—	—
Unidentified mammal	[X]	X	—	—
<b>OTHER FAUNA</b>				
<i>Aristelliger</i> sp.	—	—	—	X
<i>Cyclura</i> sp.	—	—	—	X
<i>Anolis</i> sp.	—	—	—	X
<i>Celestus</i> sp.	—	X	—	—
<i>Xenicibis xymptithecus</i>	—	—	X	—
Unidentified accipitrid	—	—	X	—
Unidentified large crustacean	—	—	—	X
Unidentified fish	[X]	—	—	X
Unidentified marine bivalve	X	—	—	X
<i>Strombus gigas</i>	X	—	—	—
<i>Pleurodonte</i> and other terrestrial gastropods	X	—	—	X
<b>ARTIFACTS</b>				
Clay pipe stems and bowls	[X]	—	—	X
Pottery sherds	X	—	—	X
Unidentified iron artifacts	—	—	—	X
Charcoal, ash	—	—	—	X
Bottle glass	—	—	—	X
Hand-forged nails	—	—	—	X

<sup>a</sup> See fn. <sup>a</sup>, table 1.

<sup>b</sup> Based on one rib fragment.

<sup>c</sup> Anthony (MS) noted recovery of monkey remains in his field journal, but Williams and Koopman (1952) named and described *Xenothrix*.

layer of fair sized rock” with few bones) could not be discriminated. Breakdown of all shapes and sizes was common in unit 2, and made excavation—which had to be carried out with a pick ax—extremely laborious (fig. 5). Bones

were comparatively scarce throughout, and not just in deeper layers as in Anthony’s experience. Most of the faunal sample, which consisted almost exclusively of hutia bones and a few lizard remains, had to be utilized

←

arrows. Worker’s right hand points to boundary between units 1 and 2. (B), Pit 2, closer view of units 1 and 2. Limits of unit 1 marked by small arrows. Dark color of the unit is evidently due to large quantities of carbon from fires. Large arrows point to shells of *Pleurodonte* and other land snails, found in great quantities in this layer. Underlying unit 2 (“yellow limestone detritus” of Anthony) is lighter in color and contains much breakdown. (C), Pit 1, southeast corner. White arrows identify thick ash layer capping original surface of unit 1. Human bone in wall (large arrow), an unrecovered part of the skeleton found in pit 1, lies at bottom of unit 1. Unit 2 has not yet been exposed.

TABLE 3  
Radiometric Age Determinations, Jamaican Fossil Mammal Localities

Locality	<sup>14</sup> C Age (yr. BP) <sup>a</sup>	Material Dated	Geochron No.
Wallingford Roadside Cave, Conglomerate ("hard breccia")	33,250 +2950/-2150	Associated turtle shell	GX-9438
Long Mile Cave, Unit I ("surface")	[Modern]	Charcoal	GX-9437
Long Mile Cave, Unit II ("yellow limestone detritus")	2145 ± 220	Miscellaneous bone	GX-9436

<sup>a</sup> Based on Libby half-life of 5570 yr. referenced to year 1950 AD, with laboratory precision rated to 1 SD statistical counting error. Listed dates are <sup>13</sup>C corrected.

for a radiometric determination of the age of unit 2. The age of the combined bone sample is on the order of 2145 years BP (table 3), which may be regarded as an "average" age for the unit.

DISCUSSION: Although we at last have a reliable age bracket for *Xenothrix*, none of the mystery surrounding this animal is cleared up. First, no new fossils were found at the type locality. Therefore, the position of *Xenothrix* in the stratigraphic section of Long

Mile is still uncertain. Secondly, although 2000 years is an insignificant period of time in most paleontological contexts, in this one it is important because the status of *Xenothrix* as a native Jamaican mammal has always been in doubt (cf. Simons, 1976). Had the <sup>14</sup>C date for the bones of unit 2 been much earlier, on the order of 20,000 BP, the notion that *Xenothrix* was merely someone's pet could finally be laid aside; even the most sanguine estimates of the age of human arrival in the Greater Antilles place the first penetration at 7000 BP or less (Rouse and Allaire, 1978). But at 2145 BP, Long Mile is old in regard to the known archaeological cultures of Jamaica only; there are dated sites of nearly twice that age in Hispaniola and Cuba, and several authorities (e.g., Howard, 1956, 1965; Rouse and Allaire, 1978) maintain that Jamaica was inhabited much earlier than the present record suggests.

The faunal and artifact lists in table 2 require little explanation. The absence of bat bones is of no significance, since a small overhang like Long Mile would be unlikely to attract a large bat population.

The "unidentified mammal" remains noted in table 2 comprise the long bones and partial pelvis noted by Williams and Koopman (1952) as "not *Geocapromys*." These authors correctly recognized that these elements (with the possible exception of the pelvic fragment) were not primate-like, but did not attempt to assign them. While inspecting Anthony's faunal remains from Long Mile, I found the shafts of two humeri in a box of *Geocapromys* remains; these do not belong

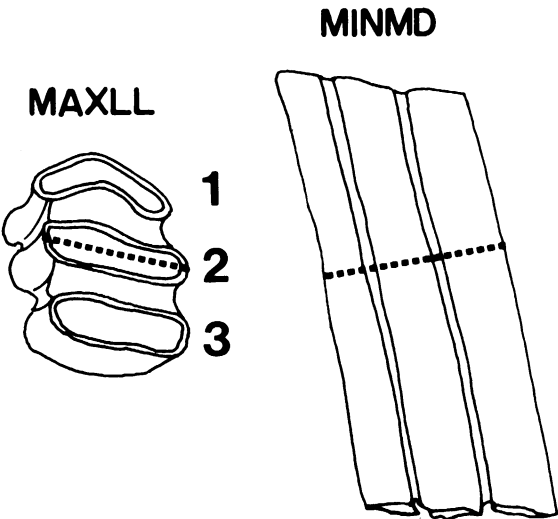


FIG. 6. Typical cheek tooth of *Clidomys*. Laminae numbered from anterior to posterior. MAXLL: maximum labiolingual width of widest lamina. MINMD: minimum mesiodistal length, taken in middle of tooth perpendicular to laminae. MAXLL formula: order of lamina widths, from largest to smallest.

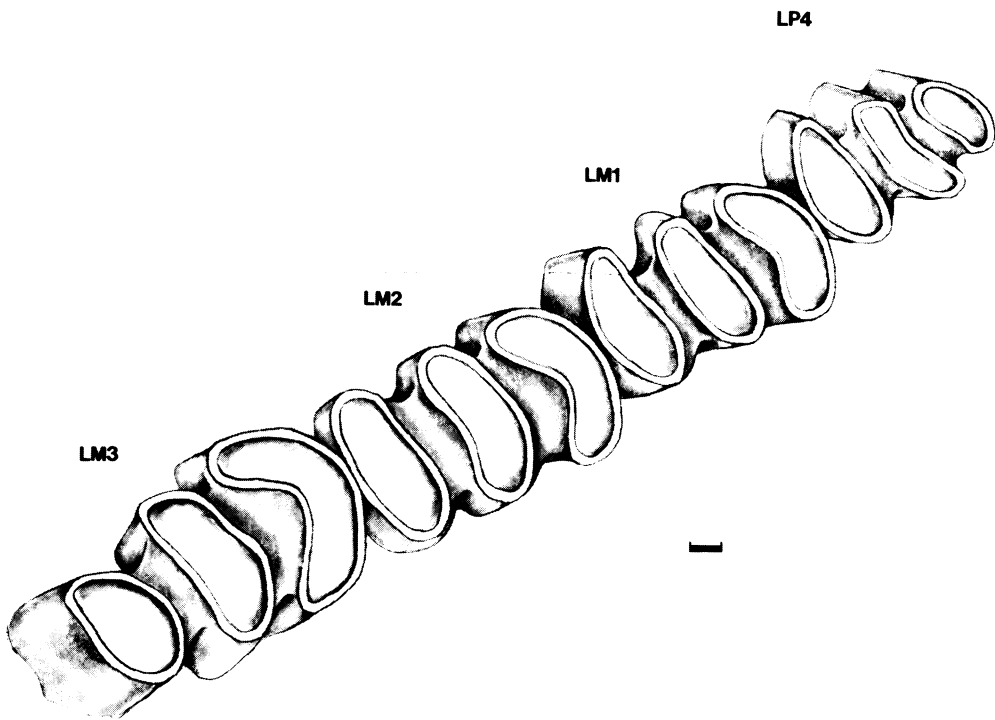


FIG. 7. Cheek teeth of *C. parvus* (left mandibular ramus, AMNH 108543), occlusal aspect. Scale = 1 mm.

to hutias either. Although they are not labeled "J5," they agree in coloration, size, and form of taphonomic alteration with the non-hutia elements grouped by Williams and Koopman. All of these remains are presently under study and will be dealt with elsewhere.

#### REVISION OF THE HEPTAXODONTID RODENTS OF JAMAICA

The purpose of this revision is to establish how many species of Jamaican heptaxodontids are valid. The relationships of the Jamaican forms to other nominal heptaxodontids and to other caviomorph families have been under study by others for some time, and, pending the publication of their findings, a protracted discussion of general heptaxodontid systematics in this paper does not seem warranted. I do, however, wish to record my doubts that heptaxodontids and echimyids (including capromyines) are sister-groups in the strict sense, as has recently been suggested. I choose to maintain the use of the family name Heptaxodontidae, and I continue to

believe that all the forms usually grouped as heptaxodontids (i.e., the Jamaican species plus *Elasmodontomys* and *Amblyrhiza* from the eastern Caribbean, but perhaps not *Quemisia* from Hispaniola) do constitute a monophyletic group. But they are certainly a very odd and primitive assemblage, a fact which may justify Patterson and Wood's (1982) recent refusal to assign them to any of the recognized superfamilies of Caviomorpha (see also Ray, 1964, 1965).

#### DENTAL MORPHOLOGY

The available sample of Jamaican heptaxodontid cheek teeth consists of about 150 individual specimens, counting teeth still in jaws, isolated finds, and large fragments. The sample is a poor one: most teeth are damaged, and only a small handful are in association with jaw parts. Anthony (1920b) provided illustrations of his types and a few referred specimens, but did not describe dental anatomy in detail.

By any standard, cheek tooth *construction*

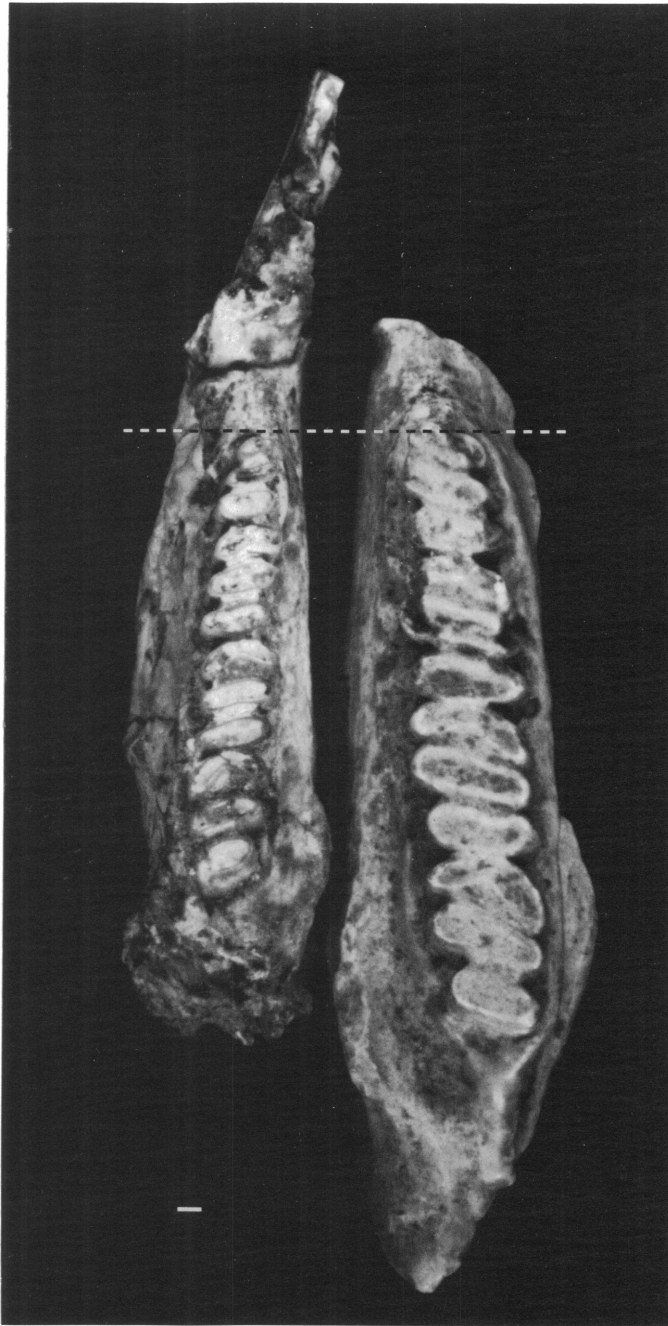


FIG. 8. Comparison of mandibular cheek teeth of *C. parvus* (left mandibular ramus, AMNH 108543) and *C. osborni* (right mandibular ramus, AMNH 17634, cast of type specimen). Dashed line aligns anterior borders of LP4s; cheek tooth row length of *C. parvus* is about 75 percent of that of *C. osborni*. Scale = 2 mm.

in Jamaican heptaxodontids is little varied (figs. 6–12); cheek tooth *dimensions*, how-

ever, are another matter. Each tooth consists of a series of enamel-enclosed laminae of

dentine which are vertically separated by thin plaques of cement. UM3 regularly possesses four laminae (fig. 11), the others three. In side view these laminae are simple flattened columns that generally neither vary in profile nor combine to form more complex shapes. For purposes of this description, laminae are numbered in m-d order from 1 to 3 (to 4 in case of quadrilaminar teeth).

In occlusal view, laminae vary somewhat in form and obliquity relative to the apparent m-d axis of the tooth row. In the best-preserved teeth, a thin sheath of cement, continuous with the intercolumnar plaques, encases all surfaces save for the occlusal and radicular. Pulp chambers are open in all specimens in which it is possible to examine the root end, implying that the cheek teeth were ever-growing. So simple is this construction plan that even heavily worn teeth differ little from unworn ones in occlusal surface patterning.

In the lower jaw, the teeth increase in size from LP4 to LM3 (m-d dimension). In the upper jaw, the first three teeth are extremely homomorphic, differing only slightly in m-d length and in laminar shape.

About 90 percent of the total sample could be sorted into upper and lower teeth using these criteria (figs. 7-12):

1. Lower teeth are generally less curved in buccal and lingual aspects.

2. The longitudinal grooves between adjacent laminae are generally deeper in lower teeth, and only lowers exhibit the highly inflected "boomerang" form of lamina 1.

3. In lower teeth, laminae are set on a marked oblique relative to the m-d axis of the entire tooth (or tooth row). In upper teeth, obliquity is small or absent.

4. Cement plaques are wider, compared with m-d lamina width, in lower teeth.

Sorting by loci was less successful. UM3s are instantly recognizable; upper and lower P4s can often be identified using a combination of morphology and wear angles, but no adequate criteria were developed for distinguishing between UM1 and UM2, or among LM1, LM2, and LM3.

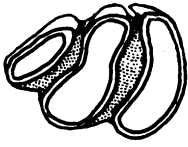
**PREMOLARS:** The species *C. parvus* was founded on a single LP4 (AMNH 17637), which Anthony distinguished from the homologous tooth of *C. osborni* on the basis of

the former's small size and diminutive lamina 1 (fig. 9). In the *C. parvus* type (correctly described by Anthony [1920b], but inadvertently labeled as "lower molar" in his figure 2), the subellipsoidal lamina 1 is only 66 percent of the b-l width of the second lamina. In contrast, in the type of *C. osborni* (AMNH 17634), LP4 is essentially molariform: lamina 1 is concave distally, and is large (80 percent of the b-l width of lamina 2).

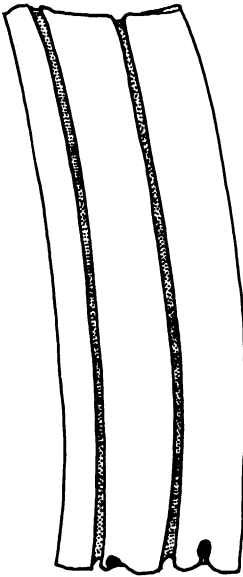
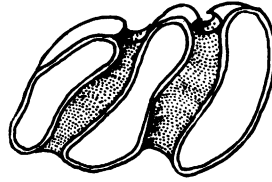
An initial sort of isolated teeth using these size/shape criteria yielded only four potential examples of the *C. parvus* pattern (first three entries in table 4 plus an incomplete tooth, AMNH 108554), but three times that many having the *C. osborni* configuration. Since molar teeth assigned to *C. parvus* on the criterion of size are nearly as numerous as those assigned to *C. osborni*, some non-random systematic error could be producing underrepresentation in the *C. parvus* LP4 class. One possibility is that some premolars have been counted as molars. This could have happened if the small lamina 1 is non-diagnostic, *contra* Anthony. Reexamination of the *C. parvus* molar sample revealed a few cases in which the first column is absolutely small (e.g., AMNH 108608, 108609), but these teeth are smaller than average in any event, and do not otherwise accord with expected premolar morphology. In any case, it is of some interest that the  $L_{10}(\text{MAXLL} \times \text{MINMD})$  distribution for LP4 is strongly bimodal (fig. 13). The MAXLL formula for the LP4 locus is  $1 < 2 < 3$ .

Anthony (1920b) did not identify or describe UP4s of either species of *Clidomys*. In the available material, only two jaw specimens (AMNH 108544, NRCD 3) retain UP4 *in situ*. These specimens establish that UP4 erupts at a considerable angle relative to the other cheek teeth (fig. 10); as a result its wear angle (dihedral angle between occlusal surface of the tooth and its shaft) is very high compared to the posterior teeth. Wear angle may or may not have increased with advancing age. (The mandibular premolar also erupts at a different angle from the other cheek teeth, but wear differences from molars are not so pronounced.) There may be variation, however; AMNH 108640/6 has a premolar-like wear angle, but its unusually large size may be an indication that it is actually an

AMNH 17637



AMNH 108553



1

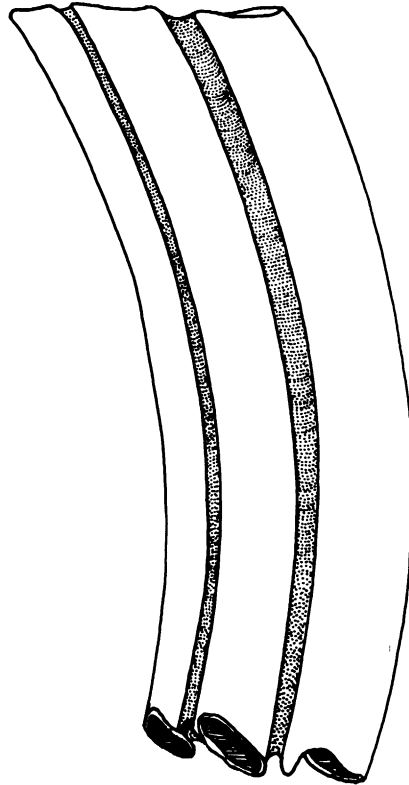


FIG. 9. Right LP4s of *C. parvus* (left, type specimen) and *C. osborni*, occlusal (top) and labial aspects; mesial surfaces face left. Note difference in conformation of lamina 1. Scale = 1 mm.

aberrant molar. Such uncertainty in identification, combined with small sample size, does not allow a ready interpretation of the wide distribution in figure 13 (see also table 5). The MAXLL formula is  $1 < 2 > 3$  for the UP4 locus.

**MOLARS:** Mandibular molars are easily distinguished from other teeth by the “boom-

erang” shape of the occlusal surface of the first lamina. This trait progressively increases in markedness from LM1 to LM3 in AMNH 17634 and 108543 (fig. 8), the only two lower jaws preserving complete dentitions. However, I do not think that the shape and size differences in the first laminae of the mandibular molars are sufficiently marked to per-

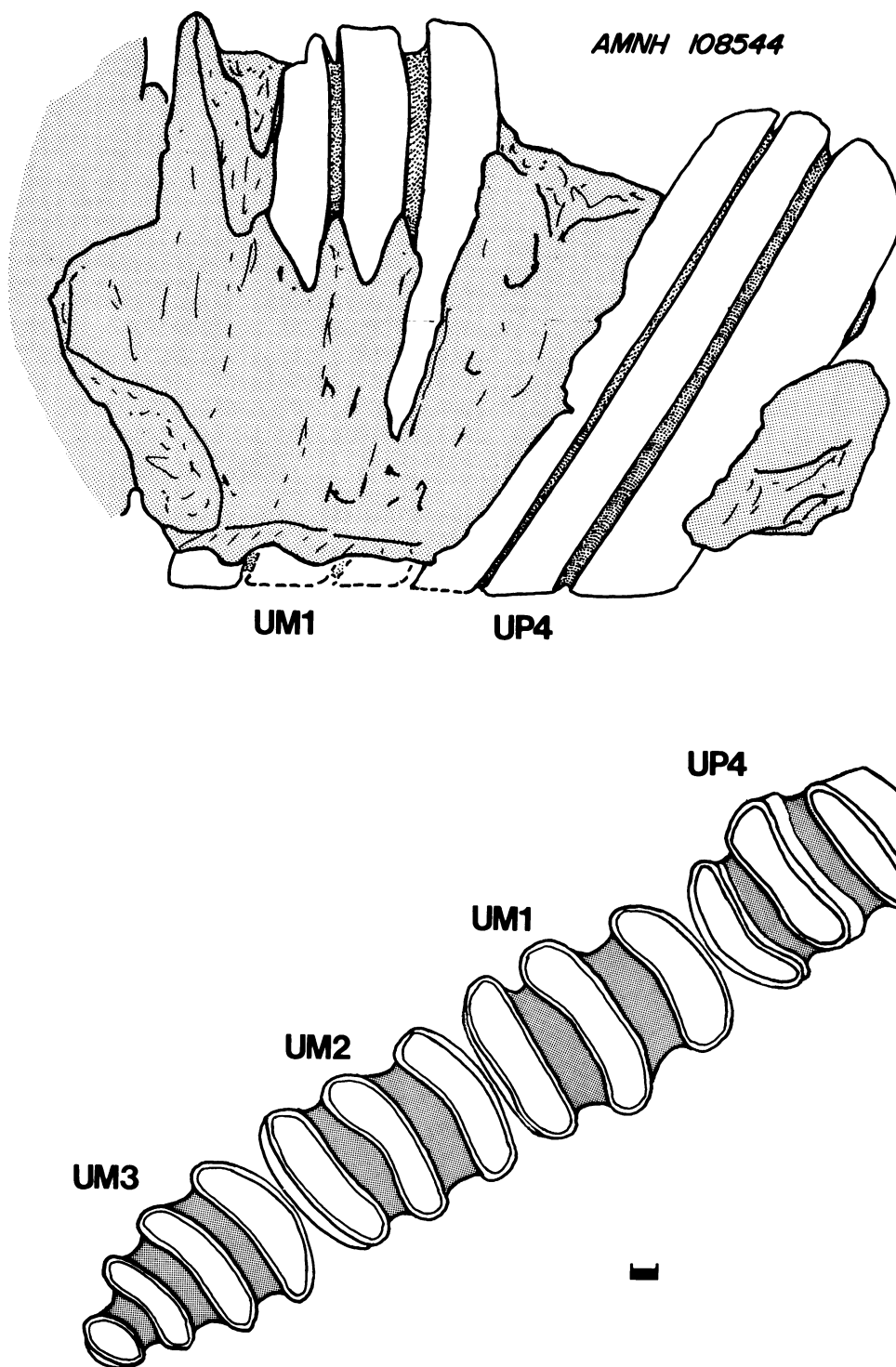


FIG. 10. The top illustration is of a left maxillary fragment referred to *C. osborni* (lingual aspect). Note obliquity of occlusal plane of UP4. In actual specimen, UM1 is rotated slightly out of position. The bottom part of the figure illustrates reconstructed occlusal aspect of left maxillary cheek teeth of *Clidomys*, based on several incomplete specimens. No recovered maxillae retain complete dentitions, and none possesses UM3 *in situ*. Scale = 1 mm (both drawings).

TABLE 4

LP4 of Jamaican Heptaxodontids (N = 13)<sup>a</sup>, Measurements (in Millimeters) and Descriptive Statistics

Specimens	MAXLL	MINMD	(MAXLL × MINMD)	L <sub>10</sub> (MAXLL × MINMD)	Descriptive Statistics (MAXLL × MINMD)
AMNH 108600	5.8	5.4	31.32	1.496	$\bar{X} = 44.08 \text{ mm}^2$
AMNH 17637 <sup>b,c</sup>	4.3	6.3	27.09	1.433	
AMNH 108543	4.3	6.3	27.09	1.433	
AMNH 108553	6.3	9.1	57.33	1.758	SD = 9.76 mm <sup>2</sup>
AMNH 17636 <sup>b,d</sup>	6.4	8.0	51.20	1.709	
AMNH 108551	6.5	7.3	47.45	1.676	
AMNH 108555	6.1	8.6	52.46	1.719	CV = 22.15
AMNH 108549	6.0	8.2	49.20	1.692	
UF 27438 <sup>e</sup>	5.7	7.1	40.47	1.607	
AMNH 108550 <sup>e</sup>	5.9	8.3	48.97	1.689	S <sub>cv</sub> (±) = 4.34
AMNH 108552	6.1	8.1	49.41	1.694	
AMNH 108556	6.0	7.6	45.60	1.659	
AMNH 108598	5.9	7.7	45.43	1.657	

<sup>a</sup> Rejected specimens (MINMD not determinable): AMNH 108554, 17634, 108542.

<sup>b</sup> Cast.

<sup>c</sup> Type of *C. parvus*.

<sup>d</sup> Type of *Speoxenus candalli*.

<sup>e</sup> Variant.

mit the allocation of isolated teeth to specific loci. In mandibular molars, the MAXLL formula is generally 1>2>3; in maxillary molars the laminae are frequently subequal.

Anthony (1920b: 474, fig. 3A, B) identified, with a question mark, the quadrilaminar teeth in his sample as UM3. His hesitation was presumably due to the fact that he did not recover any complete maxillary dentitions. I was no more fortunate in my investigations, but I have little doubt Anthony was correct in his determination. The teeth in

question are clearly from upper dentitions, and their frequency is too high within the sample for them to represent an anomalous version of some other locus.

I have considered the possibility that UM3 of *Clidomys* may be trilaminar, like the other molars, and that the quadrilaminar tooth may in fact represent DUP4. There is no evidence bearing on premolar ontogeny in *Clidomys*, and it is therefore not known whether deciduous premolars were permanently retained (as in echimyines and capromyines), or were

TABLE 5

UP4 of Jamaican Heptaxodontids (N = 9)<sup>a</sup>, Measurements (in Millimeters) and Descriptive Statistics

Specimens	MAXLL	MINMD	(MAXLL × MINMD)	L <sub>10</sub> (MAXLL × MINMD)	Descriptive Statistics (MAXLL × MINMD)
AMNH 108640/12	6.9	7.5	51.75	1.714	$\bar{X} = 47.03 \text{ mm}^2$
AMNH 108620	6.6	6.5	42.89	1.632	
AMNH 108623	6.3	6.3	39.69	1.599	
NRCD 1	5.8	6.2	35.96	1.556	SD = 15.99 mm <sup>2</sup>
AMNH 108618	5.8	6.1	35.38	1.549	
AMNH 108609	5.0	5.9	29.50	1.469	
AMNH 108640/6 <sup>b</sup>	8.9	9.3	82.77	1.918	CV = 33.94
AMNH 108640/5	7.5	7.6	57.00	1.756	
AMNH 108625	7.0	6.9	48.30	1.684	

<sup>a</sup> Rejected specimens (MINMD not determinable): AMNH 108554 and NRCD 3.

<sup>b</sup> If this specimen is excluded, descriptive statistics for (MAXLL × MINMD) become  $\bar{X} = 42.56 \text{ mm}^2$ , SD = 9.29 mm<sup>2</sup>, CV = 21.75, and S<sub>cv</sub> (±) = 5.13.



TABLE 6

## UM3 of Jamaican Heptaxodontids (N = 8), Measurements (in Millimeters) and Descriptive Statistics

Specimens	MAXLL	MINMD	(MAXLL × MINMD)	$L_{10}(\text{MAXLL} \times \text{MINMD})$	Descriptive Statistics (MAXLL × MINMD)
AMNH 108558 <sup>a</sup>	6.6	8.7	57.42	1.759	$\bar{X} = 71.34 \text{ mm}^2$
AMNH 108557	6.0	8.8	52.80	1.723	
AMNH 17635 <sup>b,c</sup>	6.0	8.5	51.00	1.708	
AMNH 108559 <sup>d</sup>	8.6	11.7	100.62	2.003	SD = 17.55 mm <sup>2</sup>
AMNH 108563	7.6	11.4	86.64	1.938	
AMNH 108562	7.8	10.5	81.90	1.913	CV = 24.60
AMNH 108560	6.8	10.4	70.72	1.849	
AMNH 108561	7.2	9.7	69.84	1.844	$S_{cv} (\pm) = 6.15$

<sup>a</sup> Variant.<sup>b</sup> Cast.<sup>c</sup> Type of *Spirodontomys jamaicensis*.<sup>d</sup> If this specimen is excluded, descriptive statistics for (MAXLL × MINMD) become  $\bar{X} = 67.19 \text{ mm}^2$ , SD = 14.02 mm<sup>2</sup>, CV = 20.86, and  $S_{cv} (\pm) = 5.58$ .

replaced by adult P4s as in caviomorphs generally (including, according to Ray's [1964] evidence, *Amblyrhiza* and *Elasmodontomys*). If deciduous premolars were retained, then the quadrilaminar teeth cannot be premolars because unequivocal premolar specimens (AMNH 108544 and NRCD 3, maxillary fragments with teeth *in situ*) are trilaminar, as are all other specimens assigned to this locus on the basis of the criteria discussed above. If replacement occurred, then it is odd that no quadrilaminar specimen shows signs of root closure or resorption, ontogenetic features commonly associated with deciduous premolars near the end of their functional life span.

UM3 may have a bimodal distribution, but the sample is too small for confidence (fig. 13).

**INCISORS:** The enamel of the incisors is colorless and coats only the outer aspect of these teeth. The enamel of lower incisors displays no obvious longitudinal grooves, but in upper incisors there are usually two faint channels, one medial and one lateral (medial deeper). In several mandibular fragments the incisor socket can be traced to a position below the third molar; the position of the upper incisors relative to other components of the rostrum is not known at this time. Incisors were not measured, but as in the case of other teeth only two size morphs are suggested by the available material.

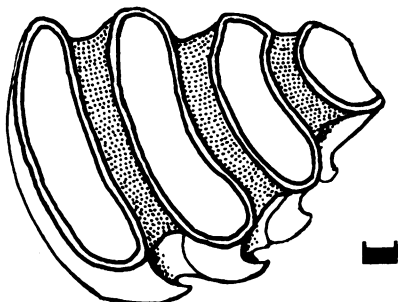
**VARIANTS:** About 11 of the 90 reasonably

complete cheek teeth in the total sample depart in some manner from the simple patterns of cementum-connected ellipses described above (fig. 12). Of these, three were designated as the types of new species by Anthony—AMNH 17635 (*Spirodontomys jamaicensis*), AMNH 17636 (*Speoxenus cundalli*), and AMNH 17638 (*Alterodon major*). The type of *Spirodontomys* resembles a small UM3 of *Clidomys*, save that laminae 3 and 4 are joined by a bridge. Similarly, the type of *Speoxenus* resembles a large LP4 of *Clidomys*, save that lamina 1 is replaced by two small, tubelike columns. The type of *Alterodon* does not resemble any other known Jamaican Pleistocene rodent tooth, but that is in part due to its incompleteness, a fact which Anthony (1920b) curiously failed to detect in making his diagnosis (MacPhee, Woods, and Morgan, 1983).

In addition to AMNH 17635a and 17635c, which Anthony (1920b) regarded as further examples of *Spirodontomys*, I found two other specimens of similar size and construction in the AMNH collections (AMNH 108558, 108565), as well as one much larger (AMNH 108545) in which only three laminae are present. This last specimen is attached to a maxillary fragment and can be securely identified as a right UM1.

Although they do not strongly resemble each other, another pair of variants, UF 27438 and AMNH 108616, differ from teeth previously described: their laminar organization

AMNH 108561



AMNH 108559

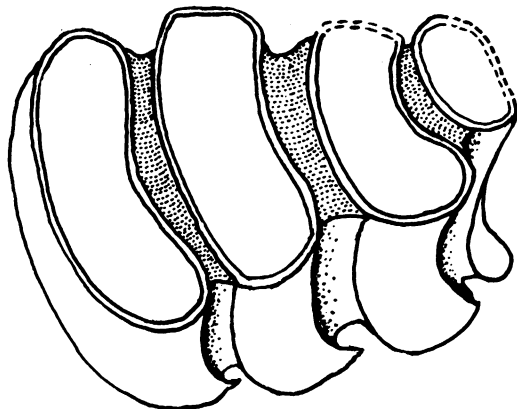


FIG. 11. UM3s referred to *C. parvus* (top) and *C. osborni*. Image of AMNH 108561 reversed to facilitate comparison with AMNH 108559. Mesial surfaces face left. Scale = 1 mm.

is not the same throughout their lengths, so that a cross-section taken at one position would not have the same aspect as one taken at another position. This, of course, is entirely unexpected on the basis of the patterns so far discussed, in which the laminae are completely separate from one another (or, if bridged, are bridged for their entire lengths). Except for the odd form of lamina 1, UF 27438 resembles a large *Clidomys* LP4. I am not sure precisely where AMNH 108616 should be placed because it is slightly damaged, but the shape of lamina 1 suggests that it is probably from the lower dentition, rather

than the upper, despite the tiny style next to lamina 3. AMNH 108550, identified as a LP4, also has a small style or projection, but in this case the style is continuous with lamina 3 for its whole length.

Anthony erected *Spirodontomys*, *Speoxenus* and *Alterodon* on the argument that the types were unlike any of the teeth he had previously allocated to *Clidomys*. This reasoning, in addition to being circular, makes no provision for distinguishing within-species and between-species variation. By application of Anthony's logic, two or three additional species (or genera) are needed to cover the new patterns described in the preceding paragraphs. This is surely unreasonable; why should several species each be represented by one or two fossils at most, while there are dozens of examples of the two forms of *Clidomys*? Clearly, in this case isolated teeth are not the best subjects for determining species boundaries. Some other approach is needed.

#### MORPHS, SPECIES, AND SEX

Loose teeth are often unhelpful or misleading indicators of the number of "good" species within a sample, especially when (as in the present case) it is extremely difficult to determine the locus of isolated specimens. Fortunately, the Wallingford Roadside sample includes some postcranial material as well. With appropriate reservations, postcranial elements can be used as the basis for making a reasonable interpretation of species diversity among the Jamaican heptaxodontids.

For the purpose of establishing a minimum number of morphs, the most useful elements in the sample proved to be calcanei and tali. Although few specimens were perfect, an adequate variety of measurements could be taken on the majority of them. Bivariate plots (fig. 15) of two combinations of these measurements (tables 7, 8) indicate that two clusters or morphs are present within the total sample, a "large" and a "small." Inspection of members of each morph establishes that there are no important differences, other than metric differences, between them. On average, the small morph's measurements are 75–85 percent of those of the large morph. Although none of the other postcrania is so well represented as these tarsal bones, the

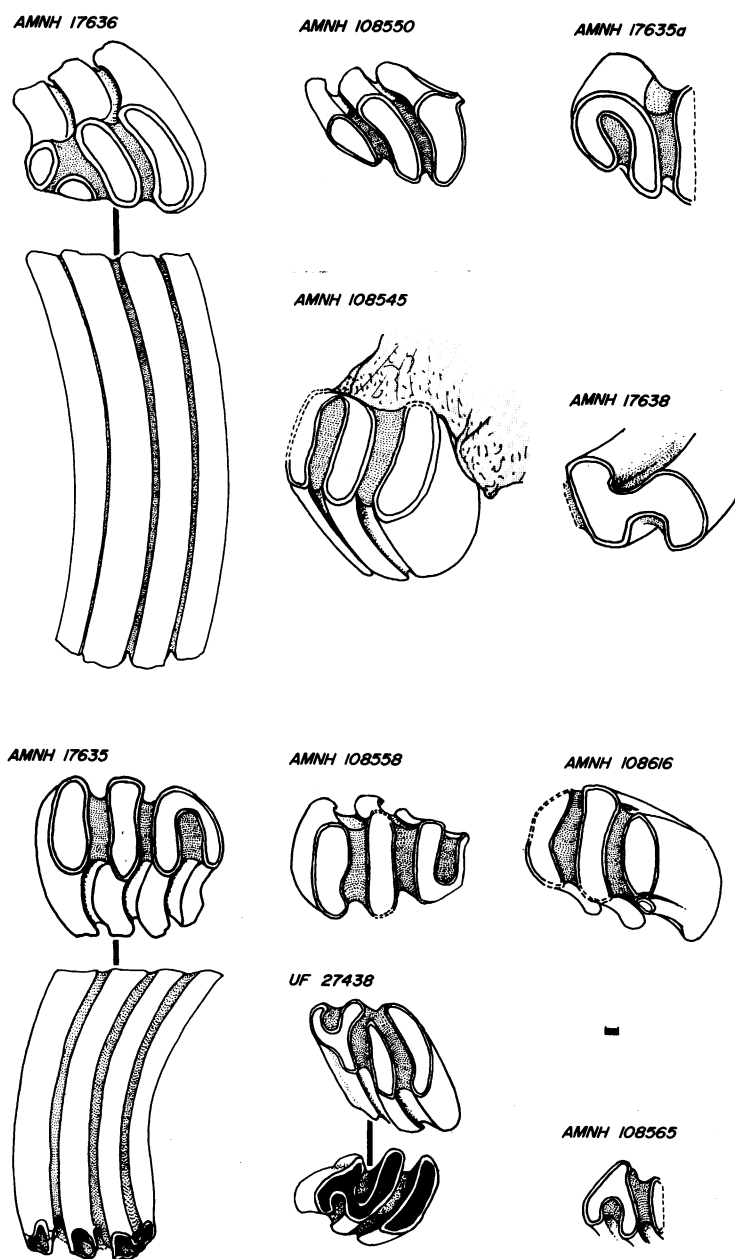


FIG. 12. Variant cheek teeth of *Clidomys* (see text). Complete teeth are oriented with mesial surface facing left, except for AMNH 108545, which faces right. Scale = 1 mm.

small/large pattern and 0.75:1 size ratio appear to be general throughout the skeleton (cf., figs. 8, 14A). Equally important, the degree of morphological correspondence between homologous skeletal elements of different size classes is universally great.

Having briefly characterized the nature of variation within the sample, it is necessary to come to some conclusion about what it means. One solution would be to recognize two species of one genus; another would be to regard the size variation within the sample

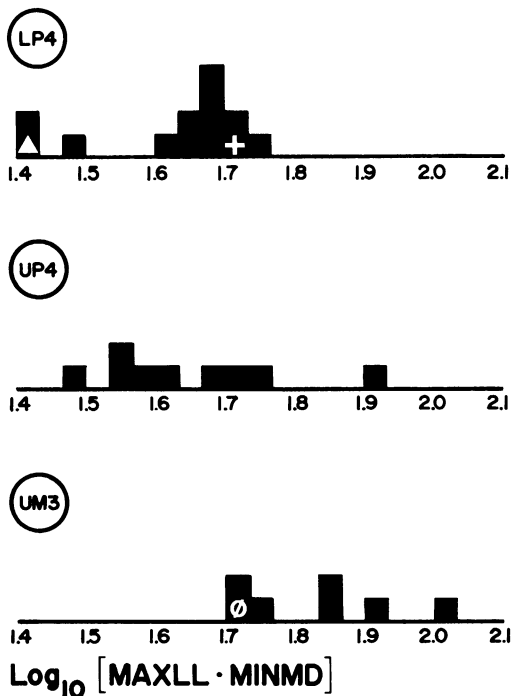


FIG. 13. Log-area variation at LP4, UP4, and UM3 loci in *Clidomys* (see fig. 6 and tables 4–6 for measurement data). White symbols identify type specimens: triangle, AMH 17637 (type of *C. parvus*); cross, AMNH 17636 (type of “*Speoxenus cundalli*”); and phi, AMNH 17635 (type of “*Spirodontomys jamaicensis*”).

as due to sexual dimorphism, in which case only one species need be retained.

Pronounced sexual dimorphism is rare among caviomorph rodents, although it does occur (e.g., in body weight in *Lagostomus* and *Chinchilla* [Walker et al., 1975]). Dimorphism has not been specifically reported for *Dinomys branickii*, a large-bodied terrestrial cavioid weighing between 10 and 15 kg (Walker et al., 1975), although analysis of Sanborn’s (1931) data points to low-order sex-related differences in the teeth (see table 9). The average female UM1, for example, is 91 percent the length of the average male UM1 in this species. It is not improbable that some extinct caviomorph “species” are actually sex morphs of one species, although I know of no investigations in which this possibility has been appropriately tested (but see Fields, 1957, on anomalously high coefficients of

variation for some teeth of the La Venta potamarchine dinomyid *Olenopsis aequatorialis*).

I used Anthony’s (1918) data on the dentition (table 10) and long bones (table 11) of the Puerto Rican heptaxodontid *Elasmodontomys obliquus*, in order to gain some idea of the level and pattern of variation in a possible relative of the Jamaican forms. As may be seen from the CVs, the teeth are moderately to highly variable (for  $\ln[L \times W]$ ), but the long bones are not. Some teeth are exceptionally variable (e.g., UM3), and isolated specimens might be uncritically used as evidence of more than one morph or species. However, since the long bones do not complement the teeth, I find no evidence for suspecting either that *Elasmodontomys* was notably dimorphic or that this genus contained a second species.

A different pattern is found in the sample from Wallingford Roadside Cave (tables 4–8). Each of the three most distinctive cheek teeth loci (UP4, LP4, UM3) is characterized by exceptionally high CV values. The values for tali and calcanei were also high in comparison to the long bone CVs computed for *Elasmodontomys*. In the absence of like measures of variation for other caviomorphs, I am forced to conclude that these high CVs imply the presence of two species at Wallingford Roadside Cave. To interpret them as sexual differences would imply a greater degree of sex-related skeletal variation than is found in any known caviomorph.

## CONCLUSIONS

1. Morphology and the pattern of variation within Jamaican Heptaxodontidae suggest that not more than two species are represented, *Clidomys osborni* and *C. parvus*.

Based on size considerations, the type of “*Spirodontomys jamaicensis*” must represent *C. parvus* and that of “*Speoxenus cundalli*” must be part of *C. osborni*.

2. The dental locus of the broken cheek tooth used to found the species “*Alterodon major*” cannot be precisely determined, but the large size of the specimen implies that it should be placed in *C. osborni*.

3. Reduction of valid heptaxodontid species from five to two essentially disposes of the

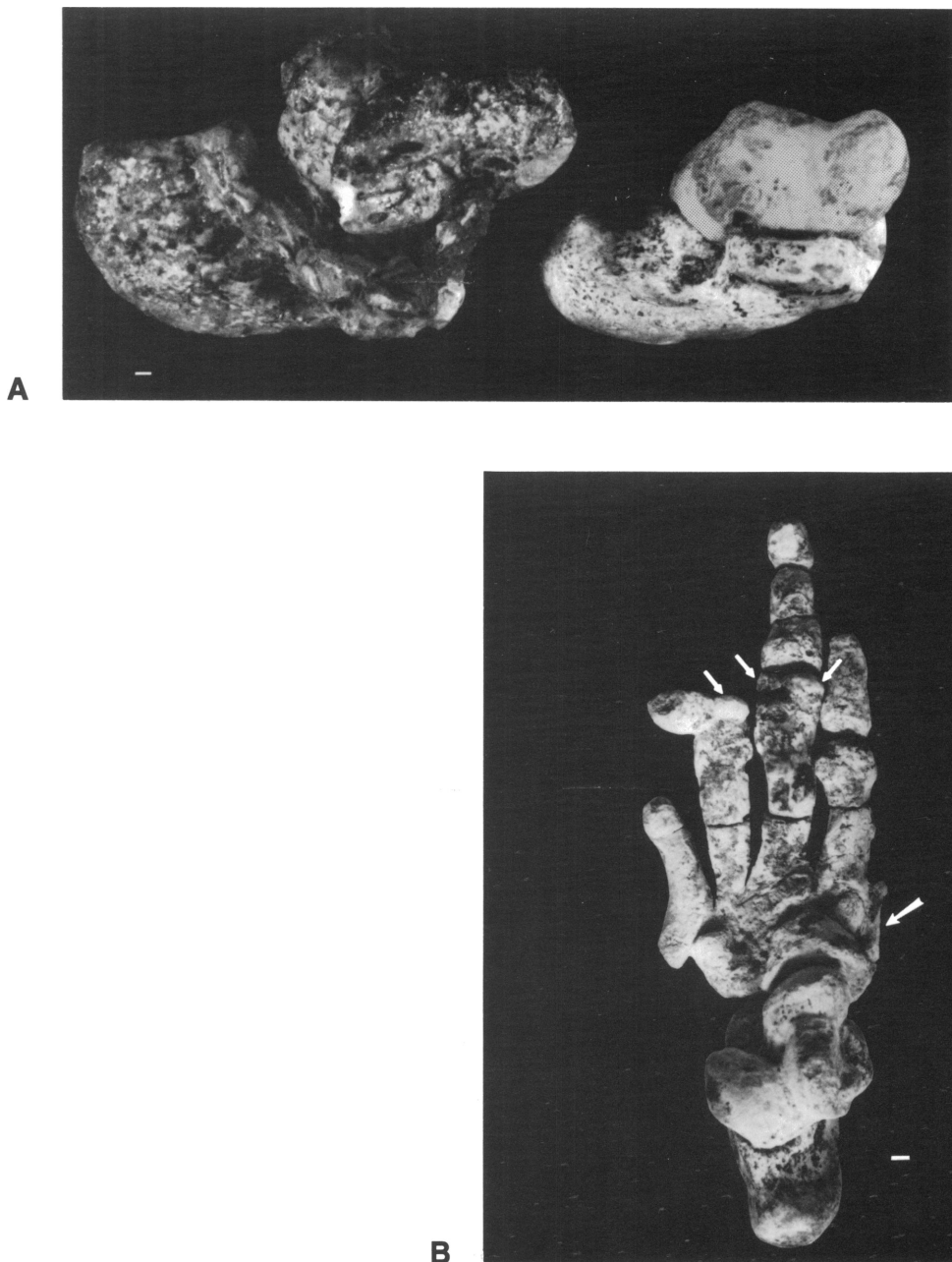


FIG. 14. (A), Calcanei and tali assigned to *C. osborni* (AMNH 108570, left) and *C. parvus* (AMNH 108596, calcaneus; AMNH 108574, talus). Elements comprising AMNH 108570 were found in articulation, although talus is rotated slightly out of position and calcaneus appears foreshortened in this photograph. Scale = 2 mm. (B), Articulated foot referred to *C. osborni* (UF 27401), found in matrix block in Patton collection from Wallingford I (Roadside Cave). Hallux evidently absent in *Clidomys*; (arrows points to entocuneiform). Small arrows point to metatarsal sesamoids, carried over toward dorsal surface as a result of postmortem shrinkage of extensor expansions and consequent hyperextension of metatarsophalangeal joints. Remarkable preservation of articulated elements proves that UF 27401 was not disturbed after initial emplacement in cave. Scale = 5 mm.

TABLE 7  
Calcanei of Jamaican Heptaxodontids (N = 7),  
Measurements (in Millimeters) and Descriptive  
Statistics<sup>a</sup>

Specimens	MEASUREMENTS	
	MAXL	MAXD
AMNH 108569	33.0	17.0
UF 27401	44.7	20.5
AMNH 108576	46.9	22.1
AMNH 108568	42.5	21.2
AMNH 108570	49.0	26.2
AMNH 108575	35.0	18.2 <sup>b</sup>
AMNH 108596	37.2	19.4

DESCRIPTIVE STATISTICS				
	$\bar{X}$	SD	CV	$S_{cv} (\pm)$
MAXL	41.2	6.2	15.0	4.0
MAXD	20.7	3.0	14.5	3.9

<sup>a</sup> Measurements are: MAXL: maximum anteroposterior distance, tuber calcanei to distal margin. MAXD: maximum superoinferior distance, highest point on talar facet to plantar surface.

<sup>b</sup> Estimate; specimen slightly damaged.

view that these late Pleistocene rodents underwent a significant radiation during their tenure in Jamaica.

4. The systematic paleontology of the Jamaican heptaxodontids may be summarized as follows:

Order Rodentia Bowdich 1821

Suborder Hystricognathi Tullberg 1899

Infraorder Caviomorpha Wood and Patterson 1958

Superfamily Uncertain

Family Heptaxodontidae (Anthony 1917) Simpson 1945

Genus *Clidomys* Anthony 1920 (incl. *Speoxenus*, *Spirodontomys*, and *Alterodon* Anthony 1920)

Species *C. osborni* Anthony 1920 (incl. *Speoxenus cundalli* and probably *Alterodon major* Anthony 1920)

*C. parvus* Anthony 1920 (incl. *Spirodontomys jamaicensis* Anthony 1920)

Definition of Genus *Clidomys*: Large rodent from late Pleistocene cave sites of

TABLE 8  
Tali of Jamaican Heptaxodontids (N = 7), Measurements (in Millimeters) and Descriptive Statistics<sup>a</sup>

Specimens	MEASUREMENTS	
	MAXL	MAXD
AMNH 108570	27.4	15.7
UF 27401	24.7	15.6
AMNH 108567	24.8	14.8
AMNH 108571	27.6	16.3
AMNH 108573	22.9	12.5
AMNH 108574	24.0	12.4
UF 27426	29.5 <sup>b</sup>	11.1

DESCRIPTIVE STATISTICS				
	$\bar{X}$	SD	CV	$S_{cv} (\pm)$
MAXL	24.4	2.8	11.3	3.0
MAXD	14.1	2.0	14.4	3.9

<sup>a</sup> Measurements are: MAXL: maximum anteroposterior distance, navicular facet to posterior notch in trochlear facet for tibia. MAXD: maximum superoinferior distance, highest to lowest points on navicular facet of head.

<sup>b</sup> Estimate; specimen slightly damaged.

Jamaica; not known to have survived into Holocene. Cheektooth dental formula 4/4; low-crowned, unrooted cheekteeth generally consisting of three independent enamel-enclosed dentine plates united by intervening cementum plaques (four plates in UM3). Premolar succession unknown. Head length of large species not less than 215 mm (based on reconstruction of fragmentary calvarium of *C. osborni* NRCD 5), or about midway between head lengths of confamilials *Elasmodontomys* (ca. 125 mm; Anthony, 1918) and *Amblyrhiza* (ca. 400 mm; Schreuder, 1933). Assuming that body length lay between 3.5 and 5 times head length (as it does in modern South American rodents), the large species of *Clidomys* was probably 750–1075 mm long, or well within the range of the largest living caviomorphs (*Agouti*, *Dinomys*, *Erethizon*, even small *Hydrochoerus*). *Clidomys parvus* was 20–25 percent smaller for equivalent measurements. Limb bones extremely robust. Foot structure resembles that of *Dinomys* more than any other living caviomorph: pedal digital rays 2 to 5 short, robust, and functional; metatarsal 1 reduced or pos-

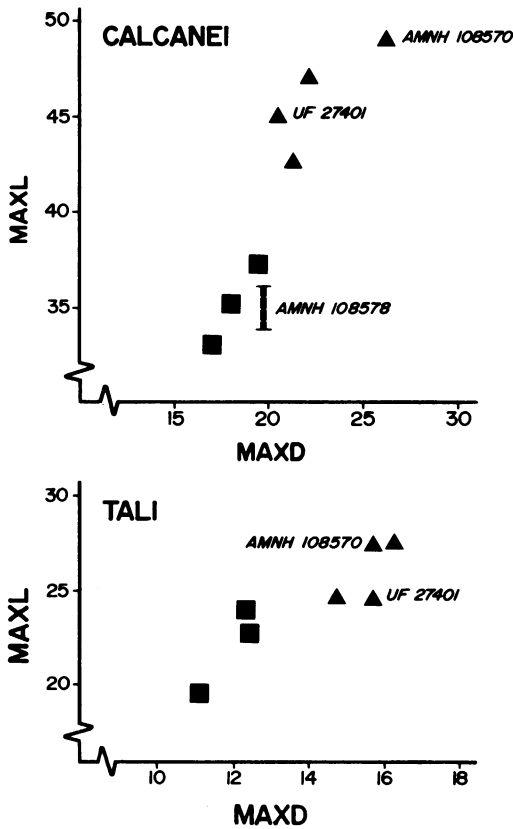


FIG. 15. Bivariate plot (in mm) of some tarsal dimensions of *Clidomys* sample (see tables 7 and 8 for measurement data). AMNH 108578, for which MAXD but not MAXL can be computed, has been included in order to extend the calcaneus sample size. Dashed line corresponds to 1SD on either side of MAXL mean (35.0 mm) for *small-sized* sample (i.e., AMNH 108569, 109575, and 108596). Other measurements, not discussed or illustrated here, yield similar clusters, with individual cluster means in approximate 0.75:1 relationship.

TABLE 9  
UM1 Crown Length (in Millimeters) in Adult and Subadult *Dinomys branickii*  
(Data of Sanborn, 1931)

	$\bar{X}$	SD	CV	$S_{cv} (\pm)$
Males (N = 5)	7.0	0.3	3.6	1.2
Females (N = 7)	6.4	0.3	4.9	1.3
Combined (N = 12)	6.6	0.4	6.3	1.8

TABLE 10  
Descriptive Statistics for the Natural Logarithm of Tooth Length Multiplied by Tooth Width ( $\ln[L \times W]$ ) in *Elasmodontomys*  
(Data of Anthony, 1918)

	N <sup>a</sup>	Range ( $\ln[L \times W]$ )	$\bar{X}$	SD	CV
UP4	6	3.99–4.22	4.13	0.09	8.8
UM1	7	3.96–4.19	4.06	0.07	7.4
UM2	9	4.05–4.33	4.17	0.10	9.9 <sup>b</sup>
UM3	8	3.74–4.20	4.00	0.17	16.4 <sup>c</sup>
LP4	8	3.89–4.08	3.92	0.09	8.7
LM1	10	3.62–4.10	3.89	0.14	13.4
LM2	11	3.94–4.26	4.09	0.09	8.8
LM3	9	3.79–4.18	4.01	0.13	12.8

<sup>a</sup> Rejected specimens: UP4 and UM1 of 17132 ("parts slightly broken") and UM3 of 17135 (tooth only partly erupted).

<sup>b</sup> AMNH 17132 was not used in this calculation. If used, CV for UM2 becomes 11.0.

<sup>c</sup> AMNH 17129 was not used in this calculation. If used, CV becomes for UM3 22.4. AMNH 17132 does not possess UM3.

sibly absent; entocuneiform gracile; and metatarsal 2 with greatly enlarged proximal styloid process on volar aspect (for long planar and plantar metatarsal ligaments?). No specializations for leaping, and almost certainly terrestrial.

5. In view of the absence of any known Cenozoic connections between Caribbean islands and continental landmasses, must one assume that the last common ancestor of the Antillean heptaxodontids was a raft-transported waif? This is perhaps an acceptable assumption given the limited facts, but one's willingness to suspend disbelief is strained in this instance by the requirement that several *additional* rafting events have to be inferred to explain the known distribution of heptax-

TABLE 11  
Greatest Length (in Millimeters) of Selected Long Bones of *Elasmodontomys*  
(Data of Anthony, 1918)

	$\bar{X}$	SD	CV	$S_{cv} (\pm)$
Femur (N = 10)	105.9	3.8	3.7	0.8
Humerus (N = 9)	84.9	4.0	4.7	1.1
Tibia (N = 10)	91.2	4.1	4.5	1.0

odontids in the Caribbean. If, for example, the heptaxodontid initiator landed on Jamaica in the mid-Tertiary, a minimum of three additional rafting events must have occurred in order to account for the existence of descendant lineages in Hispaniola, Puerto Rico, and the once-linked islands of the Anguilla Bank (Anguilla, St. Martin, and adjacent islets). It is difficult to understand how rafting among these islands could have taken place, since none of the Greater Antilles possesses rivers large enough to carry significant masses of floating vegetation. Yet the vicarist alternative—that all the important features of Caribbean vertebrate biogeography can be explained by complex plate motions—is no less improbable, since the motions involved were both initiated in and largely completed during the first half of the Mesozoic (see discussion by MacPhee, Woods, and Morgan, 1983). There were no eutherian mammals extant at that time, let alone separate lineages of insectivores, sloths, primates and rodents. For typical land mammals, a water barrier is a water barrier: the Straits of Florida, for example, were apparently formidable enough to keep North American mammals other than insectivores (MacFadden, 1980) out of Cuba, even during periods of depressed sea levels.

Given that waterways have separated the islands of the Greater Antilles from one another at least since the beginning of the Cenozoic, the routes of immigrating mammals had to have included some over-water transport, and vicariance events in the strict sense cannot have been responsible for the mammalian colonization of the Caribbean. Rafting hypotheses, it seems, still have to be preferred over others, if only because competing explanations (land bridges, foundered continents, vicariance) have more egregious weaknesses. In my view we are still far from possessing a good understanding of the processes that shaped Caribbean biogeography. The presence of a rodent as distinctive as *Amblyrhiza* in the far northeastern part of the Caribbean during the Quaternary should be considered as unusual—and as research-provoking—as the existence of a marsupial in Africa during the Oligocene (Bown and Simons, 1984). The recent discovery of an anole in a piece of Hispaniolan amber of Mio-

cene age (Rieppel, 1980) proves that obligate land vertebrates were in the Caribbean in the latter part of the Tertiary. The antecedents of many of the mammals were undoubtedly also there, and, once found, as ultimately they will be, some real light may finally be shed on the origins and vicissitudes of this remarkable fauna.

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