SUCCESSION OF MAMMALIAN FAUNAS ON TRINIDAD, WEST INDIES

By

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INTRODUCTION

Animal remains excavated from Indian middens constitute a source of valuable information to both the archeologist and the zoologist (Taylor, 1957). These materials are particularly significant, since they often can be accurately dated, in that they may provide information about the transition between Pleistocene and Recent time, a period in which world biotas underwent rapid changes (Burt, 1961). From the animals represented in a midden, much about the faunal composition of an area at a given time may be revealed. Changes in the range of certain forms may also be indicated. Such changes may in turn throw light on the nature of past ecological conditions in a given region. Midden remains occasionally include species that are new to science. More often, comparison of specimens from middens with those of the same species now inhabiting the region shows certain differences, analysis of which may lead to a better understanding of evolutionary processes. From an archeological standpoint, the study of animal remains from middens contributes to a more nearly complete understanding of the environmental milieu of the particular society under consideration. In addition it provides data on which to base cultural hypotheses as to the nature of hunting and butchering techniques, food taboos, and the non-alimentary uses of animals. By integrating data on fossil and recent faunas of the region a greater perspective on this type of assemblage is gained and thereby a better understanding of it.

Because of its dynamic geological history and attendant climatic and vegetational changes, Trinidad, West Indies, is of considerable zooarcheological interest. It has become separated from the mainland of South America, from which its fauna and aboriginal population were derived since it became inhabited by man.

The present study is an attempt to apply the zooarcheological approach in an analysis of the mammalian remains from aboriginal sites in Trinidad. These sites encompass a time-span from approximately 2750 years ago to historic times. In addition, an effort has been made to integrate this faunal assemblage with data on both pre-human and historic mammals in order to gain some knowledge of the history of the mammalian fauna of Trinidad from the Pleistocene to the present day as related to geologic, ecologic, and human factors.

MATERIALS AND METHODS

The materials upon which this study is based come from a number of sources. Many of the fossil finds on Trinidad have been made by Dr. H. G. Kugler in the course of his career as oil geologist for Texaco Trinidad, Inc. In 1922, he discovered a vertebrate-fossil-bearing stratum of oil sands while making a test pit at Apex (Trinidad) Oilfields, Inc. near Fyzabad. The fossils that were collected are in the Basel Natural History Museum collections. A similar deposit nearby at the Forest Reserve of Texaco Trinidad, Inc. was found in 1957 when the site was being cleared for oil well Number 1060. An almost complete skeleton of Glyptodon was excavated, and shipped along with some fragments to the American Museum of Natural History. None of this material has yet been prepared or catalogued. A carbon-14 date based upon wood associated with Megatherium bones was also taken at this site.

My husband and I conducted field work in Trinidad during the summer of 1959 with the objectives of collecting more fossil, midden, and Recent vertebrate material and of getting first hand knowledge of the ecology of the island. All specimens collected by us are deposited in the appropriate University of Florida Collection. An attempt to relocate the fossil locality at Apex was unsuccessful in spite of help from the Apex Company. At the site at Forest Reserve, several bones of larger mammals were collected, and a stratum containing small vertebrate fossils was discovered. The small fossils were extracted from the oil sands in which they were embedded by soaking large clumps of it

for several days in gasoline, then boiling the clumps to break them up, and finally washing the residue through screens. Initially 20, 140, and 230 gauge screens were used but since very few fossils went through the 20 gauge screen, subsequent batches were washed only through a 50 gauge screen.

The bulk of the midden materials was excavated by Dr. I. Rouse, Yale University, and Dr. J. M. Goggin, University of Florida, in 1946 and 1953, under the auspices of the Yale Caribbean Research Program and Graduate School of the University of Florida. Seven sites--St. Joseph, Mayo, St. John, Cedros, Erin, Palo Seco, and Quinam--were represented in these collections. The excavations were made by removing one or more sections two meters square. Each section was divided vertically into a number of levels 20 cm. in depth. The bones as well as the artifacts from each level were kept separate, so that stratigraphic changes could subsequently be analyzed. Another collection of midden bones which was available for study was made by Dr. Kugler at Cedros. This was not an excavation, but rather a surface collection. Additional material came from an excavation made at the Erin site by Mr. J. A. Bullbrook, of the Royal Victoria Institute. Although this site had been excavated in a manner similar to that employed by Rouse and Goggin, the bones were not kept segregated into their stratigraphic sequence.

In the summer of 1959, I visited six known archeological sites in Trinidad for the purposes of making ecological observations at each site and to collect additional surficial material. The sites

studied included Chagonaray, Palo Seco, Mayaro, Guayaguayare, Mayo, and St. John.

The zooarcheological material obtained from Trinidad middens was in quite good condition compared to similar material from other areas. Only about 50 percent of the material was too fragmentary to permit identification. Of the identifiable component, about 50 percent was mammal bones, and the remainder was fish, reptile, and bird. The mammal elements identified totaled 4884. In this study the "minimum number of individuals" is used as an index of the relative abundance of a particular species in a sample of midden remains. For each species this is determined by the count of the most numerous skeletal element in a given lot. In some cases this number may validly be increased by the addition of specimens of an age group not represented in a series of the most frequent element. For example, if the most abundant element of a given species in a level was the mandibular ramus and there were three right adult rami and one left juvenile ramus, the minimum number of individuals would be four.

Data on the modern fauna are derived largely from the literature and from my notes on Trinidad mammals. In the course of my own field work in Trinidad, Recent mammals were collected and their ecology studied, with emphasis on those forms which are of importance in middens. Smaller species were collected in traps. Since the large game animals are very scarce, I accompanied professional hunters, and acquired the unused parts of their catches. I also obtained many bones, particularly skulls and feet of wild mammals, in modern kitchen middens

around the hunters' houses. Further data on Recent mammals were obtained through the analysis of owl pellets collected by the late F. W. Urich of St. Augustine and lent to me by Dr. H. G. Kugler and Dr. S. Schaub from the Basel Natural History Museum.

Where adequate series were available, comparisons of skeletal measurements of midden and Recent mammals of the same species were undertaken with the aim of detecting differences in size that might perhaps be correlated with ecological or other factors.

POST-PLEISTOCENE HISTORY OF THE GEOLOGIC, CLIMATIC, AND VEGETATIONAL FEATURES OF TRINIDAD

For the understanding of the history of the mammalian fauna of Trinidad, a knowledge of the post-Pleistocene geological events, and the climatic and vegetational changes attendant upon them, is of primary importance. A brief sketch of these changes will, perhaps, aid in placing the history of the fauna of the island in its proper context.

Geology

Although Trinidad is commonly thought of as one of the Antilles, and is politically a member of the West Indian Federation, it is geologically and biologically closely associated with the South American mainland. The island is composed of sediments probably derived principally from the Guiana shield which extends roughly as far south as the present frontier of Brazil and includes Trinidad, and possibly Tobago, at the northern limits of its influence. According to Dr. Kugler (personal communication) several Pleistocene marine terraces are traceable, and he has recognized at least seven of these, ranging in elevation from five to 330 feet, which can be correlated closely with similar marine terraces in Venezuela. After the last glaciation, there was one continuous land mass encompassing what is now Trinidad, the Gulf of Paria, the Serpent's Mouth, and Venezuela. Thereafter a general trend of rising sea level is observable. Koldewijn (1958) states that the shoreline at an estimated 17,820 years ago was at the present 24-fathom line (Figure 1). By about 8,000

years ago (Figure 2), the shoreline had risen to the present 12-fathom mark (Nota, 1958). Roughly 700 years ago, the drainage of the Manamo Branch of the Orinoco River into the Gulf of Paria increased in volume, thereby further enlarging the Gulf, and completing the separation of Trinidad as an island from the mainland (Koldewijn, 1958). At the present time, the Island is subsiding, as is evidenced by the coastal erosion indicated by the landslips onto the beaches. Many instances can be seen of roads that have been completely undermined by wave action and of coconut palms lying uprooted on the beach. The Chagonaray site on the south coast is being washed into the sea.

Trinidad may be divided into five physiographic regions (Beard, 1946). The first of these comprises the mountains of the North Range (Figure 3). Although there are three ranges in Trinidad only the North Range, which is an extension of the coastal cordillera of Venezuela, may be considered to be actually mountainous, with elevations over 3,000 feet. The Central and South ranges constitute the second region. The elevation of these hills scarcely exceeds 1,000 feet. Just south of the North Range lies the third region, one of dissected alluvial terraces, formed of material from the mountains. The fourth and most extensive region is the dissected peneplain. This division includes all of the rest of the land except for a few coastal swamps which comprise the fifth and final region.

Climate

As a result of its insular nature and varied physiographic features, Trinidad has a somewhat varied climate. The most notable

Figure 1: The shoreline of Trinidad about 17,820 years ago. The solid line is the present 24-fathom mark which corresponds to the former shoreline, and the dotted line denotes the present geographic features of the area.

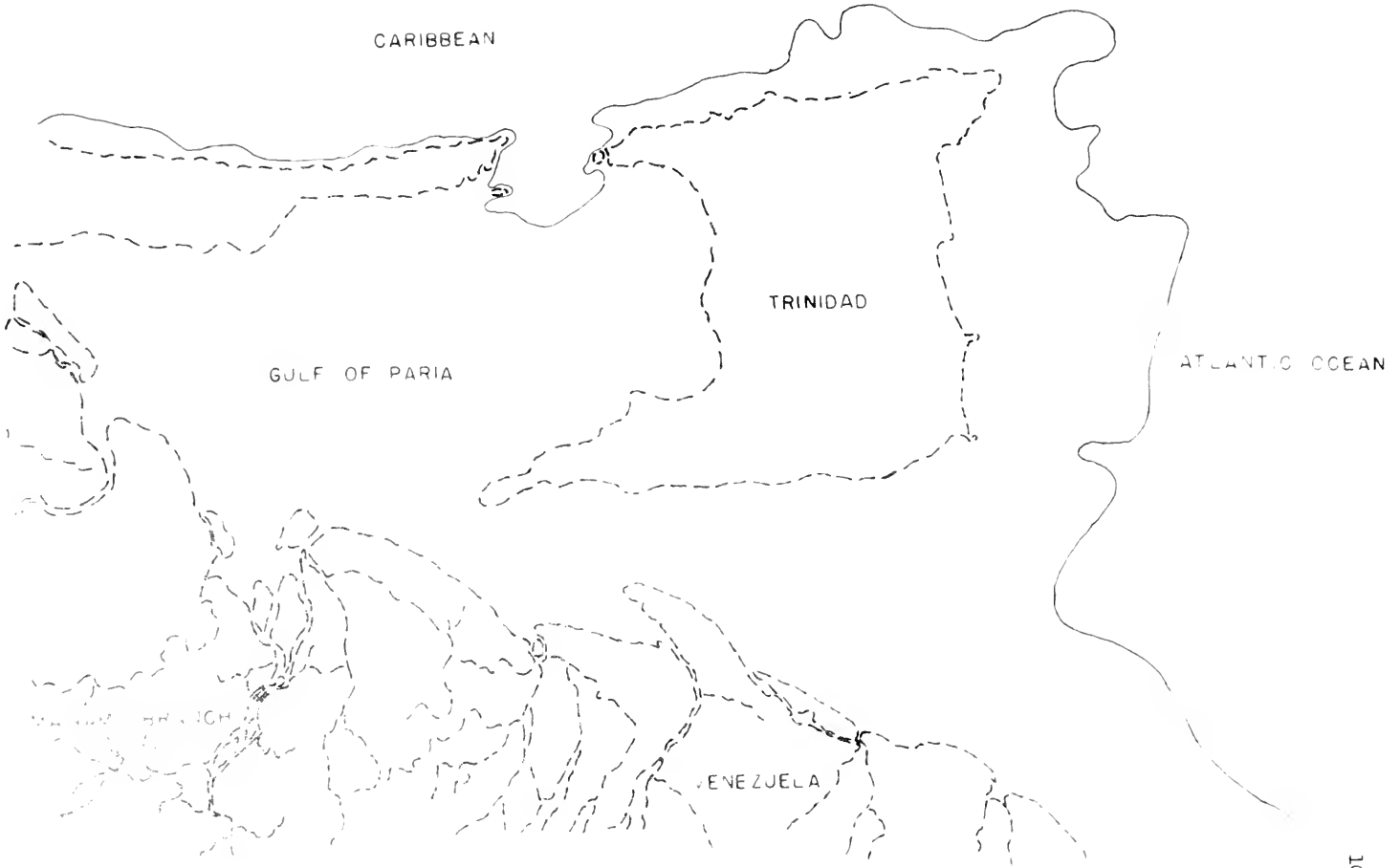

CARIBBEAN
TRINIDAD
GULF OF PARIA
ATLANTIC OCEAN
VENEZUELA

Figure 2: The shoreline of Trinidad about 8,000 years ago. The solid line is the present 12-fathom mark which corresponds to the former shoreline, and the dotted line denotes the present geographic features of the area.

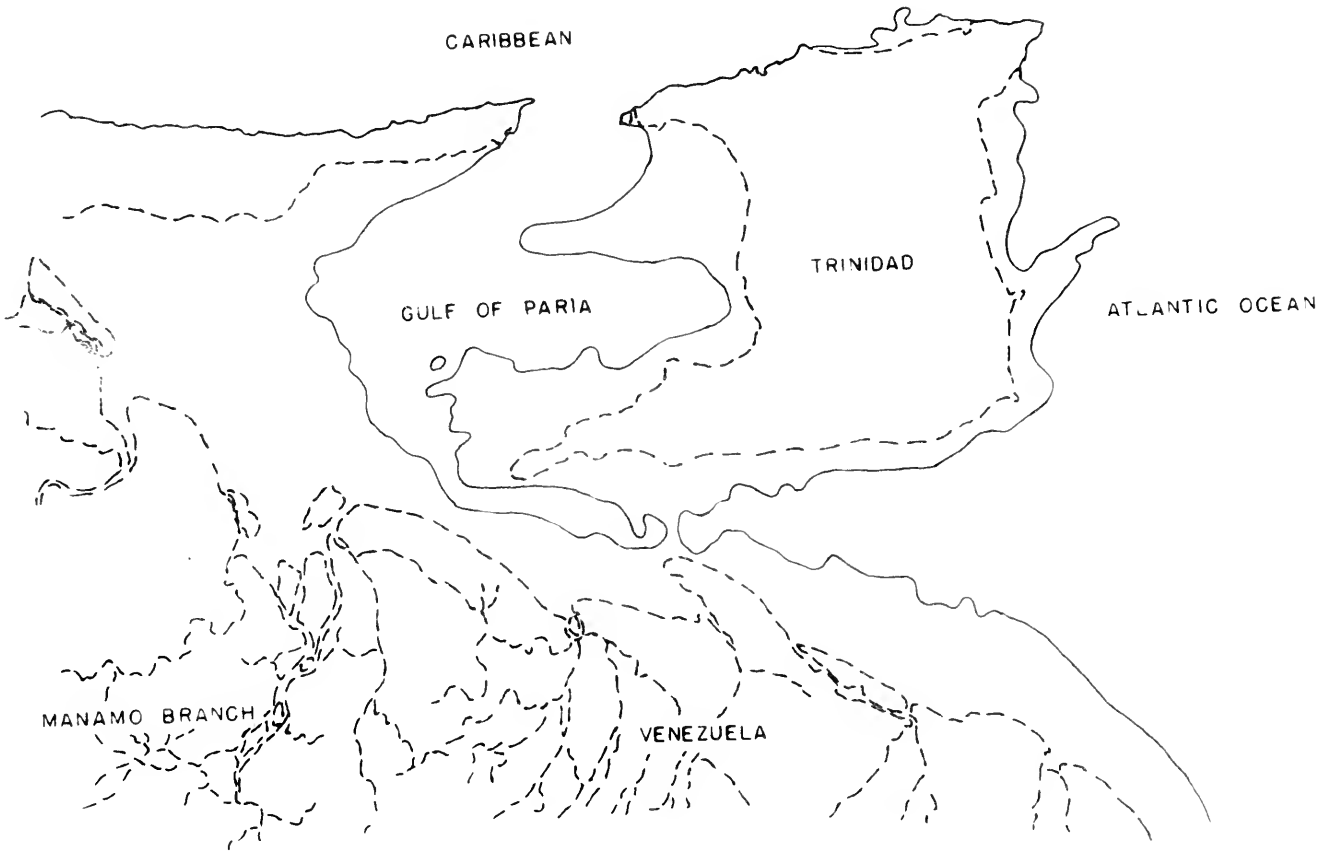
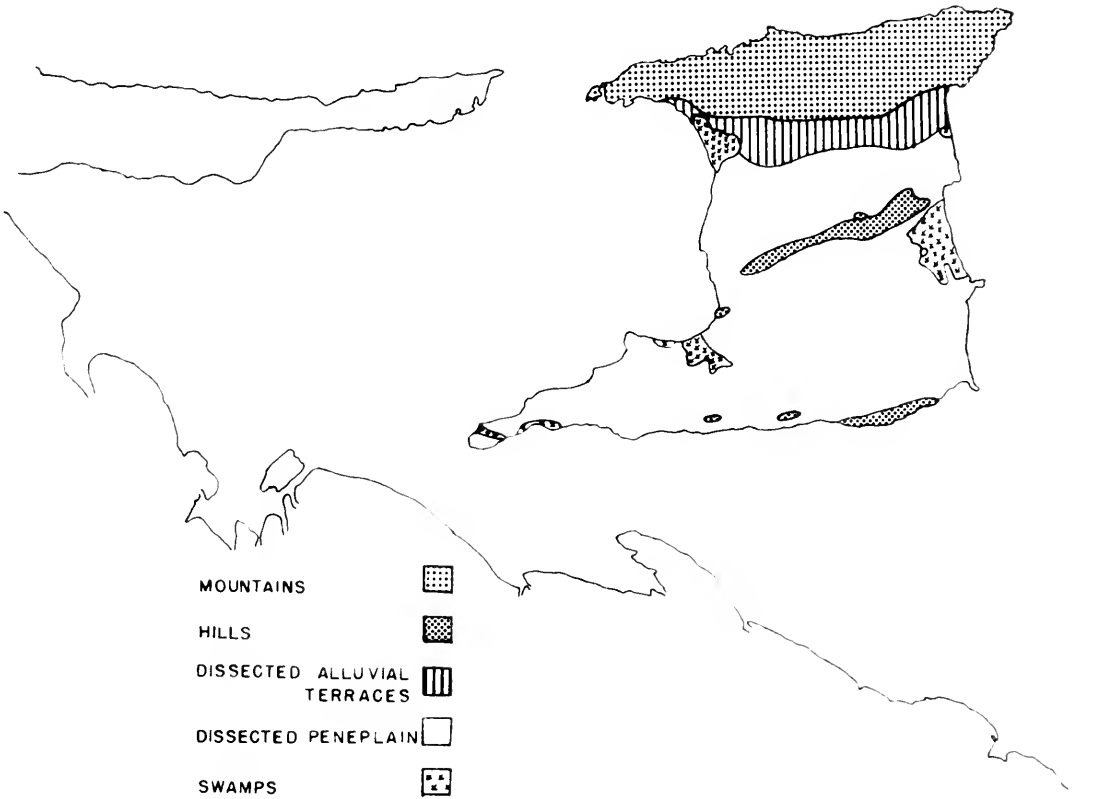

CARIBBEAN
TRINIDAD
GULF OF PARIA
ATLANTIC OCEAN
MANAMO BRANCH
VENEZUELA

Figure 3: The physiographic regions of Trinidad.
(after Beard)


MOUNTAINS
HILLS
DISSECTED ALLUVIAL TERRACES
DISSECTED PENEPLAIN
SWAMPS

climatic zone is the montane region of the North Range, which is characterized by heavy rainfall of at least 200 inches per year and an almost continual cloud cover. The remainder of the island experiences a seasonal climate, with two dry seasons from January through April and September through October, and two rainy seasons, as the result of shifts in the tradewinds from northeast to southeast. The windward coastal strip is affected by the wind and salt spray, and is therefore somewhat drier than the rest of the island. Rainfall data for selected stations, provided by the West Indies Meteorological Service, are presented in Table 1.

Evidence indicates that temperatures in the area of Trinidad underwent an increase, beginning about 16,500 years ago, reaching a maximum at 6,000 years ago, and thereafter declining slightly (Emiliani, 1955). The enlargement of the Gulf of Paria may have had a moistening influence on Trinidad. Present day temperatures vary in the different parts of the island, but on the whole are generally equable. The temperature ranges at Port-of-Spain, representative of the seasonal climate, vary from the average monthly maximum of 86.4° F. in January to 89.8° F. in May, and from the average monthly minimum of 67.6° F. in February to 71.8° F. in September. Daily temperature fluctuation is almost constant, ranging from a maximum of 18.9° F. in February to a minimum of 16° F. in September. Humidity always exceeds 50 percent and often approaches 100 percent at night (Beard, 1946).

TABLE 1

RAINFALL DATA (IN INCHES) FOR SELECTED STATIONS ON TRINIDAD

Station	Number of Years	Jan. - April	May - August	Sept. - October	Nov. - December	Total
Oropouche Police Station near St. John's site	20	9.33	30.30	12.68	12.34	64.65
Perseverance Estate, Cedros	20	13.06	25.46	8.61	11.69	58.82
Erin Police Station	16	9.53	23.05	6.87	9.52	48.97
Mayaro Police Station	20	14.91	35.45	13.98	18.89	83.23
Brothers Estate, Williamsville, Montserrat Hills	20	11.61	37.22	15.40	18.40	82.63

Vegetation

Striking changes in the vegetation of Trinidad have accompanied the geologic and climatic events that have influenced the island. The following discussion of the vegetation is based upon Beard's monograph (1946) The Natural Vegetation of Trinidad. At the time when there was a continuous land mass including Trinidad and the mainland, there was also an extension of the vegetation types of Venezuela into Trinidad (Figure 4). The North Range was forested, as were some of the higher parts of the Central and South ranges, while the remainder of what is now Trinidad and the Gulf of Paria were occupied by savannah. The savannah was dissected by streams bordered by gallery forest. The savannah formation which is now widespread in Venezuela as the "llanos," reaches to within 50 miles of the Gulf of Paria and persists as relics in a few small areas on Trinidad itself. The distribution of savannahs on Trinidad is controlled by edaphic factors. They occur in flat areas where the soil is poorly drained and the subsoil is impermeable. The soils became rejuvenated, accompanying geological changes in the area, and this resulted in the spread of forests from the streams and hills, eventually to cover nearly the entire island.

Particular climatic and edaphic factors influenced the development of several vegetational types. Beard (1946) recognizes six major plant formations (Figure 5): seasonal forest; dry evergreen forest; montane forest; intermediate forest; swamp; and marsh. Four of these are further divisible into associations. The seasonal formation

includes evergreen, semi-evergreen, and deciduous forest depending upon the availability of moisture.

The evergreen seasonal forest requires 70 inches or more of available moisture, and is characterized by a discontinuous emergent stratum more than 100 feet in height, and " . . . an almost continuous canopy layer at 40-90 feet, and almost continuous lower story at 10-30 feet" (Beard, 1946, p. 38). Lianas and epiphytes are common. Conspicuous species of trees are Spondias mambin (hogplum), Carapa guianensis (crappo), Eschweilera subglandulosa (guatecare), Pantaclethra macroloba (bois mulatra or fineleaf), Maximiliana elegans (cocorite palm), and Mora excelsa (mora). The largest trees are buttressed, and many are important sources of food for wild animals.

The semi-evergreen seasonal forest exists where 50-70 inches of available moisture occurs. It is an open forest characterized by " . . . a discontinuous emergent layer at 60-80 feet, and an almost continuous layer at 20-40 feet" (Beard, 1946, p. 38). Lianas are very abundant, but epiphytes are not. Buttressed trees are rare. Common species are Bravasia integerrima (jigger-wood), and Hura crepitans (sandbox).

The third form of seasonal forest, the deciduous, occurs in areas of 30-50 inches of available moisture. It is characterized by having a continuous canopy at 10-30 feet, and a few emergent trees up to 60 feet in height.

The dry evergreen or littoral woodland formation occurs along the coastal strip which is exposed to continual wind off the ocean.

Figure 4: The Pleistocene vegetation of Venezuela and Trinidad. (after Beard)

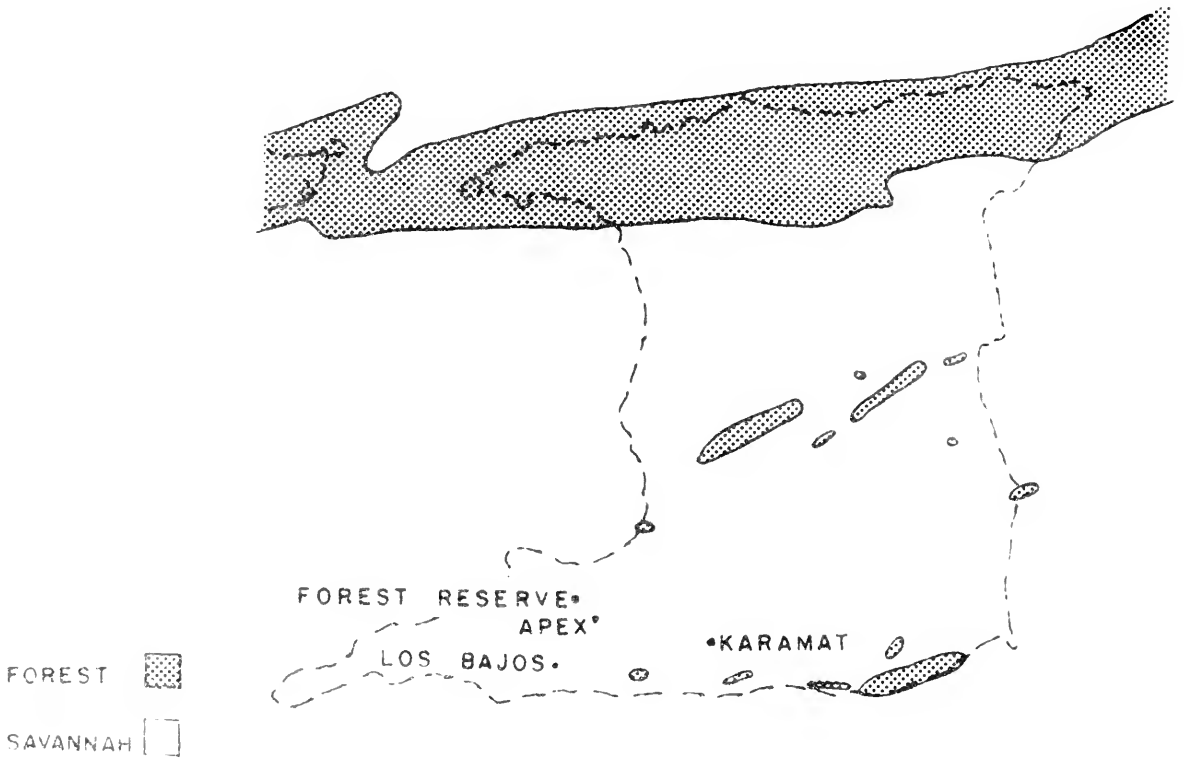
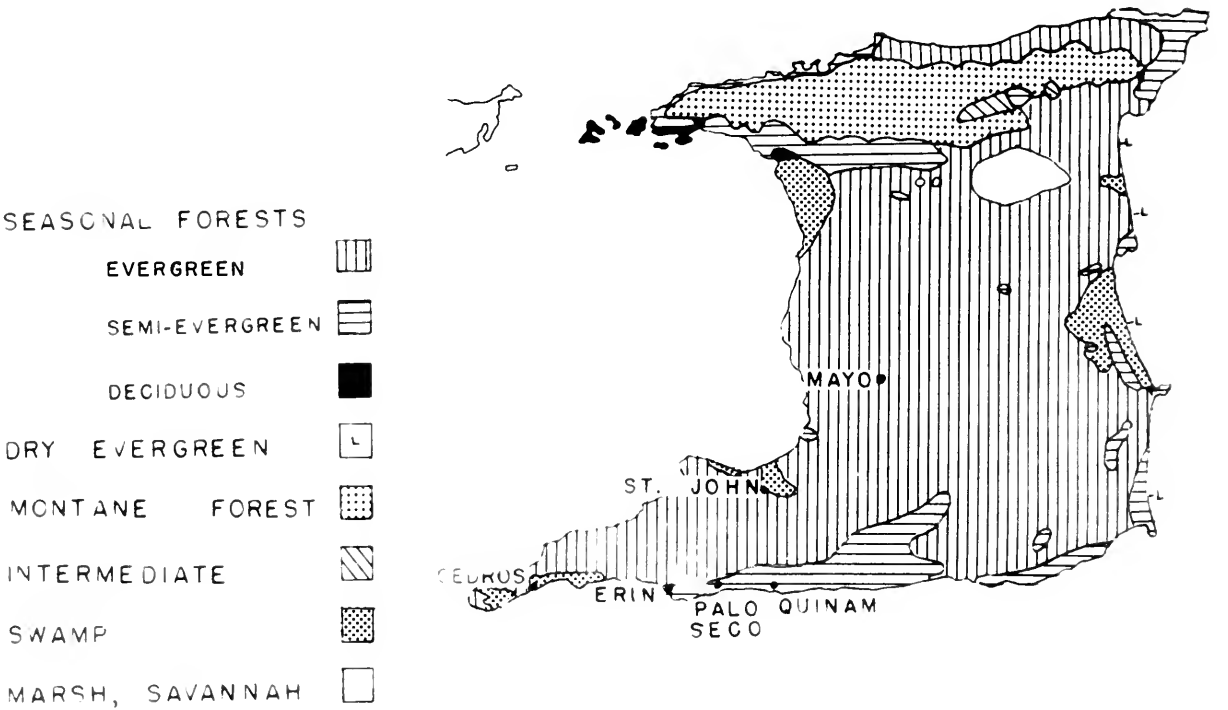

FOREST RESERVE
APEX
KARAMAT
LOS BAJOS
FOREST
SAVANNAH

Figure 5: The pre-Columbian vegetation of Trinidad.
(after Beard)


SEASONAL FORESTS
EVERGREEN
SEMI-EVERGREEN
DECIDUOUS
DRY EVERGREEN
MONTANE FOREST
INTERMEDIATE
SWAMP
MARSH, SAVANNAH
MAYO
ST. JOHN
ERIN
PALO SECO
QUINAM

Two associations of this formation exist in Trinidad: the Coccoloba uvifera-Hippomane mancinella (sea grape-manchineel), and Roystonea oleracea-Manilkara bidentata (palmiste-balata).

Beard divides the montane formation into three association: lower montane rain forest, montane rain forest, and elfin woodland. These replace one another at successively higher altitudes. The height of the canopy decreases with increasing altitude, from 70-100 feet in the lower montane rain forest, to 60 feet in the montane forest, to 15-25 feet in the elfin woodland.

The intermediate or seasonal montane formation is intermediate in characteristics between the seasonal and the montane formations.

The swamp formation is composed of four types: swamp forest, palm swamp, herbaceous swamp, and mangrove woodland. The greatest area of swamp forest is the Oropouche swamp. In it the principal tree species is Pterocarpus officinalis (swamp blackwood), which form a closed canopy at 60 feet and is conspicuously buttressed. The species of palm occurring in the palm swamps near the sea is Roystonea oleracea. The marsh formation consists of marsh forest, palm marsh, and savannah. The swamp and the marsh formations develop under the influence of particular edaphic factors. The marsh formation is characterized by only seasonal inundation and the swamp formation by permanent inundation. Savannahs of the marsh formation are characterized by a dominant short bunch-grass, and a scattering of gnarled shrubs attaining a height of up to 12 feet. Several species of grasses occur, and the chief shrubs are Byrsonima crassifolia

(Savanna serratta) and Curatella americana (roughleaf) or Chrysobalanus pellocarpus (fat pork). These fire-resistant shrubs have in some areas replaced the former Myrcia-Roupala association which still occurs widely in the Venezuelan llanos.

The natural condition of the vegetation as sketched above has been markedly modified in recent times by the agricultural activities of man. About half of the Island is still forested. The land that is under cultivation was formerly principally seasonal forest. Cocoa and coffee are grown mainly in the North and Central Ranges, whereas sugar cane is grown in the flatter area between these ranges. Rice is cultivated in the swamp areas and coconuts along the coast, particularly the east coast. There has been some reforestation with teak in the southern watershed.

THE PRE-HUMAN MAMMALIAN FAUNA OF TRINIDAD

The samples of the mammalian fauna from the three different time periods to be treated will be considered separately. The oldest period, represented by fossils, may be designated the pre-human. The Recent fauna, representing two periods, is composed of Indian midden bones and of specimens from a period that may be termed the historic. The time range for the pre-human period includes the Pleistocene epoch and probably the early post-Pleistocene as well. A carbon-14 date of greater than 34,000 years has been determined from wood associated with Megatherium remains at a depth of 12 feet at Trinidad's most important fossil locality at Forest Reserve, the so-called Glyptodon site. During this time Trinidad was still broadly connected with the South American mainland, and savannah dissected by streams edged with gallery forest covered the area.

The pre-human fauna of Trinidad known at present is small, reflecting the limited amount of collecting carried out in this field. The fauna is represented by three orders: Edentata, Rodentia, and Proboscidea. The edentates are represented by the families Megatheriidae, Mylodontidae, and Glyptodontidae, the rodents by the Cricetidae, and the proboscidians by the Gomphotheriidae. All of these families, excepting the Cricetidae, are now extinct.

Fossil Mammals of Trinidad

Megatheriidae

This family is represented by Megatherium americanum Blumb.,

which has been found at several localities. An astragalus was found at Karamat mud volcano and identified by Schaub (1935). Parts of a skeleton were found at Los Bajos. The site at Forest Reserve also yielded Megatherium remains. Part of a tooth found at the time the Glyptodon skeleton was excavated (1957), and along with the other materials, was sent to the American Museum of Natural History. In 1959 I found many dermal bones, a complete fourth tarsal, a complete tibia and fibula, part of a mandibular ramus, a rib, and three thoracic vertebrae. This fossil site is by far the most productive on Trinidad. It is a river bed cut to a depth of 15 feet into Miocene sands and clays, and filled with oil impregnated silt, sand, clay stone pebbles, plant remains ranging from large logs to twigs and stems, and vertebrate and insect fossils. This site is known locally as the "Glyptodon site."

Mylodontidae

A single tooth of Mylodon sp. was excavated along with other materials at the "Glyptodon site" and has been identified by me. It is now deposited in the collection of the American Museum of Natural History.

Glyptodontidae

An almost complete Glyptodon skeleton, from which the "Glyptodon site" takes its name, was found while the oil well site was being prepared in 1957. Almost the entire skeleton was found in place, and is now, unprepared, at the American Museum of Natural History.

I found abundant dermal bone but no other skeletal parts while working at this site.

Cricetidae

At the "Glyptodon site" I found a layer with a concentration of small vertebrate remains two feet above the layers containing the large bones and logs. A single mammal was represented which is referable to the genus Zygodontomys. Associated with the Zygodontomys are unidentified remains of a few birds, a turtle, a frog, and many insects. Another site containing small vertebrate fossils is at Apex near the "Glyptodon site" and geologically similar to it was found by Dr. Kugler. Zygodontomys sp., the only mammal represented, is associated with bird and insect remains (Blair, 1927).

Named species of the genus Zygodontomys are distributed in northern South America and southern Central America. Forms of Zygodontomys have been described from south of the Amazon River, from northeastern Brazil and the Matto Grosso, but these are included correctly in the genus Akodon (Tate, 1939). Tate (1939) divides the Zygodontomys into two primary groups of small and large size. Included in the group of large-sized species is Zygodontomys brevicauda, which occurs abundantly on Trinidad, and other species distributed in Panama and northern Colombia. The group of small-sized species include ones distributed in Central America, Colombia, Venezuela, and the Guianas. Tate (1939) also reports that among the specimens referable to Zygodontomys microtinus stellae from the Esmerelda savannahs at the foot of Mt. Duida there are some individuals

with a normal upper molar tooth row of 4.2 mm. and there are others with the shortest known tooth row of 3.7 to 3.8 mm. for this genus. Gyldenstolpe (1932) notes that Zygodontomys thomasi distributed in the Cumana district of Venezuela is allied to Zygodontomys brevicauda but is much smaller. The fossil Zygodontomys from Trinidad is also similar to Zygodontomys brevicauda but a great deal smaller.

Since the fossil material is largely fragmentary only a few measurements could be taken. The most useful ones were the alveolar length of the upper and lower cheek tooth rows. A comparable set of measurements was taken on Zygodontomys brevicauda from owl pellets found by F. W. Urich on Trinidad, Zygodontomys microtinus stellae from Esmeralda Savannah, Venezuela, and Zygodontomys thomasi from Cristobal Colon, Venezuela. These were taken to the nearest one tenth of a mm. and appear in Table 2.

The fossil Zygodontomys differs from the other species of Zygodontomys available for comparison in several respects. The most outstanding characteristic of the fossil form is its small size (Table 3). Additional characteristics that distinguish the fossil are exceptionally long anterior palatal foramina and deeply concave zygomatic plate. In the younger individuals (specimens with unworn teeth) the foramina extend posterior to the level of the posterior lingual root of the first molar. In the oldest individuals of the fossil (with heavily worn teeth) and in young individuals of other species the foramina extend posteriorad only to the anterior root of the first molar. Diagnostic dental characteristics include a deep anterior median fold in M^1, a broad U-shaped

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF THE ALVEOLAR CHEEK TOOTH ROW OF VARIOUS SPECIES OF ZYGODONTOMYS

		Number	Mean	Range
Zygodontomys sp.	upper	7	3.7	3.3-4.1
	lower	24	3.6	3.1-4.3
Z. thomasi	upper	5	4.6	4.2-4.9
	lower	6	5.1	4.9-5.2
Z. brevicauda	upper	13	5.1	4.7-5.6
	lower	--	--	--
Z. microtinus stellae	upper	6	4.1	3.8-4.2
	lower	6	4.1	4.0-4.3

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF FOSSIL ZYGODONTOMYS

Specimen Number	Length of Nasals	Length of Frontals	Least Inter-orbital Breadth	Length of Palatal Foramen	Width of Zygomatic Plate	Length of Mandible	Height of Mandible
1	7.6	--	3.7	--	2.3	11.5	3.0
2	8.0	--	--	--	2.0	--	--
3	7.4	7.1	3.3	5.0	2.3	11.5	3.0
4	--	--	--	4.8	2.0	--	--
43	8.5	7.8	3.4	6.2	2.8	13.0	3.2

first primary fold, and presence of a mesostyle, anterior labial style, anterior lingual style, or enterostyle in the M^1 and M^2. The anterior median fold is exceedingly well developed and is present in all specimens except those in which it is obliterated by excessive wear. This fold is otherwise present in only a few specimens of Zygodontomys brevicauda and in these it is merely a vestige. The first primary fold is broad in the fossil specimens and narrow in the other species. In the M^1 the mesostyle is present in all of the specimens and the other three styles occur in between 64 percent and 73 percent of the 16 specimens. In the M^2 the enterostyle is present in 78 percent of the nine specimens and the mesostyle in 67 percent. No styles are found in any of the other species. In the lower cheek tooth series the mesostylid is present on the M_2 in 94 percent of the 17 specimens. The articular process of the mandible is also distinctive, being short and broad, whereas in the other species it is long and narrow.

According to Tate (1939), "The South American Zygodontomys appear to be a grassland-inhabiting group of mice. I have little doubt they extend southward from Sucre across the llanos to the Orinoco and continue into Guiana wherever savannas exist." It appears, therefore, that when the llanos extended into Trinidad there was opportunity for the spread of this genus into Trinidad from South America.

Gomphotheriidae

Cuvieronius hyodon (Fischer) is represented by two teeth found at Los Bajos and identified by Schaub (1935), part of a tooth found oridinally at the "Glyptodon site," and another fragment of a tooth found by me at the same site.

Zoogeographic Significance of Pre-human Fauna

The known fossil fauna of Trinidad is sparce in numbers of species. Further collecting will probably increase this number considerably. The Edentates are of South American origin but the three genera, Megatherium, Mylodon, and Glyptodon, found in Trinidad were distributed throughout much of both North and South America in the Pleistocene. Megatherium ranged from South America to southeastern United States in the Pleistocene. Mylodon ranged from South America to southwestern United States and was contemporaneous with man. Glyptodon was apparently very numerous throughout South America and southern United States in the Pleistocene. Of the Proboscidea, the genus Cuvieronius probably originated in southwestern United States (Osborn, 1936) and was distributed widely in South America and in southern North America in the Pleistocene. The rodent Zygodontomys evolved in South America and exists now in South America north of the Amazon River and in Central America as far north as Costa Rica. Certain forms south of the Amazon River which have been referred to the genus are probably referable instead to the genus Akodon (Tate, 1939). All known representatives of the fossil fauna of Trinidad are herbivores and are characteristic of grassland habitats, which were widespread in Trinidad during the Pleistocene.

MAMMALIAN FAUNA AS REPRESENTED IN INDIAN MIDDENS

The present knowledge of the pre-Columbian mammalian fauna of Trinidad is based on skeletal material excavated from nine Indian sites. These sites represent all the cultural levels known on Trinidad. The sites, like all those known from the island, are located near the coast, indicating an orientation of the people toward the sea. The pre-ceramic sites are, of course, the oldest, dating here from 2,750 (± 130) years ago. These are followed by sites exhibiting four distinct ceramic styles (Bullbrook, 1953) that span the time from the pre-ceramic period to contact with the Spanish after 1532. The first of these periods is characterized by the Cedros style, the second by the Palo Seco style, the third by the Erin style, and the last by the Bontour style. Pottery of the last period is sometimes associated with Spanish ceramic work (Table 4).

Description of Sites

1. St. John

The St. John site is located on a high bluff south of the Godineau River above the Oropouche Swamp, and at the end of the St. John Road. This location takes advantage of the evergreen seasonal forest on the hill and the mangrove swamp habitats. This site was excavated in 1953 by Drs. Rouse and Goggin (Rouse, 1953). The soils are light sands that are freely drained. The shell midden at this site is extensive, reaching four feet in depth and 125 feet in diameter. Material of two successive occupations has been obtained

TABLE 4

CORRELATION OF PERIODS OF OCCUPATION ON TRINIDAD AND CERAMIC STYLES

(after Cruxent and Rouse)

Venezuelan Periods of Occupation	Trinidad Ceramic Styles
V	St. Joseph
IV	Bontour
III	Erin --- Palo Seco
II	Cedros --- Preceramic
I	?

here. The first of these is pre-ceramic and is comparable to the Ortoire site, for which there is a carbon-14 date of about 2,750 years. The second period of occupation is characterized by pottery of the Bontour style, with some European ware. This excavation consisted of 13 level units, four of which were pre-ceramic, five protohistoric, and four a mechanical transition between the two. Each of these three groups of levels has approximately the same proportion of each mammal species in them, but the pre-ceramic group contains more bones (Table 5). This is probably the result of differences in the economy of the two cultures, the pre-ceramic population depending exclusively on hunting and fishing, while agriculture also contributed to the food economy of the protohistoric population. Another factor that might explain the difference in the relative quantities of bones and artifacts could be that in the ceramic sites a larger proportion of the bulkier artifacts would correspondingly reduce the number of bones found in a given area and level.

List of Species Identified

Didelphis marsupialis, opossum: 10 individuals.

Dasypus novemcinctus, nine-banded armadillo: 27 individuals. As in all other sites there is a far higher proportion of bone fragments to minimum number of individuals for the armadillo than for any any other mammal because of the numerous bones in the shell. On the average for every 4 to 5 individuals, there were over 75 armadillo bones identified, but fewer than 50 bones identified for the same number of any of the other mammals.

TABLE 5

RELATIVE ABUNDANCE OF MAMMALS AT DIFFERENT TIME PERIODS WITHIN THE ST. JOHN SITE

	Preceramic	Mechanical Transition	Protohistoric
Didelphis	3	3	4
Dasypus	15	6	6
Alouatta	5	3	2
Rhipidomys	1		
Coendu	1	2	1
Agouti	11	7	8
Dasyprocta	4	3	6
Echimys	2	1	1
Proechimys	9	2	1
Procyon	1		2
Lutra		1	
Felis	1		
Pecari	27	18	12
Mazama	10	7	7

Alouatta seniculus, red howler monkey: 10 individuals.

Rhipidomys couesi: 1 individual.

Coendu prehensilis, porcupine: 4 individuals

Agouti paca, paca: 26 individuals in all; 8 in the proto-historic group of levels, and 11 in the pre-ceramic group. The remaining 7 were found in the levels of mechanical transition.

Dasyprocta aguti, agouti: 13 individuals in all; 6 in the proto-historic group of levels, and 4 in the pre-ceramic group; 3 in the transitional group of levels. The paca and agouti were represented numerously enough in all sites to allow useful comparison.

Echimys armatus, spiny rat: 4 individuals.

Proechimys guyannensis, spiny rat: 12 individuals.

Procyon cancrivorus, crab-eating raccoon: 3 individuals.

Lutra enudris, otter: 1 individual.

Felis pardalis, ocelot: 1 individual.

Pecari tajacu, collared peccary: 57 individuals in all; 12 in the protohistoric group of levels, and 27 in the pre-ceramic group; 18 in the transitional group of levels.

Mazama americana, brocket: 24 individuals in all; 7 in the proto-historic group of levels, and 10 in the pre-ceramic group; 7 in the transitional group of levels. As with the paca and agouti, the peccary and brocket were sufficiently well represented at each site to allow comparison.

Other vertebrates: As at all other sites there were very few birds represented, Cairina moshata (muskovy duck) being identified.

There were a few land turtles, but no sea turtle remains at this site. Fish remains, particularly cat fish, were abundant here as at all other sites.

2. Cedros

The Cedros site is situated on the United States Army's Green Hill Reservation in the extreme southwest corner of the island and is located on a slight elevation within one fourth mile of the sea. The area is now a coconut plantation and is inhabited; it was, however, formerly palm swamp surrounded by evergreen seasonal forest. The sandy soil in this area is classified as having impeded drainage, since it is close to sea level and the water table. Cedros is a shell mound yielding purely Cedros style pottery. The materials studied were from an excavation made by Dr. Rouse and Mr. Bullbrook (Rouse, 1953), consisting of 25 level units, and from two random surface collections made by Dr. Kugler and by me. The economy of this culture, as is true for all the ceramic cultures known on Trinidad, was probably based on hunting, fishing, gathering, and agriculture.

List of Species Identified

Didelphis marsupialis, opossum: 5 individuals.

Dasypus novemcinctus, nine-banded armadillo: 15 individuals.

Tamandua longicaudata, ant eater: 2 individuals.

Alouatta seniculus, red howler monkey: 1 individual.

Agouti paca, paca: 16 individuals.

Dasyprocta aguti, agouti: 14 individuals.

Proechimys guyannensis, spiny rat: 1 individual.

Canis cf. familiaris, dog: 3 individuals. These were represented only in the surface collection, and were undoubtedly added in recent times.

Procyon cancrivorus, crab-eating raccoon: 2 individuals.

Herpestes auropunctatus, mongoose: 4 individuals. This species, like the dog, was found only in the surface collection and was deposited in recent times.

Pecari tajacu, collared peccary: 14 individuals.

Mazama americana, brocket: 23 individuals.

Bovid: 1 individual. This was found only in surface collections and was deposited in recent times.

Trichechus manatus, manatee: 2 individuals.

3. Palo Seco

The Palo Seco midden is on the south coast of Trinidad. It is located on a ridge at an elevation of 90 feet and is surrounded by hills. The shoreline is approximately 200 yards distance. The Palo Seco site is now at the center of the Trinidad Petroleum Development camp, but it was formerly in semi-evergreen forest habitat. The soils of this area are predominantly clays and silts with impeded drainage. The excavation, made by Dr. Rouse (Rouse, 1953) at this site consisted of 57 level units, and yielded two pottery types, Cedros and Palo Seco.

List of Species Identified

Didelphis marsupialis, opossum: 14 individuals.

Dasypus novemcinctus, nine-banded armadillo: 18 individuals.

Tamandua longicaudata, ant eater: 2 individuals.

Alouatta seniculus, red howler monkey: 3 individuals.

Coendu prehensilis, porcupine: 6 individuals.

Agouti paca, paca: 41 individuals.

Dasyprocta aguti, agouti: 47 individuals.

Proechimys guyannensis, spiny rat: 2 individuals.

Felis pardalis, ocelot: 1 individual.

Pecari tajacu, collared peccary: 26 individuals.

Mazama americana, brocket: 76 individuals.

Bovid: 1 individual. This was found at the surface, presumably from recent occupation.

Tapirus sp., tapir: 1 individual. A right lower second pre-molar was found. This animal occurs on the mainland of South America.

Trichechus manatus, manatee: 1 individual.

Cetacean: 1 individual.

Other vertebrates: Sea turtle remains were abundant at this site and at the other south coast site. There were few or no remains of land turtles.

4. Erin

The Erin midden is just west of Palo Seco in the center of the town of Erin under the present police station. It is on a hill that was covered with semi-evergreen forest, about one-half mile from the

beach and the Erin River. The soils here, as at Cedros and Palo Seco, are poorly drained clays and silts. The site yielded Palo Seco and Erin style pottery. The materials that were examined came from an excavation made by Dr. Rouse (Rouse, 1953) that consisted of 69 level units, and one excavation made by Mr. Bullbrook, in which, however, the specimens from different levels were not kept separate.

List of Species Identified

Didelphis marsupialis, opossum: 18 individuals.

Caluromys philander, woolly opossum: 2 individuals.

Dasypus novemcinctus, nine-banded armadillo: 10 individuals.

Tamandua longicaudata, ant eater: 2 individuals.

Alouatta seniculus, red howler monkey: 3 individuals.

Sciurus granatensis, squirrel: 1 individual.

Nectomys squamipes: 1 individual.

Coendu prehensilis, porcupine: 4 individuals.

Agouti paca, paca: 14 individuals.

Dasyprocta aguti, agouti: 59 individuals.

Echimys armatus, spiny rat: 2 individuals.

Proechimys guyannensis, spiny rat: 2 individuals.

Canis cf. familiaris, dog: 1 individual. This came from a surface level.

Procyon cancrivorus, crab-eating raccoon: 1 individual.

Lutra enudris, otter: 1 individual.

Felis pardalis, ocelot: 2 individuals.

Herpestes auropunctatus, mongoose: 1 individual. This came from Mr. Bullbrook's collection and presumably was collected from the surface.

Pecari tajacu, collared peccary: 11 individuals.

Mazama americana, brocket: 61 individuals.

Trichechus manatus, manatee: 1 individual.

5. Mayaro

This site is just back of the Atlantic coast shore in a coconut grove belonging to the St. Bernard Estate, a short distance directly south of Cape Mayaro. The ceramic style at this site is predominantly Palo Seco. The bones available for study consisted of two small surface collections, one made by Dr. J. Hill of Port-of-Spain and the other by me, both in 1959.

List of Species Identified

Dasypus novemcinctus, nine-banded armadillo: 2 individuals.

Agouti paca, paca: 1 individual.

Dasyprocta aguti, agouti: 1 individual.

Proechimys guyannensis, spiny rat: 1 individual.

Pecari tajacu, collared peccary: 3 individuals.

Mazama americana, brocket: 2 individuals.

6. Quinam

The Quinam midden is located in semi-evergreen forest east of the Palo Seco site, near the beach and the Palmiste River. The soil is similar to that of Erin and Palo Seco. The excavations made

by Dr. Rouse (Rouse, 1953), consisting of 58 level units, produced pottery of Palo Seco, Erin, and Bontour styles.

List of Species Identified

Didelphis marsupialis, opossum: 4 individuals.

Dasypus novemcinctus, nine-banded armadillo: 10 individuals.

Tamandua longicaudata, ant eater: 2 individuals.

Alouatta seniculus, red howler monkey: 2 individuals.

Agouti paca, paca: 16 individuals.

Dasyprocta aguti, agouti: 26 individuals.

Lutra enudris, otter: 1 individual.

Felis pardalis, ocelot: 2 individuals.

Pecari tajacu, collared peccary: 23 individuals.

Tayassu pecari, white-lipped peccary: 5 individuals. This was the only site where remains of this species were found.

Mazama americana, brocket: 77 individuals.

7. Chagonaray

This site is half way between Palo Seco and Quinam on Chagonaray Point. It has quite the same ecological conditions as Quinam, but is undergoing coastal erosion. The pottery found was principally of Erin and Bontour style, but also included some of the Barrancas style typical of the Lower Orinoco region (Rouse, personal communication). The mammal material examined was from a surface collection made by me.

List of Species Identified

Dasypus novemcinctus, nine-banded armadillo: 1 individual.

Agouti paca, paca: 1 individual.

Dasyprocta aguti, agouti: 1 individual.

Proechimys guyannensis, spiny rat: 1 individual.

Pecari tajacu, collared peccary: 3 individuals.

Mazama americana, brocket: 2 individuals.

8. Mayo

Mayo is a Spanish mission site located in the Montserrat Hills of the Central Range, seven miles from the Gulf of Paria. A Catholic church has been built over the site. Formerly this area was covered by evergreen seasonal forest. The soil is light and freely drained. On the basis of the Bontour style pottery and the European ware found, this site has been dated (Goggin, personal communication) from the late seventeenth or early eighteenth centuries. The material examined came from an excavation of 8 level units made by Dr. Goggin (Rouse, 1953) and from my surface collection.

List of Species Identified

Dasypus novemcinctus, nine-banded armadillo: 14 individuals.

Tamandua longicaudata, ant eater: 3 individuals.

Alouatta seniculus, red howler monkey: 6 individuals.

Coendu prehensilis, porcupine: 2 individuals.

Agouti paca, paca: 12 individuals.

Dasyprocta aguti, agouti: 5 individuals.

Canis cf. familiaris, dog: 1 individual.

Pecari tajacu, collared peccary: 17 individuals.

Mazama americana, brocket: 8 individuals.

9. St. Joseph

St. Joseph was the first Spanish capital of Trinidad, and the site is located in the town of St. Joseph on a branch of the Caroni River on the south side of the North Range. This area was semi-evergreen forest. The excavation made by Dr. Rouse and Dr. and Mrs. Goggin (Rouse, 1953), consisting of 13 level units, yielded Bontour style pottery and European ware.

List of Species Identified

Coendu prehensilis, porcupine: 1 individual.

Agouti paca, paca: 1 individual.

Dasyprocta aguti, agouti: 3 individuals.

Mazama americana, brocket: 2 individuals.

Bovid: 2 individuals.

Cetacean: 1 individual.

TABLE 6

RELATIVE ABUNDANCE OF MAMMALS IN TERMS OF MINIMUM NUMBERS OF INDIVIDUALS, RECORDED FROM NINE MIDDENS

Mammals	Mayo	St. John	Cedros	Erin	Palo Seco	Chago-naray	Quinam	Mayaro	St. Joseph
Didelphis		10	5	18	14		4		
Caluromys				2					
Dasypus	14	27	15	10	18	1	10	2	
Tamandua	3		2	2	2		2		
Alouatta	6	10	1	3	3		2		
Sciurus				1					
Rhipidomys		1							
Nectomys				1					
Coendu	2	4		4	6				1
Agouti	12	26	16	14	41	1	16	1	1
Dasyprocta	5	13	14	59	47	1	26	1	3
Echimys		4		2					
Proechimys		12	1	2	2	1		1	
Canis	1		3	1					
Procyon		3	2	1					
Lutra		1		1			1		
Felis		1		2	1		2		
Herpestes			4	1					
Pecari	17	57	14	11	26	3	23	3	
Tayassu							5		
Mazama	8	24	23	61	76	2	27	2	2
Bovidae			1		1				2
Tapirus					1				
Trichechus			2	1	1				
Cetacean					1				1

Intersite Comparisons

The mammals that have been identified from Indian middens comprise a surprisingly complete list of the larger animals found in Trinidad today. One group of animals that is, however, entirely missing is the bats, although there are a great number of bats (Goodwin and Greenhall, 1961) now living on Trinidad. Another group, the cricetid rodents, is represented in the middens only by the two largest genera, Rhipidomys and Nectomys. Of the four species of marsupials now occurring on Trinidad, two species of the genus Marmosa were not found in the middens. Presumably the bulk of the animals represented were used by the Indians for food. This automatically excludes from the middens a certain portion of the natural fauna of the area, either because the Indians would make no effort to catch animals they considered useless, or because they might not have the technological ability to catch otherwise edible forms. Thus, for example, although there seems no reason to suppose that the bat population on Trinidad was markedly inferior to that at the present time, it is not wholly surprising that no bat remains are to be found in the middens.

The smallest animal represented in the middens is Rhipidomys. With three exceptions, all larger animals now known from Trinidad occur in the middens. One of those not represented is the small arboreal anteater, Cyclopes didactylus. This animal, aside from being relatively small, emits a very mournful wail, which may have caused it to be avoided. The capuchin monkey, Cebus albifrons, was also not found. This species has a large gap in its distribution on the mainland, and

the closest ally to the Trinidadian form occurs around the Maracaibo Basin in eastern Venezuela and nowhere in the area closer to Trinidad. Hershkovitz (1949) has suggested two possible explanations for its appearance on Trinidad: that Cebus albifrons may at an earlier time have had a wider distribution than it does at present, or that it was brought to Trinidad by early inhabitants as a pet. In regard to the second of these suggestions, it seems highly doubtful that, had the monkey been kept about the camps, no remains of it would be found. The absence of this species from the midden material does not, however, seem necessarily to invalidate the first suggestion that it was indigenous to Trinidad. Possibly the explanation lies in the fact that the monkey is of relatively small size, and may have been undesirable as an article of food. The third animal which might have been expected but was not recorded is the tayra, Eira barbara. However, remains of it have been recorded by Bullbrook (1953) from his excavations at Palo Seco.

Remains of two other large animals which may exist on Trinidad--the coati-mundi, Nasua, and the water opossum, Chironectes--were also absent from the middens. Probably individuals of these species find their way over from the mainland from time to time. Mr. L. Wehekind (personal communication) has informed me that the coati-mundi possibly occurs in the North Range. There is a somewhat better record of the water opossum (Greenhall, 1956) based on a photograph, and the description of a strange opossum shot by a hunter in Guayaguayare at the southeastern tip of Trinidad. The absence of remains of these animals in the middens, taken together with their present status on Trinidad, would

seem to indicate that in the past as now they were either merely occasional visitors to the island, or, if native, so rare as to be of no consequence to the fauna.

Only one mammal not previously reported from Trinidad was represented in the midden samples. This is the tapir, Tapirus, of which the remains found consisted of a single premolar. The tapir now exists on the mainland, and it is quite conceivable that the tooth found at Palo Seco was brought there by man. The white-lipped peccary, Tayassu pecari, has been reported from Trinidad, but it is questionable whether it still exists there or ever did in considerable numbers. Remains of it were found at Quinam. Another mammal, the savannah deer, Odocoileus gymnotis, which does not at present occur on the island, was identified from the Erin midden by Dr. S. Schaub, according to a personal communication by Dr. Kugler. I found no remains of this animal, however.

The surface levels at the Cedros, Palo Seco, and Erin sites contained remains of introduced animals that were probably deposited at the site subsequent to occupation by the Indians. Each of these sites is in a populated area, making this supposition even more likely. At Mayo and St. Joseph, as a result of colonial contact, these introduced forms were incorporated in the middens. Bovid remains appear in the Cedros, Palo Seco, and St. Joseph Middens. The mongoose, Herpestes a. auropunctatus, that was introduced into Trinidad in 1870, occurred in the Cedros and Erin sites. Remains of a small dog, Canis familiaris, were found at Mayo and Cedros.

In Trinidad, considering all sites together, 25 species of mammals are represented (Table 6). Much can be learned from those species which were caught in sufficient quantities to make them, on the basis of the evidence of the remains found in the middens, the chief sources of meat in the Indian's diet. In every site, the five most abundant species were the armadillo, Dasypus novemcinctus; paca, Agouti paca; agouti, Dasyprocta aguti; collared peccary, Pecari tajacu; and brocket, Mazama americana. These five forms make up more than 75 percent, in number of individuals, of the animals at each of the sites. The incidence of these forms at the six largest sites was analyzed statistically for randomness by a contingency table. The results (x^2 = 115.09, 4 degrees of freedom) show that the observed differences are highly significant. There are two possibilities to explain this difference; either food preference by the Indians or the local animal population. Since there is no cultural evidence to indicate a difference in food preference, the conclusion that is drawn is that the three smaller ones, the armadillo, paca and agouti, and the two larger ones, the peccary and the brocket, were probably equally sought. Therefore, the relative abundance of each at the different sites probably reveals their actual abundance in each area rather than selection by the Indians.

At the three south coast sites of Quinam, Palo Seco, and Erin, the percentage of armadillo among the mammals represented within each site is one half or one third as great as within the sites of Mayo, St. John, and Cedros (see Table 6). This distribution may well be correlated with the soil best suited to the burrowing activity of the armadillo.

At the three south coast sites, the soils are predominantly clays and silts with relatively poor drainage. Thus soil conditions would not be as favorable for burrowing as light soils with free drainage or excessive drainage found in the area of the Mayo and St. John site. The sandy soil at the Cedros site, although classified as having impeded drainage because it is close to sea level and the water table, would, however, provide suitable substrate for burrows. The evidence suggests, therefore, that the relative abundance of these animals is related to the character of the soil as indicated by midden remains.

The relative abundance of agouti and paca at the various sites would also appear to be correlated with the ecology around each site. At the two sites in the denser evergreen seasonal forest--Mayo and St. John--paca were found to be approximately twice as abundant as agouti, whereas the reverse was found to be true at the three sites--Erin, Palo Seco, and Quinam--located in more open semi-evergreen forest. At Cedros near evergreen forest, but actually in palm swamp, paca and agouti remains are almost equally abundant. The paca is characteristically a forest animal, feeding on fruits and eggs laid on the ground, although it does venture into the edge of clearings as well. The agouti is usually found in more open forest.

A similar pattern is seen when the relative abundance of deer and peccary remains are compared. At the Mayo and St. John sites, the remains of peccary are more than twice as abundant as those of deer, whereas at the Erin, Palo Seco, and Quinam sites, deer are almost three times as abundant as peccary. At the Cedros site also, more deer than peccary

remains were found. The Quinam site revealed a few bones referable to the white-lipped peccary, Tayassu pecari, as well as remains of the collared peccary. Peccary are often found in forested areas, and particularly along river bottoms, where their feeding habits are similar to those of pigs (Seton, 1929, quoting Audubon and Bachman). Ideal habitat of this kind is present at the St. John site. This habitat was also found at Mayo with the Mayo River providing the river bottom conditions. Deer, although numerous in densely forested areas, prefer the open forests found along the south coast.

With the exception of the St. John site, which is a special case, no significant trends in the numbers of individuals of a given species at different levels of excavation in the other sites could be discovered. Moreover, when the faunas from the various Indian middens are compared on the basis of the total fauna rather than by levels, no striking differences are found in their composition. Animals that are found only in a few sites appear to be incidental, and are represented by only a bone or two. As has been noted, differences in the faunas can be observed in the relative abundance of certain forms which were locally numerous and presumably equally sought after by the Indians.

HISTORIC MAMMAL FAUNA

One of the first lists of Recent mammals of Trinidad was published by De Verteuil (1884). It included 24 species of large, conspicuous land mammals. Three of these--Gulo, Viverra vittata (= Grison vittata), and Cachicamus septemcinctus (= Dasypus septemcinctus)--have since been found not to occur on the island. De Verteuil's list was followed in 1892 by a preliminary list of 24 species published by Oldfield Thomas. This number of species was enlarged by the work of J. A. Allen and F. M. Chapman which was based on material collected in Trinidad by Chapman in 1893 and 1894. In their first publication (1893), these authors listed 37 land mammals, 13 of which had not been previously reported. New species that were described included Nectomys palmipes (Holochilus squamipes listed by Thomas is later synonymized with this), Tylomys couesi, Oryzomys speciosus, Oryzomys trinitatis, Oryzomys velutinus, Oryzomys brevicauda, Loncheres castaneus, and Echimys trinitatis. In the second paper (1897) they omitted Myrmecophaga jubata, Choloepus didactylus, Cercoleptes caudivolvulus, Loncheres castaneous (= Loncheres guianae = Echimys armatus), and Dicotyles labiatus (= Tayassu pecari). However, recent evidence has been obtained to indicate that the last two forms do, in fact, occur on Trinidad. Allen and Chapman also added the following species: Oryzomys delicatus, Akodon frustrator, and Thylamys carri. The most recent list of Trinidad mammals is that of Vesey-Fitzgerald (1936), while the Chiroptera have been dealt with in a monograph by Goodwin and Greenhall (1961).

One form included in the Vesey-Fitzgerald list, Akodon fru trator, evidently was described from a juvenile specimen of Zygodontomys brevicauda, and had earlier been synonymized (Gyldenstolpe, 1932). A second species given, Oryzomys brevicauda, had previously been referred to the genus Zygodontomys (Gyldenstolpe, 1932).

A list of the Recent land mammals of Trinidad is presented below. Although by far the largest segment of the mammal fauna of the island is made up of bats, 58 species having been reported, the Chiroptera are not included in the following list, since they have been the subject of a very recent monograph, and are of comparatively little importance archeologically. The list is essentially that of Vesey-Fitzgerald except for the addition of two species, and certain nomenclatural changes. Most of the nomenclatural changes follow the work of Hershkovitz (1947, 1948, 1949, 1955, 1960) and Cabrera (1957). The synonymy for the species concerns only the references to the occurrence of these species on Trinidad. The list includes observations that I made during the summer of 1959.

List of Terrestrial Mammals

Didelphis marsupialis insularis Allen, Bull, Amer. Mus. Nat. Hist., XVI, 1902.

Didelphys marsupialis Thomas, Jour. Trinidad Field Nat. Club, I, 1893.

Didelphis marsupialis Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Didelphis karkinophaga Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897.

The opossum or "Manicou" appears to be quite common, particularly around plantations. One male was shot on 3 September 1959 on a cocoa estate in the North Range, Arima Valley, Spring Hill Estate. Its measurements were 744-399-55-En 48. Mango, insect and rodent remains were contained in the stomach. One skeleton from Biche was obtained from a hunter.

Caluromys philander trinitatis (Thomas)

Didelphis (Philander) philander Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Didelphis (Philander) trinitatis Thomas, Ann. and Mag. Nat. Hist. (6) XIII, 1894.

"Manicou gros-yeux" is also quite common around plantations. One male was shot on 3 September 1959 at Spring Hill Estate. The measurements were 536-322-34-En 30. His stomach contained fruit and insect remains.

Marmosa robinsoni chapmani Allen

Didelphis (Miscoureus) murina Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Marmosa murina Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897.

Marmosa chapmani Allen, Bull. Amer. Mus. Nat. Hist., XIII, 1900.

One immature male was trapped on 31 July 1959 at the base of a large clump of bamboo at Pointe-a-Pierre. His measurements were 192-111-14.

Marmosa carri (Allen and Chapman)

Thylamys carri Allen and Chapman, Bull. Amer. Mu . Nat. Hist., IX, 1897.

Marmosa carri, in Trouessart Cat. Mamm. viv. foss. Suppl. 856.

Alouatta seniculus insularis Elliot

Mycetes seniculus (Linn.), Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897.

Alouatta seniculus insularis Elliot, Ann. and Mag. Nat. Hist. Ser. 8, V, 1910.

Howler monkeys were often heard in the late afternoon or before rain at Guayaguayare. They were usually in bands of 3 to 10, each band appearing to have a fixed route through the forest. We observed a small band, composed of several adults with at least one young of that season, feeding on Mora flowers at Guayaguayare on 26 August 1959. One young male of this band was shot. His measurements were 1214-651-155-En 30. Hog plum seeds were contained in his stomach and intestine. Two skulls were found on the trail to La Table in Guayaguayare on 26 August 1959.

Cebus albifrons trinitatis Pusch

Cebus sp., Thomas Trinidad Field Nat. Club I, 1893.

Cebus apella, Vesey-Fitzgerald (nec. Linnaeus), Tropical Agr. (Trinidad), 13(6), 1936.

Cebus albifrons trinitatis Pusch, Zeitschr. für Säuget, 16, 1941.

Capuchin monkeys move in large bands, 15 or more. They will come quite close to investigate a call. One band attracted in such a way was seen in Guayaguayare forest. One male specimen, formerly a pet,

was obtained from the Trinidad Regional Virus Laboratory. Its measurements were 810-404-123-En 35.

Tamandua longicaudata longicaudata Wagner

Tamandua tetradactylus (Linn.), Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Tamandua longicaudata Wagner, Vesey-Fitzgerald, Tropical Agr. (Trinidad), 13(6), 1936.

One ant eater or "mataperro" was shot at Guayanguayare on 27 August 1959. A partial skeleton was found on the trail to La Table on 26 August 1959.

Cyclopes didactylus didactylus (Linn.)

Cyclothurus didactylus (Linn.), in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

Cyclopes didactylus didactylus (Linn.) in Vesey-Fitzgerald, Tropical Agr. (Trinidad), 13(6), 1936.

Dasypus novemcinctus novemcinctus Linn.

Tatusia novemcinctus (Linn.) in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

The armadillo or "tatou" is widely distributed and common. It is the most common large mammal in the Mora forest of southeastern Trinidad according to hunters. One male was shot on 31 August 1959 in Guayaguayare with measurements of 813-385-91-En 30. Three more individuals were shot in the same area on 27 August 1959. An immature female was run down in the cocoa at Spring Hill Estate, 13 August 1959, with measurements of 670-345-80-En 37.

Sciurus granatensis chapmani Allen

Sciurus aetuans hoffmani Peters, in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

Sciurus chapmani Allen, Bull. Amer. Mus. Nat. Hist., XII, 1899.

These are fairly common.

Nectomys squamipes palmipes Allen and Chapman

Holochilus squamipes (Brants) in Thomas, Jour. Trinidad Field Nat. Club I, 1893.

Nectomys palmipes Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

These are commonly found at the edge of ponds or streams. Two were trapped at the edge of a shallow pond in a logged area and one was shot along a stream in Guayaguayare forest. The two males were both in breeding condition and were caught the 29 and 30 August 1959. They measured 437-220-51-En 23, 346-177-45-En 21, respectively. One pregnant female with three embryos which averaged 27 mm. crown-rump was caught the 31 August 1959 with measurements of 340-183-45-En 20.

Oryzomys concolor speciosus Allen and Chapman

Oryzomys speciosus Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

Oryzomys trinitatis Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

One pregnant female with two very early embryos was trapped at Pointe-a-Pierre on 28 July 1959. Its measurements were 241-136-23.

Oryzomys laticeps velutinus Allen and Chapman

Oryzomys velutinus Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1910.

Three were trapped between 13 and 16 August 1959 at Spring Hill Estate between the cocoa and the uncleared land. There were some gnawed cocoa pods on the ground. One female was a subadult, one was in breeding condition, and one was pregnant with six embryos of which one was resorbing. The measurements were 163-75-24-En 16, 210-109-27-En 18, 207- injured tail 87-28-En 20, respectively.

Oryzomys (Oligoryzomys) delicatus Allen and Chapman

Oryzomys delicatus Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897.

Twelve skulls and 52 rami of this species were found in owl pellet material. This form is rare in collections.

Rhipidomys couesi (Allen and Chapman)

Tylomys couesii Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Rhipidomys couesi (Allen and Chapman), Bull. Amer. Mus. Nat. Hist., IX, 1897.

Zygodontomys brevicauda brevicauda (Allen and Chapman)

Oryzomys brevicauda Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Akodon frustrator Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897.

Forty-three skulls are represented in the owl pellet material. This form is commonly trapped.

Akodon urichi Allen and Chapman

Abrothrix caliginosus (Tomes), provisional reference in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Akodon urichi Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897.

Sigmodon cf. hirsutus

Twenty-one skulls referable to Sigmodon are represented in the owl pellet material. All the owl pellets studied were collected by the late F. W. Urich at St. Augustine, to the best of everyone's knowledge. St. Augustine is located eight miles east of Port-of-Spain and the Gulf of Paria and 35 miles from the nearest point on the mainland. Both the numbers of animals represented and the distance from the mainland would suggest that, if the owl pellets were indeed collected at St. Augustine, these rats must have been caught on Trinidad and as such represent a new record. Only minor differences were noted when they were compared with four skulls referred to Sigmodon hirsutus. Three of these Sigmodon hirsutus came from Caracas and one from Rancho Grande which is the closest record of this species to Trinidad. Sigmomys, characterized by grooved upper incisors, has a range nearest to Trinidad. Hershkovitz (1955) suggests that probably all species of Sigmodon and Sigmomys are synonymous with Sigmodon hispidus. This material tends to support the idea that at least the skulls from Trinidad, the four skulls studied from Venezuela, and the skulls studied of Sigmodon hispidus from Florida

are very close. Some measurements taken on the skulls from Trinidad are given in Table 7.

Heteromys anomalus anomalus (Thompson), in Thomas, Trinidad Field Nat. Club I, 1892.

These are commonly trapped.

Rattus rattus (Linn.)

Five were trapped in areas under cultivation, inhabited areas, and in the deep forest. One was from Pointe-a-Pierre, two were from Spring Hill Estate, and two were from Guayaguayare.

Rattus norvegicus (Berkenhout)

Mus musculus Waterhouse

Coendu prehensilis (Linn.)

Synetheres prehensilis (Linn.), in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

A skeleton was obtained from a specimen killed about 10 August 1959 in Guayaguayare and a jaw of another was found. Another skeleton was obtained from a hunter from Biche.

Agouti paca (Linn.)

Coelogenys paca (Linn.), in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Paca or "Lappe" is a delicacy and as a result have become very rare. It and the peccary are probably the most difficult game animal to obtain in Trinidad. A skeleton of one was procured from a hunter from Biche.

TABLE 7

MEASUREMENTS (IN MILLIMETERS) OF SIGMODON CF. HIRSUTUS

Measurement	Number	Mean	Range
Skull length	1	36.6	
Zygomatic breadth	3	20.0	19.5-20.6
Interorbital breadth	18	5.9	5.5- 6.3
Length of palate	16	6.9	6.3- 7.7
Alveolar length of upper molar row	16	6.3	5.8- 6.9
Length of incisive foramen	16	7.5	6.6- 8.5
Breadth of rostrum	14	9.3	8.2-10.1

Dasyprocta aguti (Linn.)

Dasyprocta rubrata Thomas, Ann. and Mag. Nat. Hist. (7)II, 1898.

Dasyprocta aguti (Linn.), in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

In Guayaguayare the "guti" is thought by hunters to be next in abundance after the armadillo. One was shot at Guayaguayare on 20 August 1959. One was obtained from Biche.

Echimys armatus castaneous (Allen and Chapman)

Loncheres guianae Thomas, Trinidad Field Nat. Club I(7), 1892.

Loncheres castaneus Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Echimys armatus Geoff.

Proechimys guyannensis trinitatis (Allen and Chapman)

Echimys trinitatis Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

The "Pilori" inhabit the stream banks. One male in breeding condition was shot in Guayaguayare on 29 August 1959. Its measurements were 478-212-56-En 30. One partial skull was found at the edge of the Aripo River.

Procyon cancrivorus cancrivorus (Cuvier) in Thomas, Trinidad Field Nat. Club I(7), 1892.

Eira barbara trinitatis (Thomas)

Galictis barbara (Linn.) in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Tayra barbara trinitatis Thomas, Ann. and Mag. Nat. Hist. (7) V, 1900.

Lutra enudris enudris (Cuvier)

Lutra insularis Thomas, Ann. and Mag. Nat. Hist. (8) I, 1908

Herpestes auropunctatus auropunctatus

Felis pardalis Linn.

Felis tigrina Erxl., Allen and Chapman, Bull. Amer. Mus. Nat. Hist., IX, 1897

Leopardus pardalis Linn., in Vesey-Fitzgerald, Tropical Agr. (Trinidad), 13(6), 1936.

Pecari tajacu (Linn.)

Dicotyles tajacu (Linn.), in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Tayassu Pecari Fischer

Dicotyles labiatus Cuvier, in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Mazama americana trinitatis (Allen)

Cariacus (Coassus) nemorivagus (Cuvier), in Allen and Chapman, Bull. Amer. Mus. Nat. Hist., V, 1893.

Mazama rufa (Cuvier)

Mazama trinitatis Allen, Bull. Amer. Mus. Nat. Hist., XXXIV, 1915.

Deer are less abundant than Dasyprocta and must be hunted increasingly further away from the population center, Port-of-Spain. They have one or two young, dropping them mainly in the summer. One hunter killed a deer with a well formed fetus in the middle of August. The skull and leg of one specimen was obtained which was killed during the spring of 1959 in Siparia Forest Reserve. A hunting party with dogs

killed a lactating doe with a single corpus luteum in the ovary at Tabaquit on 26 June 1959. One buck was shot on 23 August 1959 at Guayaguayare that dressed out at 35 pounds. One deer was seen in the Guayaguayare Forest.

Zoogeographic Affinities

Trinidad is part of the savannah region of South America as defined by Cabrera (1940). In addition to savannah, however, the region also includes the forested coastal range which is the mountainous extension of the Andes. Trinidad is included in this forested section, and may be considered as the extreme northeastern end of the coastal range. This geographic character is reflected in the present mammal fauna which is composed to a large extent (38 percent) of arboreal forms. The savannah faunas which existed on the island in the Pleistocene is represented by only one relict form, Oryzomys delicatus, in the present fauna, and by one other, Odocoileus gymnotis, of the pre-Columbian fauna.

Westermann (1953) has stated that "The flora and fauna of Trinidad and Tobago have strong affinities to those of the neighboring South American continent, but quite a number of species common to the Guianas are absent here. Their absence is due to natural circumstances and not to extermination by man." When the present land mammals of Trinidad are compared with the mammals of the Guiana Region and Rancho Grande, Venezuela, as reported by Tate (1939, 1947), and those of Northern Colombia as reported by Hershkovitz (1947, 1948, 1949, 1960), it is found that more than twice as many (28 percent) have affinities

to the west of Trinidad in Venezuela, Colombia, and the Andes than have affinities to the south in the Guiana region. Those forms with allies to the west are: Cebus albifrons, Alouatta seniculus, Sciurus granatensis, Oryzomys delicatus, Rhipidomys couesi, Akodon urichi, Heteromys anomalus, and Marmosa carri, whereas those with allies to the south are Oryzomys concolor, Lutra enudris, and Caluromys philander. The remaining forms (59 percent) have relatively extensive ranges. This association again reflects the geographic ties which Trinidad has had with Venezuela and its recent ecological relationship with the forested areas. It also suggests that the Orinoco River constitutes an important barrier to many widely ranging mammal species.

DISCUSSION

Since a large part of this study is based on animal bones associated with archeological remains it is appropriate that some of the problems involved in the use of such materials for zoological interpretation be discussed. It is important to understand the nature of the deposit in which the bones are found, the method of sampling, and the cultural background of the human population represented. The nature of the deposit may be ceremonial where animals are buried as part of a ritual, but more often animal remains are associated with kitchen middens. The number of different forms represented in a midden may often be correlated with the economy of the aborigines that made the midden. Usually gathering, hunting, and fishing peoples will depend on a greater variety of animal foods than agricultural people. Middens are sampled by the archeologist either randomly by a surface collection that may be preliminary to an excavation or by an excavation that systematically samples all parts of the midden. Each level, the smallest unit of the sample, is of known volume and all that is found in each level is kept separate for analysis. The zooarcheologist bases his analysis on material sampled in the same manner.

The archeologist's goal is to reconstruct the life of the aboriginal group he is studying whereas the zooarcheologist's objective is to reconstruct as far as possible the faunal characteristic of that period. Such data contribute to the archeologist's interpretation of the relationship of the human population to its natural environment. The

analysis of particular faunal associations must rest upon a foundation of accurate identifications. For this purpose as large series of skeletons as possible must be obtained and prepared. Usually between 25 percent and 75 percent of the material will be too fragmentary to identify. From the identifiable portion, the relative number of individuals of each species may be determined by calculating the minimum number of individuals. This must be done to give equal consideration to each form and not favor those with more bones. With these data a better picture of the former ecology and various changes in the fauna may be revealed. Certain changes in the fauna within one site may become apparent when the materials are analyzed stratigraphically, or between the fauna of the site and the more distant past or present fauna of the same area. Work with the individual species may reveal new forms, certain variations of recognized forms, or osteological properties of a species or genus. This material may provide much valuable information when analyzed with its origin in mind.

In this study of samples of past and present mammalian faunas of Trinidad an effort was made to determine the composition of the faunas and to gain some insight into the possible factors that might have played a role in the formation of the faunas. It is obvious that the fauna will be composed of such forms as have had geographic access to the area and whose habitats are represented. The fossil fauna existed at a time when what is now Trinidad was connected to the mainland, and savannahs covered most of the area. Forests grew at higher elevations and along streams. The known fossil fauna reflects these conditions in

that it is composed principally of large herbivores of grassland habitats. The geological events that resulted in the isolation of Trinidad as an island also resulted in the rejuvenation of the soils and thereby the spread of forest vegetation. Isolated in this habitat is a recent fauna of entirely different nature. As many as 38 percent of these mammals are arboreal and a great many more are forest dwelling forms.

As would be expected, accompanying the changes in the composition and isolation of the faunas are changes in its affinities and percentage of endemism. The fossil fauna was composed largely of species with very wide ranges. There is no endemism among the fossil species (with the possible exception of Zygodontomys) since there was no isolation in the uninterrupted expanse of savannah that spread across Venezuela and Trinidad. The Recent fauna is composed to a large extent of widespread forms that originated principally from the west of Trinidad. Evidently the Orinoco River presented a barrier to the movement of certain species from the south to Trinidad. Due to the gradual separation of the island from the mainland, species became isolated. This is reflected in the extent of endemism now found in Trinidad. Of the 29 land mammals now known from Trinidad, two Marmosa carri, and Akodon urichi, are endemic. Twelve endemic subspecies are also recognized.

Since the colonization of Trinidad by Europeans the isolation of the island fauna has in one sense broken down and as a result of man's activities the composition of the fauna has been altered. At the present time the forest forms are decreasing in numbers as the forest habitat is replaced by agricultural and industrial areas. With the

increase in the human population from about 635,843 in 1950 to 825,700 in 1960 a drastic change has been seen in the abundance of game animals. This situation is particularly serious because of three principal factors. The first of these is unemployment resulting from the increase in population. The second is the good market for wild meats that stimulates hunting by the people. Finally the game laws, although reasonably strict, are poorly enforced. Hunters hunt without licenses, shoot protected animals, and animals out of season without hesitation. The clearing of land provides habitats for rodents and particularly Rattus and Mus at the expense of the native forms. A few of the native forms such as Zygodontomys adapted to habitats resulting from cleared land have been able to compete successfully with the introduced forms. However, the persecution of game species would appear inevitably to lead to their extermination if no reservoirs are provided. Perhaps the most practical resolution would be to set aside sanctuaries that could be managed and stringently protected for the replenishment of game in other forested areas. The one area which is absolutely protected now is the United States base at Chagaramus where game is said to be plentiful. As Westermann (1953, p. 12) has said, "The relatively small size of these islands, and their rapidly growing population, make the outlook for the preservation of nature rather precarious, unless large forest and nature reserves can be kept in perpetuity."

SUMMARY AND CONCLUSIONS

Three samples of mammal bones representing different time periods were studied to see what changes have taken place since the late-Pleistocene and to determine the cause of these changes.

The first of these samples was deposited more than 34,000 years ago in a stream edged by gallery forest when Trinidad and Venezuela were broadly connected. The mammal fauna represented was composed of large herbivorous forms as Cuvieronius, Glyptodon, Mylodon, and Megatherium of which all are now extinct. In addition to these large mammals one small rodent referable to the genus Zygodontomys was represented. Although a species of Zygodontomys now exists on Trinidad it is not the same species as the fossil form. The fossil Zygodontomys is characterized by its very small size. The ecological situation indicated by the fossil mammals is that the area's habitat was grassland and forest.

The second sample was composed of bones excavated at six Indian middens. The mammals represented comprise almost all the larger land mammals native to Trinidad. Those larger than the cricetid rodent Rhipidomys couesi that were not found are Cyclopes didactylus, Cebus albifrons, and Eira barbara, although the latter has previously been reported from a midden. Species that do not now occur on the island are Odocoileus gymnotis, which probably constitutes a relict; Tayassu pecari, which is probably now extinct on the island but did appear in the early lists of Trinidad mammals; and Tapirus represented by one tooth which may have been a trade object.

The principal difference between sites was not found to be the presence or absence of certain animals, but rather the percentage of comparable and abundant forms. The armadillo was found to be more abundant at sites where the soils are more friable. At the three sites situated on the south coast in open forest, deer and agouti were more abundant than peccary and paca, respectively. At the site in palm forest surrounded by heavy forest agouti and paca were almost equally abundant but deer were more abundant than peccary. The two sites located in heavy forest had far more paca and peccary than agouti and deer, respectively. These differences in the percentage of various forms reveal more subtle differences in the ecology of an area than are revealed by the presence or absence of an incidental form.

The last sample is composed of specimens that were collected by us, and by mammal remains from owl pellets, and includes a compilation of published records. The only unreported form found is a rodent referable to Sigmodon cf. hirsutus. This record is based on 21 skulls from owl pellets collected originally by F.W. Urich. The Recent fauna is composed to a large extent of forest forms that are allied principally to species from the west of Trinidad or with widespread ranges. These affinities with the west reflect the past land connection of Trinidad and Venezuela and the barrier of the Orinoco River to the dispersal of certain forms. Today with the removal of forests by man many of the native mammal populations are dwindling.

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BIOGRAPHICAL SKETCH

Anne Elizabeth Schwarz was born in Cambridge, Massachusetts, March 5, 1932. She attended the Winsor School in Boston, Massachusetts, and was graduated in 1951. In 1955 she received her Bachelor of Arts degree from Mount Holyoke College in South Hadley, Massachusetts, and in 1957 she received her Master of Science degree from the University of Florida.

During her graduate studies she has held graduate assistantships in the Department of Biology and Florida State Museum. In the summer of 1959 she was awarded a National Science Foundation Summer Fellowship for Graduate Teaching Assistants. She is presently employed as a research associate of the Florida State Museum on a zooarcheological project supported by the National Science Foundation, Grant 17948.

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On April 18, 1957, she was married to James E. Wing, Jr. and has one child, Mary Elizabeth, born September 12, 1961.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of the committee. It was submitted to the dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

February 3, 1962

Dean, College of Arts and Sciences

Dean, Graduate School

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