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CONTENTS

NEW TAXA

No new taxa were described in Volume 53.

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VERTEBRATES FROM ARCHAEOLOGICAL SITES ON MONTSERRAT, WEST INDIES

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Abstract

We report our identifications of fish, reptile, bird, and mammal bones from two archaeological sites on Montserrat. The sites, known as Trant's and Radio Antilles, both represent the Saladoid culture, a ceramic-producing people who colonized the Lesser Antilles approximately 2000 years ago. As indicated by the vertebrate remains we have identified, the Saladoid peoples of Montserrat used both the marine and terrestrial vertebrates of the region. The former are represented by fish and sea turtles. The fish remains include forms characteristic of both deep and shallow waters. Terrestrial vertebrates are represented by iguanas, a variety of birds (mostly pigeons and doves), at least two species of extinct oryzomyine rodents, and a bat. Two other mammals recovered from the sites, the agouti and the dog, are not indigenous to Montserrat but were transported there by Saladoid peoples. Although this sample of 746 bones reveals some important new records for the vertebrate fauna of Montserrat (especially the extinct rodents), it is too small to provide a definitive picture of the prehistoric man-animal relationships on this island.

Introduction

Montserrat is a lush, green island in the eastern Caribbean, between lat. 16°40′ to 16°49′N and long. 62°09′ to 62°15′W. It lies 43 km

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southwest of Antigua, 64 km northwest of Guadeloupe, and 24 km southeast of Redonda, and is one of the islands comprising the inner volcanic arc of the northern Lesser Antilles (Fig. 1). Montserrat has an area of 102 km^2 (39.5 mi^2), although the area was often erroneously listed in the past as 32 mi^2. The island is about 17 km from north to south and 9 km from east to west.

Montserrat is a volcanic island with rocky cliffs, limited sandy beaches, very few mangrove swamps, no significant estuaries, and a relatively narrow insular shelf. It is the sole emergent feature on the Montserrat Bank, and is surrounded for the most part by deep water (Fig. 2). The scattered and sparse patch reefs and seagrass beds on the bank are present mainly to the north, west, and south of the island (ECNAMP, 1980: Map 6). Above water, Montserrat's landscape is dominated by three major volcanic centers, Silver Hill, Centre Hills, and Soufrière Hills, trending north to south and differing greatly in degree of erosion. The greatest elevation is 912 m (3002 ft) at Soufrière Hills. These volcanoes have extruded mostly andesitic lavas and pyroclastics, although some basaltic magma is known (Rea, 1974). Lang (1967) identified four major soil groups, Protosols, Young Soils, Latosolics, and Smectoid Clays, each of which is derived from differentially weathered igneous parent materials.

Most of the east and part of the west coast is formed of rugged cliffs. Open bays with black-sand pocket beaches are scattered along the coastline, which is not significantly indented. Major beach formation occurs only in the southwest near the capital of Plymouth. Permanent or seasonal streams radiate from the volcanic masses, flowing to the sea through steeply sided ravines (called "ghauts"). The upper slopes of the Soufrière and Centre Hills (Fig. 3) are now densely covered in secondary rain forest (Beard, 1949:104–107). The original forests were cleared extensively in the early historic period for cultivation of commercially important plantation crops such as tobacco and sugarcane.

ARCHAEOLOGY

Columbus sighted and named Montserrat on 11 November 1493, during his second voyage to the New World. He was told by Arawak Indians he had rescued from captivity on Guadeloupe that Montserrat no longer was inhabited, the occupants having been driven off by Carib raids. It is not certain whether Indians were living on Montserrat in the 1630's when the island was colonized by the English and Irish. On several occasions these new inhabitants were subjected to Carib raids launched from nearby islands (Watters, 1980:137–145).

Very little was known about the prehistory of Montserrat prior to the completion of a year-long archaeological field project by Watters in 1979. Results of the project, which also involved study of the nearby

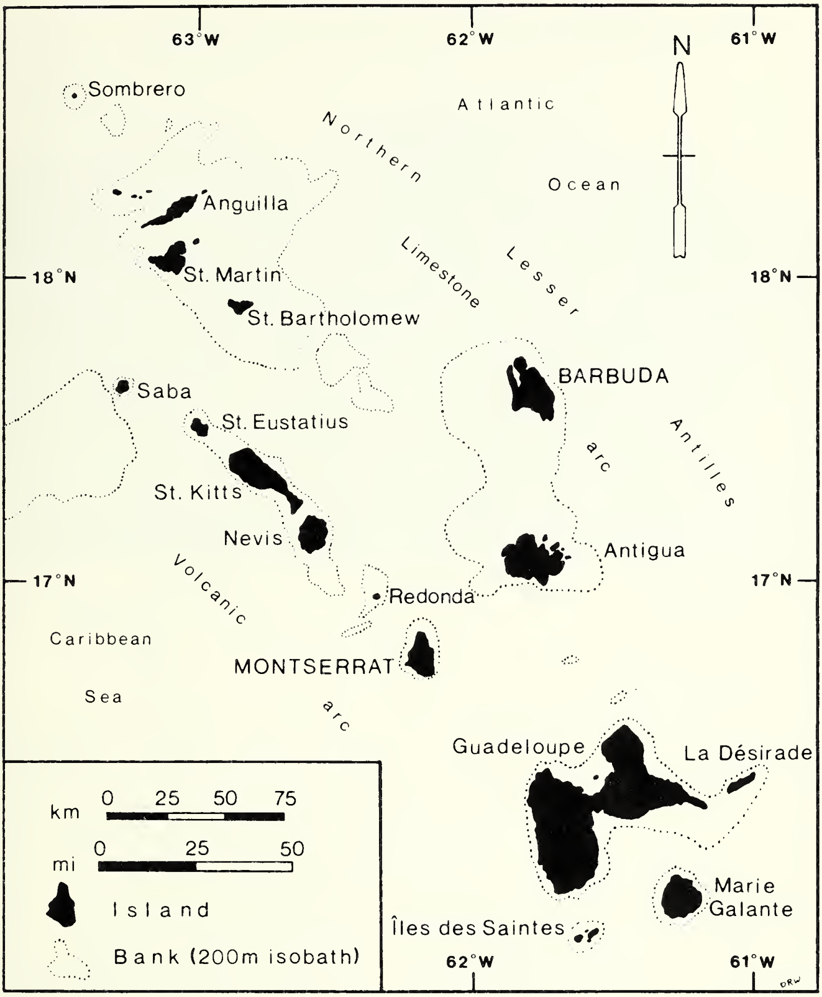

Fig. 1.—Islands and banks of the northern Lesser Antilles, showing the relationship of Montserrat to surrounding islands.

island of Barbuda (Fig. 1), are reported in detail elsewhere (Watters, 1980). In a separate paper we will present information on the prehistory of Barbuda and the faunal remains from its archaeological sites.

Ceramic assemblages from Montserrat correspond quite well with those of other volcanic islands in the Lesser Antilles. They indicate that the first ceramic-bearing populations to occupy Montserrat arrived

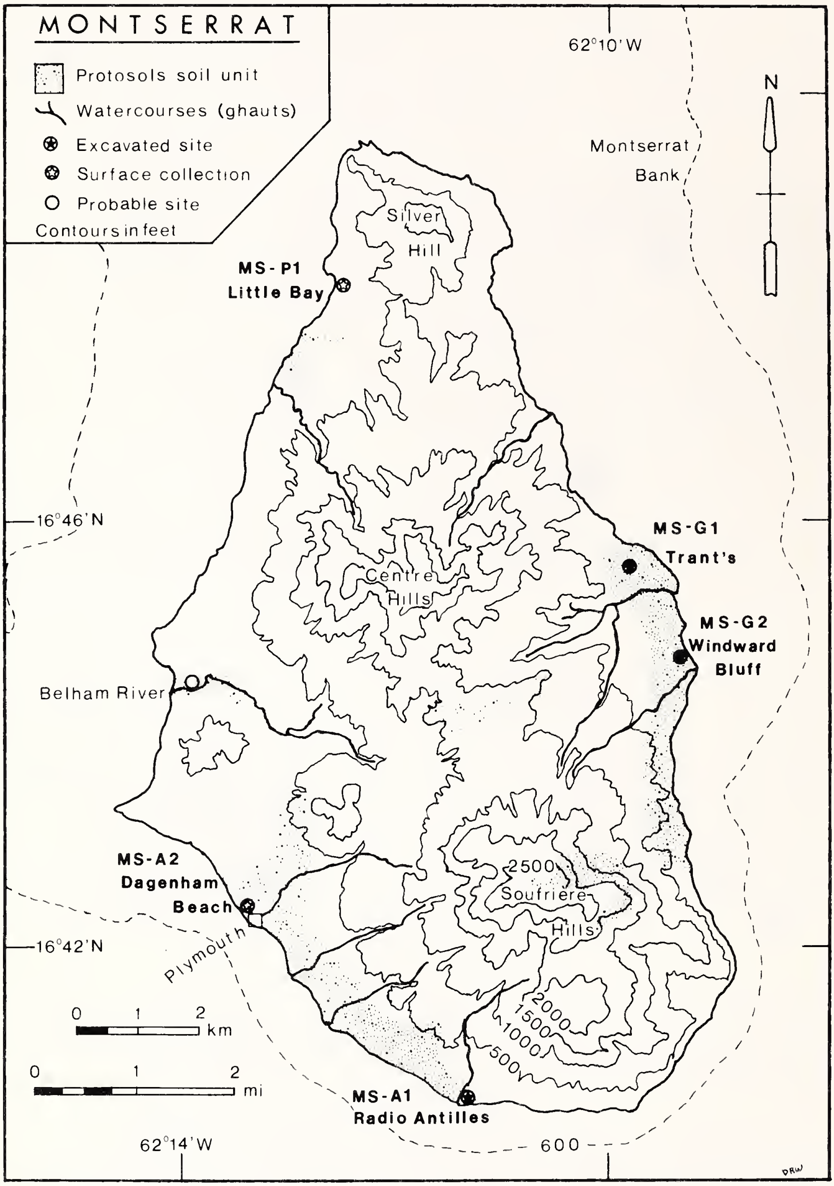

Fig. 2.—Physiographic units and prehistoric sites on Montserrat.

Fig. 3.—The cliffed coast and secondary forest on the western flank of the Centre Hills volcanic formation, Montserrat.

in the first centuries A.D. From the Orinoco region of South America, these populations dispersed through and rapidly colonized the Lesser Antilles and ultimately the Greater Antilles. Distinctive white-on-red (WOR) and zone-incised-crosshatch (ZIC) pottery associated with this Saladoid colonization occurs throughout the volcanic Lesser Antilles (Rouse and Allaire, 1978), and on Montserrat this pottery is known from test pits at the sites of Trant's (MS-G1) and Radio Antilles (MS-A1). Judging from surface collections or limited excavation, the other three confirmed sites on Montserrat—Windward Bluff, Dagenham Beach, and Little Bay (Fig. 2)—do not contain WOR or ZIC pottery but instead have only post-Saladoid materials. No sites predating the Saladoid occupation have been discovered on Montserrat, although such Archaic (preceramic) sites are known from nearby Antigua and St. Kitts.

A single 2 by 2 m test pit was dug in the eastern part of the Trant's site (Fig. 4) at an area where a concentration of artifacts had been discovered on the surface. At the Radio Antilles site, two 1 by 2 m test pits were made. Test pit 1 had a depth of only 10 cm, was underlain by bedrock, and contained few artifacts, whereas test pit 2 had much greater depth and contained many more artifacts and faunal remains.

Fig. 4.—General view of the Trant's site and background terrain, on the eastern coast of Montserrat. Test pit 1 is located (but not visible) to the right of the cow, just before the treeline.

At both sites, test pits were excavated in 10 cm units within natural strata. Sediments were dry-screened through ⅛ in. mesh, and materials were segregated by 10 cm units and natural stratum. Flotation samples yielded nothing when processed. No vertebrate remains were recovered at the Windward Bluff site (MS-G2), the third site where a test pit was dug, and it is not discussed further.

Three strata were identified in the Trant's test pit (Fig. 5A). Stratum I reaches a depth of 30 cm and contains units 1–3 . It is a very compacted and dark grayish brown soil (Munsell notation dry 10YR4/2, wet 7.5YR3/2). Stratum II occurs from 30 to 60 cm (units 4–6). It is a fine-grained, loosely compacted soil that is light brownish gray (dry 10YR6/2, wet 10YR3/2). Stratum III was colored similarly (dry 10YR6/3, wet 10YR3/3) and was also loosely compacted, but had a somewhat coarser texture. It was dug to 80 cm (units 7–8), at which point a rock-laden unit without artifacts was encountered. The volume of soil removed from the test pit was approximately 3.2 m^3. Greatest quantities of cultural materials occur in units 2 through 4. Units 1 and 2 definitely are disturbed as historic ceramics were found to a depth of 20 cm. Below approximately 20 cm, however, cultural materials were in pri-

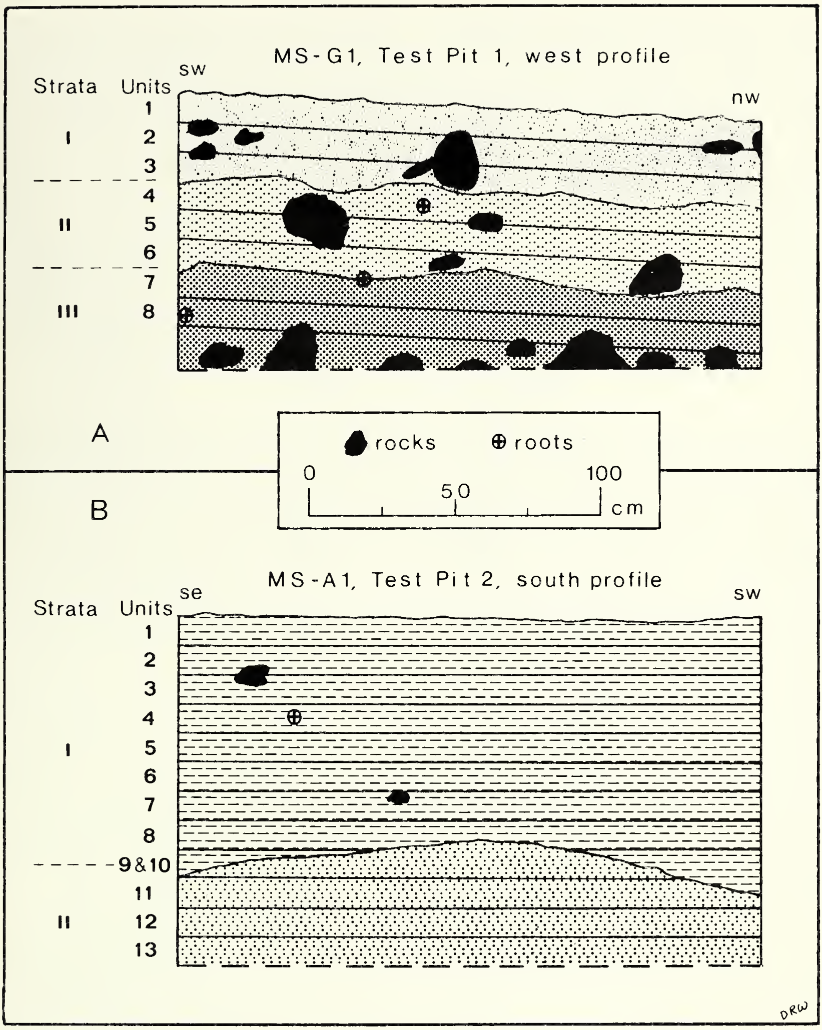

Fig. 5.—Stratigraphic profiles of Test Pit 1 at the Trant's site (A), and Test Pit 2 at the Radio Antilles site (B), Montserrat.

mary context. The faunal assemblage from the Trant's test pit includes vertebrates, mollusks, crab, and coral.

Test pit 2 at the Radio Antilles site contained two strata (Fig. 5B). Stratum I is a brown (dry 10YR5/3, wet 10YR3/2), loosely compacted soil reaching a depth of 80 cm in the center of the test pit and slightly deeper on the sides. Nine units of 10 cm each were dug in Stratum I. The upper levels are disturbed since historic artifacts were found down to 40 cm. This disturbance probably resulted from bulldozing associated with construction of the nearby Radio Antilles broadcasting facility, as well as cultivation during historic times. The cultural materials below 40 cm are in primary context. Stratum II is a somewhat coarser textured, light yellowish brown soil (dry 10YR6/4, wet 10YR3/4) that includes units 10 to 13. The interface between Strata I and II was an undulating, sloping surface. Cultural resources occur in greatest numbers to a depth of 70 cm. Faunal remains from Radio Antilles includes vertebrates, sea urchins, chiton valves, other mollusks, crabs, and corals. Approximately 2.4 m^3 of soil was removed from test pit 2.

The Vertebrate Fauna

Analysis of archaeological faunal remains can provide important new information for zoologists and archaeologists alike. The faunal remains from the Trant's and Radio Antilles test pits are important for several reasons. First, if these sites actually do represent the initial human occupation of Montserrat, then the vertebrate remains are indicative of the indigenous fauna encountered and used by those colonizers, and in turn suggest the kinds of habitats that existed at that time. Second, they establish the contemporaneity of prehistoric peoples with species now extirpated from Montserrat. Third, the remains provide information about species that were exploited by human inhabitants, and thus provide data on human subsistence patterns. For Montserrat, these subsistence data are limited by the small number of bones presently available. Fourth, these vertebrate remains can be compared to those found in prehistoric archaeological sites elsewhere in the West Indies. In this paper, such comparisons are limited in scope because a broader treatment of the topic is planned for a future publication after the Barbudan vertebrate remains are analyzed and published.

Species accounts of the vertebrates from Trant's and Radio Antilles are presented below in standard systematic order. Compilations of our analyses are presented in Tables 1 and 2, which directly precede the species accounts. The fish identifications and interpretations are by Reitz, those of reptiles are by Pregill, and those of birds and mammals are by Steadman.

All of the vertebrate specimens from Trant's are from test pit 1 (the only test pit at this site), whereas all remains from Radio Antilles are from test pit 2, so individual test pits are not distinguished in the "Material" portion of the species accounts. All specimens are catalogued in the collections of the Division of Vertebrate Paleontology of the United States National Museum of Natural History, Smithsonian

Table 1.—*The vertebrate fauna from Trant's and Radio Antilles, Montserrat, segregated by Stratum. The first number is the number of specimens identified. The second number is the MNI. For both sites, Stratum I (D) represents the disturbed upper units that contain both historic and prehistoric artifacts. Because they cannot be associated unequivocally with Amerindian culture, the faunal remains from the disturbed units constitute no MNI.*

Taxa	Trant's			Radio Antilles		
	I (D)	I	II	I (D)	I	II
Fish						
Epinephelus sp.	3, —	18, 3	21, 3			
Mycteroperca sp.			1, 1			
Carangidae sp.					1, 1	
Lutjanus sp.		3, 2	2, 1			
Lutjanidae sp.	1, —					
Anisotremus sp.	3, —		3, 1			
Haemulon sp.		1, 1				
Haemulidae sp.		1, 0				
Sparidae sp.	1, —					
Labridae sp.	5, —	1, 1	1, 1			
Scarus sp.	1, —		1, 1			
Sparisoma sp.	2, —				1, 1	
Scaridae sp.				1, —		
Euthynnus sp.	6, —		7, 1			
Scomberomorus sp.		1, 1				
Scombridae sp.	29, —	21, 0	31, 0	3, —	21, 1	3, 1
Fish sp.	68, —	78, 0	91, 0	4, —	13, 0	
Reptiles						
Cheloniidae sp.	2, —	5, 1	6, 1	1, —	74, 2	
Iguana sp.	4, —	5, 1	13, 2		3, 2	
Birds						
Gallinula chloropus		2, 1	2, 2			
Columba squamosa	1, —	1, 1	10, 2			
Zenaida aurita	1, —	3, 1	5, 3			
Columbina passerina		1, 1				
Geotrygon mystacea	6, —	9, 3	13, 3			
Columbidae sp.	6, —	8, 0	11, 0			
Margarops fuscus		2, 1	4, 2			
Margarops fuscatus	1, —	2, 1	5, 2			
Cinclocerthia ruficauda			1, 1			
Passeriformes sp.			1, 1			
Bird sp.		2, 0		2, —		
Mammals						
Brachyphylla cavernarum					1, 1	
Homo sapiens					20, 1	
Canis familiaris			2, 1			
Oryzomyine sp. A	5, —	12, 2	11, 3	1, —	1, 1	
Oryzomyine sp. B	4, —	4, 1				

Table 1.—*Continued.*

	Trant's			Radio Antilles		
Taxa	I (D)	I	II	I (D)	I	II
Mammals (cont.)						
cf. Oryzomyine (large)	2, —	1, 1				
cf. Oryzomyine (small)	1, —		1, 1			
Dasyprocta aguti	1, —			1, —		
Mammal sp.	4, —			1, —		
Vertebrate sp.	4, —	2, 0	1, 0	1, —	5, 0	
Total fish	119, —	124, 8	158, 9	8, —	36, 3	3, 1
Total reptiles	6, —	10, 2	19, 3	1, —	77, 4	
Total birds	15, —	30, 9	52, 16	2, —	0, 0	
Total mammals	17, —	17, 4	14, 5	3, —	22, 3	
Grand total (includes "Vertebrate sp.")	161, —	183, 23	244, 33	15, —	140, 10	3, 1

Institution (USNM), and this 6-digit catalogue number appears for each taxon under "Material."

The Minimum Number of Individuals (MNI) was determined using paired elements, size, age, and excavation provenience as criteria. In calculating MNI, the sample from each Stratum was considered as a single, homogeneous unit. This consideration rests upon the relative uniformity of the sediment within each Stratum. The fauna from disturbed levels was not included in these calculations because our main interest is the relationship between prehistoric man and fauna. In disturbed levels, it is impossible to associate unequivocally any faunal remains with prehistoric man because bones of historic times may have been introduced into these sediments. None of the vertebrate taxa from either site, however, is restricted to the historic period, and so it is likely that the bones from disturbed upper levels actually have an archaeological origin.

Two basic problems confront zooarchaeological use of MNI. First, MNI usually is based upon paired elements. Two right dentaries, for example, indicate two animals. Occasionally, however, a species is identified only from non-paired elements such as scales or vertebrae. When this happens, the MNI count may be too low. Second, MNI is subject to bias from sample size. Samples of fewer than 200 individuals or 1400 bones may be too small for certain interpretations (Grayson, 1979; Wing and Brown, 1979). With our small samples, the relative abundances of species probably have little meaning. It is not possible

Table 2.—*The vertebrate fauna from Trant's and Radio Antilles, Montserrat, combining all undisturbed strata. These figures represent MNI of taxa that are definitely associated with Amerindian cultures.*

Taxa	Trant's	Radio Antilles	Both sites
Fish			
Epinephelus sp.	6		6
Mycteroperca sp.	1		1
Carangidae sp.		1	1
Lutjanus sp.	3		3
Anisotremus sp.	1		1
Haemulon sp.	1		1
Labridae sp.	2		2
Scarus sp.	1		1
Sparisoma sp.		1	1
Euthynnus sp.	1		1
Scomberomorus sp.	1		1
Scombridae sp.		2	2
Reptiles			
Cheloniidae sp.	2	2	4
Iguana sp.	3	2	5
Birds			
Gallinula chloropus	3		3
Columba squamosa	3		3
Zenaida aurita	4		4
Columbina passerina	1		1
Geotrygon mystacea	6		6
Margarops fuscus	3		3
Margarops fuscatus	3		3
Cinclocerthia ruficauda	1		1
Passeriformes sp.	1		1
Mammals			
Brachyphylla cavernarum		1	1
Homo sapiens		1	1
Canis familiaris	1		1
Oryzomyine sp. A	5	1	6
Oryzomyine sp. B	1		1
cf. Oryzomyine (large)	1		1
cf. Oryzomyine (small)	1		1
Total fish	17	4	21
Total reptiles	5	4	9
Total birds	25	0	25
Total mammals	9	3	12
Grand total	56	11	67

to determine the nature or extent of this bias, or to correct for it, until the sample is made much larger through additional excavations. We cannot provide a definitive discussion of Saladoid subsistence on Montserrat from our sample, but our data document some interesting taxa and provide guidelines for additional research.

Our interpretation of the faunal remains is complicated further by how poorly the modern fauna of Montserrat is known. Thorough faunal surveys are needed before definitive statements can be made about the present status of Montserratian vertebrates. From 24 to 30 January 1983, Watters, Steadman, and Pregill were part of a team that visited Montserrat to begin such work, but our cursory examination produced more questions than answers. Soon we hope to survey the vertebrates of Montserrat much more completely.

FISH

The fish were identified using the comparative skeletal collection of the Zooarchaeology Laboratory, Florida State Museum, Gainesville. None of the fish bones had been modified either as tools or in subsistence activities. Only four atlases were suitable for measurement (width of atlas in mm—*Epinephelus* sp., 5.8; Lutjanidae, 9.0; *Haemulon* sp., 7.5; Sparidae, 4.4). These figures indicate a fairly uniform size in these four individuals. However, several very large individuals were also identified for each of these taxa. Weights for the fish remains have been recorded and are available on request from Reitz.

Also of interest are the types of elements that were identified. Most taxa were identified from cranial fragments, but mackerels were identified only from their distinctive vertebrae. The absence of mackerel cranial bones in this sample may be due to the fragility of the bones. However, their absence also may indicate that mackerel's heads were discarded elsewhere, or it may simply be an artifact of small sample size.

Order Perciformes
Family Serranidae
Epinephelus sp.—grouper

Material.—Trant's, Stratum I: unit 1—premaxilla (359367); unit 2—dentary (359372), atlas (359377); unit 3—quadrate (359384), 4 premaxillae, 2 dentaries, 3 hyomandibulars, epihyal, 2 ceratohyals, 3 articulars (359386), quadrate (359389), maxilla (359393). Stratum II: unit 4—maxilla (359401), premaxilla, 2 dentaries, 2 epihyals, 2 ceratohyals, quadrate, articular (359403), articular, hyomandibular (359409); unit 5—2 premaxillae, quadrate (359419); unit 6—2 epihyals, 2 hyomandibulars, 2 quadrates (359423). MNI = 6.

Mycteroperca sp.—grouper

Material.—Trant's, Stratum II: unit 5—dentary (359415). MNI = 1.

Mycteroperca has been known to cause ciguatera or fish poisoning.

Family Carangidae

Carangidae sp.—jack

Material.—Radio Antilles, Stratum I: unit 6—maxilla (359426). MNI = 1.

Carangids are an extremely diverse group of carnivorous fishes that includes jacks, pompano, bumpers, scads, and runners.

Family Lutjanidae

Lutjanus sp.—snapper

Material.—Trant's, Stratum I: unit 3—quadrate (359390), 2 maxillae (359394). Stratum II: unit 4—dentary, quadrate (359404). MNI = 3.

Lutjanidae sp.—snapper

Material.—Trant's, Stratum I: unit 2—atlas (359378). MNI = 0.

Snappers are predators that are mainly demersal and nocturnal. Large snappers may cause ciguatera.

Family Haemulidae

Anisotremus sp.—porkfish

Material.—Trant's, Stratum I: unit 2—maxilla, 2 premaxillae (359373). Stratum II: unit 4—phyraengeal grinding platform, maxilla (359405), articular (359410). MNI = 1.

Haemulon sp.—grunt

Material.—Trant's, Stratum I: unit 3—atlas (359398). MNI = 1.

Haemulidae sp.—grunt

Material.—Trant's, Stratum I: unit 3—hyomandibular (359387). MNI = 0.

There are many species of *Haemulon* in West Indian waters, so species-level identification is not possible in our sample.

Family Sparidae

Sparidae sp.—porgy

Material.—Trant's, Stratum I: unit 2—atlas (359379). MNI = 0.

Family Labridae

Labridae sp.—wrass

Material.—Trant's, Stratum I: unit 1—dentary (359368); unit 2—2 phyraengeal grinding platforms, 2 dentaries (359374); unit 3—premaxilla (359396). Stratum II: unit 4—quadrate (359406). MNI = 2.

Wrasses are a diverse family of carnivorous fish.

Family Scaridae

Scarus sp.—parrotfish

Material.—Trant's, Stratum I: unit 1—premaxilla (359369). Stratum II: unit 4—premaxilla (359407). MNI = 1.

Sparisoma sp.—parrotfish

Material.—Trant's, Stratum I: unit 1—phyraengeal grinding mill (359370); unit 2—phyraengeal grinding platform (359375). MNI = 0. Radio Antilles, Stratum I: unit 8—phyraengeal grinding platform (359362). MNI = 1.

Scaridae sp.—parrotfish

Material.—Radio Antilles, Stratum I: unit 4—phyraengeal grinding platform (359353). MNI = 0.

Family Scombridae

Euthynnus sp.—tunny

Material.—Trant's, Stratum I: unit 2—6 vertebrae (359381). Stratum II: unit 4—7 vertebrae (359413). MNI = 1.

Scomberomorus sp.—mackerel

Material.—Trant's, Stratum I: unit 3—tooth (359391). MNI = 1.

Scombridae sp.—mackerel

Material.—Trant's, Stratum I: unit 1—23 vertebrae (359366); unit 2—6 vertebrae (359380); unit 3—21 vertebrae (359399). Stratum II: unit 4—22 vertebrae (359412); unit 5—2 vertebrae (359417); unit 6—7 vertebrae (359420). MNI = 0. Radio Antilles, Stratum I: unit 4—3 vertebrae (359352); unit 5—7 vertebrae (359355); unit 6—8 vertebrae (359358); unit 7—4 vertebrae (359359); unit 8—1 vertebra (359361). Stratum II: unit 9—1 vertebra (359365); unit 10—2 vertebrae (359363); unit 11—1 vertebra (359564). MNI = 2.

Fish sp.

Material.—Trant's, Stratum I: unit 2—18 fragments (359371), 50 fragments (359376); unit 3—fragment (359382), 2 fragments (359383), 11 fragments (359385), 20 fragments (359388), 4 fragments (359392), fragment (359395), 40 fragments (359397). Stratum II: unit 4—8 fragments (359400), 16 fragments (359402), 19 fragments (359408), 8 fragments (359411); unit 5—10 fragments (359414), 5 fragments (359416), 14 fragments (359418); unit 6—fragment (359421); 9 fragments (359422); unit 7—fragment (359424). MNI = 0. Radio Antilles, Stratum I: unit 3—fragment (359351); unit 4—3 fragments (359354); unit 5—9 fragments (359356); unit 6—3 fragments (359357), fragment (359425); unit 7—fragment (359360). MNI = 0.

These undiagnostic specimens cannot be identified beyond the level of class.

REPTILES

The herpetofauna of Trant's and Radio Antilles sites consists solely of scattered, fragmentary remains of adult sea turtles and iguanas. None of this material is remarkable in extent, diversity, or quality of preservation. The bones were compared with reference specimens in the osteology collections of the Department of Herpetology, San Diego Natural History Museum.

Order Testudines
Family Cheloniidae
Cheloniidae sp.—sea turtle

Material.—Trant's, Stratum I: unit 1—worn marginal scute (359246); unit 2—carapace fragment (359247); unit 3—carapace fragment (359248), 3 phalanges (359249), phalanx (359250). Stratum II: unit 4—carpal, phalanx (359251), 4 phalanges (359252). MNI = 2. Radio Antilles, Stratum I: unit 4—metatarsal (359253); unit 6—17 fragments of carapace and plastron (359254); unit 7—2 phalanges (359255), 55 fragments of carapace and plastron (359256). MNI = 2.

Nothing of the fragmentary remains of sea turtles from either Trant's or Radio Antilles lends confidence to their identification. On purely speculative grounds, assignment could be made to the Hawksbill, *E. imbricata,* only because this species is the most abundant sea turtle in the Lesser Antilles. However, the Green Turtle, *Chelonia mydas,* and the Loggerhead, *Caretta caretta,* also range throughout the Caribbean and therefore cannot be dismissed. Rebel (1974) reported briefly on the limited modern turtle fisheries of Montserrat.

Wing et al. (1968) reported *Caretta caretta* from the Mill Reef site on Antigua, and we have examined superficially other sea turtle bones from that site. Wing (1973) also recorded unidentified sea turtle remains from St. Kitts and Marie Galante.

Order Squamata
Family Iguanidae
Iguana sp.—iguana

Material.—Trant's, Stratum I: unit 1—metatarsal (359257); unit 2—metatarsal, 2 phalanges (359258); unit 3—4 caudal vertebrae (359259), tibial (?) shaft (359260). Stratum II: unit 5—metatarsal, ulna, tibia, 2 phalanges (359261), caudal vertebra, phalanx (359262); unit 6—humerus, tibia, metacarpal, metatarsal (359263), thoracic vertebra, vertebral centrum (359264). MNI = 3. Radio Antilles, Stratum I: unit 5—metacarpal with scraps (359265); unit 6—ulna (359266); unit 9—humerus (359267). MNI = 2.

I. iguana and *I. delicatissima* are distinguishable from one another on skull characters, but the fragmentary post-cranial remains listed above do not permit identification to species. We are reluctant to refer the bones to *I. iguana* simply because it alone now inhabits Montserrat. There is no compelling reason to believe that *I. iguana* is not native to Montserrat (and elsewhere in the Lesser Antilles), as has been proposed by Underwood (1962). Lazell (1973) has argued persuasively against this theory, citing such evidence as character discordance between insular and mainland populations and the largely hearsay nature of earlier speculation to the contrary.

Iguanas have become severely restricted in most areas of the Lesser Antilles because of habitat destruction and predation; the modern distribution of both species probably does not reflect their prehistoric range. *I. iguana* and *I. delicatissima* occur erratically throughout the Lesser Antilles, but are sympatric only on Les Iles des Saintes in the Guadeloupeen archiepelago. *I. delicatissima* occurs from Anguilla south to Martinique, whereas *I. iguana* ranges from the Virgin Islands south to the Venezuelan coast, and on the mainland from Mexico to southern Brazil and Paraguay. On Montserrat the species is found in scattered areas around the island and is locally common in certain places along the southern coast, including near the Radio Antilles site.

Other prehistoric reports of *Iguana* from the Lesser Antilles are *I. iguana* from the Spring Bay fossil site on Barbados (Swinton, 1937; Ray, 1964) and *I. delicatissima* from the Mill Reef site, Antigua (Wing et al., 1968), both amply represented by bone reported to have been compared adequately to both species. An undetermined species from the Paquemar archaeological site, Martinique, was reported by Wetmore (1952), and "Iguanidae probably *Iguana*" was reported from archaeological sites on St. Kitts and Marie Galante by Wing (1973).

BIRDS

Of the 97 avian specimens recovered from Trant's site, 69 could be identified to species. Only two bird bones were found at the Radio Antilles site, neither of which could be identified even to family. Identifications were made using the skeletal collection of the Division of Birds, USNM. Sequence and nomenclature for birds mainly follows Bond (1956 and supplements). Subspecies are not distinguished herein because they generally are not determinable osteologically. Whenever feasible, osteological nomenclature follows that of Baumel (1979). Our comments on the modern status of birds on Montserrat are taken from Danforth (1939), Lack and Taylor (1974), and our own observations.

Order Ralliformes

Family Rallidae

Gallinula chloropus (Linnaeus, 1758)—Common Gallinule

Material.—Trant's, Stratum I: unit 3—2 femora (359427). Stratum II: unit 4—humerus (359268); unit 6—humerus (359269). MNI = 3.

Among large rallids of the West Indies, the humerus in *G. chloropus* is smaller overall than in *Fulica americana* or *F. caribaea,* shorter and stouter than in *Rallus longirostris,* and has a differently shaped Incisura capitis and Margo caudalis than in *Porphyrula martinica.* The shaft of the femur in *G. chloropus* is more slender than in *F. americana* or *F. caribaea,* shorter than in *R. longirostris,* and has a deeper depression on the caudal surface between Condylus medialis and Condylus lateralis than in *P. martinica.*

Gallinules occur on Montserrat today, but they are very restricted by the lack of their preferred habitat, which is thickly vegetated swamps, marshes, and slowly moving rivers. During our visit to Montserrat, we observed gallinules only at the brackish swamp at Foxes Bay Bird Sanctuary, where Steadman saw approximately 10 adults and five immatures on 28 January 1983. Foxes Bay was the only area we explored on the island that seemed capable of sustaining gallinules, although they could occur at Little Bay as well. Their occurrence at Trant's suggests the nearby presence of some sort of body of fresh or brackish water. In an undisturbed state, the mouth of the stream near Trant's may have been vegetated sufficiently to attract gallinules.

This is the first prehistoric record of *G. chloropus* from the Lesser Antilles. Other prehistoric West Indian records are from Cuba and St. Croix (Brodkorb, 1967:135).

Order Columbiformes
Family Columbidae

Bones of West Indian columbids can be very difficult to identify, especially the medium-sized species of the genera *Zenaida* and *Geotrygon.* Olson and Hilgartner (1982:35), for example, found it very difficult to distinguish the bones of *Z. aurita* from *G. chrysia* in their study of Bahaman fossils. For most skeletal elements of West Indian columbids, size is the only diagnostic character, and even size is complicated by significant interspecific overlap. Six species of columbids have been recorded or could be expected to occur on Montserrat. These are *Columba squamosa, C. leucocephala, Z. aurita, Geotrygon montana, G. mystacea,* and *Columbina passerina,* each of which is widespread in the Antilles. (*C. leucocephala* is known from Montserrat only by sight records [Bond, 1974; our field party in 1983]; it is a nomadic species and is locally common on nearby Antigua. *Geotrygon montana* has not been reported from Montserrat, but occurs on nearby Guadeloupe and has been reported by sight records [Holland and Williams, 1978] from Antigua.) Of the six species, *Columba squamosa* and *Columbina passerina* have, respectively, the largest and smallest skeletal elements, and therefore are the easiest species to identify (except for the tarsometatarsus of *C. squamosa*; see below). The differences in size among the remaining four species are more subtle, and vary from element to element. In order of decreasing size, these generalized patterns emerge for the major skeletal elements of the four middle-sized species: coracoid, scapula, carpometacarpus—*Columba leucocephala* = *Geotrygon mystacea* > *Zenaida aurita* = *Geotrygon montana*; humerus, ulna—*C. leucocephala* = *G. mystacea* > *Z. aurita* > *G. montana*; femur—*G. mystacea* > *C. leucocephala* > *Z. aurita* (stout) > *G. montana* (slender); tibiotarsus—*G. mystacea* > *C. leucocephala* > *Z. aurita* > *G. montana* (long, but slender); tarsometatarsus—*G. mysta-*

cea (longest, slender) > *G. montana* (long, most slender) > *C. squamosa* (broad) > *C. leucocephala* (broad) > *Z. aurita.* The amount of pneumaticity in the dorsal surface of the sternal end of the coracoid varies greatly within a species, and so appears to be undiagnostic for identification. We note this because great differences in this character may be evident between two species if only one or two coracoids are compared. One apparent difference was found to distinguish the similarly-sized humeri of *G. mystacea* and *C. leucocephala,* namely the more slender shaft and less pointed Tuberculum dorsale of the former.

Columba squamosa Bonnaterre 1792—Red-necked Pigeon

Material.—Trant's, Stratum I: unit 2—ulna (359270); unit 3—coracoid (359271). Stratum II: unit 4—2 coracoids, 2 ulnae, radius, femur, 3 tibiotarsi (359272); unit 5—ulna (359273). MNI = 3.

Columba squamosa occurs commonly today in many forested regions of Montserrat, especially in riverine forests along the ghauts. It is not found now in the immediate vicinity of Trant's, but this is due to historic destruction of the surrounding forest. Nevertheless, *C. squamosa* may still be found on wooded slopes within 1 km of the site.

Elsewhere in the West Indies, *C. squamosa* has been reported from a variety of archaeological and paleontological sites (see Brodkorb, 1971:196), including Martinique in the Lesser Antilles (Wetmore, 1952).

Zenaida aurita (Temminck, 1810)—Zenaida Dove

Material.—Trant's, Stratum I: unit 1—coracoid (359274); unit 3—sternum (359275), coracoid, femur (359276). Stratum II: unit 4—2 coracoids, femur (359277); unit 5—coracoid (359278); unit 6—femur (359279). MNI = 4.

The Zenaida Dove is the most common columbid on Montserrat today, including at Trant's. *Z. aurita* is also the most versatile West Indian columbid in its habitat requirements, occurring in and around clearings, shrubby or aborescent second growth, and at the edge of, or just within, primary forest. Because Zenaida Doves thrive in areas of habitat disturbance, they probably are more abundant on Montserrat today than during the time of Amerindian occupation.

Z. aurita has been reported from many prehistoric sites in the Antilles (see Brodkorb, 1971:198), including Martinique in the Lesser Antilles (Wetmore, 1952).

Columbina passerina (Linnaeus, 1758)—Common Ground Dove

Material.—Trant's, Stratum I: unit 3—humerus (359280). MNI = 1.

This tiny dove lives only in rather open or completely open habitats, such as cultivated or shrubby fields, pastures, roadsides, and creekbeds. As with the Zenaida Dove, ground doves are common today at Trant's, and probably are more abundant on Montserrat today than in prehistoric times.

Other West Indian records of prehistoric remains of *C. passerina* are listed in Brodkorb (1971:198), none being from the Lesser Antilles.

Geotrygon mystacea (Temminck, 1811)—Bridled Quail-dove

Material.—Trant's, Stratum I: unit 1—sternum (359281); unit 2—sternum, coracoid, 2 tibiotarsi, tarsometatarsus (359282); unit 3—3 coracoids, 2 femora, tibiotarsus, 3 tarsometatarsi (359283). Stratum II: unit 4—humerus, 2 femora, tibiotarsus, 2 tarsometatarsi (359284); unit 5—humerus (359285), humerus, carpometacarpus, tarsometatarsus (359286); unit 6—coracoid, humerus, tibiotarsus (359287). MNI = 6.

Geotrygon mystacea occurs in forested areas of Montserrat, tending to prefer primary forest and to avoid second growth. Like *Columba squamosa,* Bridled Quail-doves are not found at Trant's today, but may be encountered on forested slopes within 1 km of the site. *G. mystacea* seems to be less common than *C. squamosa.*

This is the first report of *G. mystacea* from any archaeological or paleontological site in the West Indies.

Columbidae sp.

Material.—Trant's, Stratum I: unit 1—tibiotarsus (359288); unit 2—humerus, ulna, 3 radii (359289); unit 3—2 humeri, 3 ulnae, radius, pedal phalanx (359290), sternum (359291). Stratum II: unit 4—sternum, scapula, 2 ulnae, tibiotarsus (359292); unit 5—ulna, femur, tibiotarsus (359293); unit 6—humerus, femur, tibiotarsus (359294). MNI = 0.

These specimens are all in the approximate size ranges of *Zenaida aurita, Geotrygon mystacea,* or *G. montana,* but otherwise lack diagnostic features. They are not included in the MNI because of stratigraphic overlap with *Z. aurita* and *G. mystacea.*

Order Passeriformes
Family Mimidae

All diagnostic passerine bones from Trant's represent relatively large species in the broad size range of mimids (mockingbirds, thrashers) or turdids (thrushes). These bones were compared with skeletons of all species of mimids and turdids that occur on Montserrat, as well as these extralimital species—*Mimus gundlachii, M. polyglottos, M. gilvus, Turdus plumbeus,* and *Myadestes genibarbis.* No skeletons were available for *Ramphocinclus brachyurus* of Martinique and St. Lucia. Within the Mimidae and Turdidae, size alone can often eliminate all but several species, thus greatly facilitating the identification of fragmentary remains.

Margarops fuscus (Muller, 1776)—Scaly-breasted Thrasher

Material.—Trant's, Stratum I: unit 3—femur, tibiotarsus (359295). Stratum II: unit 4—2 humeri (359296); unit 5—humerus (359297; only tentatively referred); unit 6—tibiotarsus (359298). MNI = 3.

The humerus of *Margarops fuscus* is similar in size to that of *Mimus gundlachii, Cichlherminia lherminieri,* and *Turdus plumbeus,* but is distinguished from these species by its shallow medial Fossa pneumotricipitalis, its less prominent Margo caudalis, its shallow Fossa musculus brachialis, and its small (less bulbous) Condylus ventralis in distal aspect. The femur of *Margarops fuscus* is similar in size to that of *Mimus gundlachii, Cinclocerthia ruficauda,* or *Turdus plumbeus,* but is distinguished from these species by its relatively small Facies articularis acetabularis, its straighter shaft in medial aspect, its less pointed Crista tibiofibularis, and its differently shaped proximo-medial portion of Condylus medialis. The tibiotarsus of *Margarops fuscus* is similar in size to that of *Mimus gilvus, Mimus polyglottos, Cinclocerthia ruficauda,* and *Turdus plumbeus,* but is distinguished from these species by its very protrudent and perpendicularly oriented (from the shaft) Condylus medialis and Epicondylus lateralis, its deep and differently excavated Sulcus cartilaginis tibialis, and its more circularly shaped Epicondylus lateralis in lateral aspect.

Margarops fuscus is common along forested ghauts of Montserrat, and occurs regularly but in lower numbers in other types of forest. This thrasher does not occur at Trant's today, but may be found just inland in forested areas.

This is the first prehistoric record for *M. fuscus.*

Margarops fuscatus (Vieillot, 1807)—Pearly-eyed Thrasher

Material.—Trant's, Stratum I: unit 2—humerus (359299); unit 3—humerus, tibiotarsus (359300). Stratum II: unit 4—femur, tibiotarsus (359301); unit 6—coracoid, humerus, tibiotarsus (359302). MNI = 3.

The humerus and coracoid of *Margarops fuscatus* are larger than in all other passerines of Montserrat or nearby islands. The femur and tibiotarsus of *M. fuscatus* are larger than in all pertinent passerines except *Cichlherminia lherminieri,* from which the femur of *M. fuscatus* is distinguished by its more pointed proximo-medial and disto-medial portions of Condylus medialis. The tibiotarsus of *M. fuscatus* is distinguished by its stouter shaft, its more circular shape of Epicondylus lateralis in lateral aspect, and its more proximally located tubercle on the medial side of the shaft near Sulcus extensorius.

The status and habitat requirements of *Margarops fuscatus* seem to be very similar to those of *M. fuscus,* although it may be somewhat more common than its congener. A study of the interactions between these two thrashers would be interesting, for they are clearly the most common large passerines in much of the forest on Montserrat. Lack and Taylor (1974) noted that some calls of these two thrashers were indistinguishable, with which we concur.

This is the first prehistoric record for *M. fuscatus* in the Lesser Antilles. It has been reported from archaeological settings in Puerto Rico (Wetmore, 1922), but this identification is apparently erroneous (S. L. Olson, personal communication). The record from Bahamas (Wetmore, 1937) has been shown by Olson and Hilgartner (1982:51) to be based upon a specimen that is actually referable to "*Sturnella* sp." (Icteridae).

Cinclocerthia ruficauda (Gould, 1836)—Trembler

Material.—Trant's, Stratum II: unit 5—tibiotarsus (359303). MNI = 1.

The tibiotarsus of *Cinclocerthia ruficauda* is generally similar in size to that of *Mimus gilvus, Mimus polyglottos,* and *Margarops fuscus,* but is distinguished by its relatively stout shaft, its more obtuse (less perpendicular) angle between the shaft and Epicondylus lateralis and Condylus medialis, and by its shallower Sulcus cartilaginis tibialis.

The Trembler is another forest-dwelling species that lives alongside the two species of *Margarops,* but seems to occur in somewhat lower densities. As with the two thrashers, Tremblers do not live at Trant's today, but occur in the nearby forest.

The only other prehistoric record of *C. ruficauda* is from Burma Quarry, Antigua (Olson, 1982), a paleontological and archaeological site with radiocarbon ages ranging from 4300 to 2500 years B.P. A detailed report on this site is being prepared by G. K. Pregill, D. W. Steadman, and S. L. Olson.

Passeriformes, family and species indeterminate

Material.—Trant's, Stratum II: unit 4—femur (359304). MNI = 1.

This fragmentary specimen is larger than, for example, *Myadestes genibarbis,* but is smaller than in *Margarops, Cinclocerthia, Cichlherminia,* or *Turdus.* It is approximately the size of *Mimus gilvus* or *Mimus polyglottos,* neither of which occurs on Montserrat.

Bird, order and species indeterminate

Material.—Trant's, Stratum I: unit 3—synsacrum (359305), tibiotarsus (359306). MNI = 0. Radio Antilles, Stratum I: unit 1—carpometacarpus (359307); unit 4—tibiotarsus (359308). MNI = 0.

These very fragmentary specimens are wholly undiagnostic. Although those from Radio Antilles represent the only bird bones from that site, they are from disturbed units and therefore archaeologically meaningless.

MAMMALS

The mammalian remains from Trant's and Radio Antilles differ significantly from those of fish, reptiles, and birds in that all taxa identified except one (the bat *Brachyphylla cavernarum*) owe their current status on Montserrat solely to human activities. The surviving agouti and dog arrived as Amerindians' baggage, whereas the native rice rats are extinct, presumably because of alien rats (*Rattus rattus*) introduced from Europe and/or Africa in historic times. Skulls and skeletons in the collections of the Division of Mammals, USNM, were used for identifications, except for the extinct rice rats, which were compared to fossils from paleontological and archaeological sites on Anguilla, St. Kitts, Barbuda, Antigua, Montserrat, Guadeloupe, and Marie Galante. Sequence and nomenclature generally follow Varona (1974).

Order Chiroptera
Family Phyllostomatidae
Brachyphylla cavernarum Gray 1834—large leaf-nosed bat

Material.—Radio Antilles, Stratum I: unit 7—edentulous dentary (359309). MNI = 1.

This bat occurs today on Montserrat, as documented by many specimens. From an archaeological context, *B. cavernarum* has been reported from the Mill Reef site, Antigua (Wing et al., 1968).

Order Primates
Family Hominidae
Homo sapiens Linnaeus 1758—man

Material.—Radio Antilles, Stratum I: unit 6—3 cranial fragments, 2 ribs (359310); unit 7—7 ribs (359311), 4 sacral fragments (359312), 3 cranial fragments (359313); unit 8—fragmentary long bone (359314). MNI = 1.

All of these bones appear to be from an infant. Certain of the unidentified mammal bones could represent an adult human, but much better material is needed to be sure. These bones are all from uncontaminated units, and therefore represent an Amerindian rather than a European or African.

Order Carnivora
Family Canidae
Canis familiaris Linnaeus 1758—dog

Material.—Trant's, Stratum II: unit 4—2nd lower premolar (359315); unit 5—3rd lower incisor (359316). MNI = 1.

These two teeth are from a young adult dog approximately the size of a Labrador Retriever. Known only from undisturbed units, these limited remains give us only a glimpse at the type of dog kept on Montserrat by Amerindians. Elsewhere in the Lesser Antilles, dogs have been reported from prehistoric sites on Grenada, Barbados, St. Lucia, and St. Kitts (Wing and Reitz, 1982).

Order Rodentia
Family Cricetidae
Tribe Oryzomyini
Undescribed species A

Material.—Trant's, Stratum I: unit 2—dentary with Ml-2 (359319), 2 pelves, 2 tibiofibulae (359320); unit 3—pelvis, calcaneum (359321), lower incisor, 2 tibiofibulae (359322), humerus, pelvis, femur, tibiofibula (359323), maxilla with Ml-3 (359324), dentary with Ml-3 (359325), dentary with Ml-2 (359326). Stratum II: unit 4—humerus, 3 pelves, 3 femora, femur, 2 tibiofibulae (359327), pelvis (359328). MNI = 5. Radio Antilles, Stratum I: unit 4—tibiofibula (359329); unit 6—dentary with Ml-2 (359330). MNI = 1.

This relatively small species of rice rat is known on Montserrat only from the material reported here. Descriptions of this and the next species are being prepared by D. W. Steadman and Michael D. Carleton as part of their review of the systematics, paleontology, and evolution of West Indian oryzomyines. Of a similar size to Undescribed species A are the undescribed rice rat remains reported from late Holocene archaeological and paleontological sites on St. Kitts (Hoffman, 1973; Wing, 1973), and Anguilla (Steadman, personal observation). Pending completion of Steadman and Carleton's studies, we believe that it is premature to make definitive statements about species limits in Lesser Antillean rice rats.

Undescribed species B

Material.—Trant's, Stratum I: unit 2—cranial fragment, humerus, 2 ulnae, pelvis (359331); unit 3—edentulous dentary (359332), 2 humeri (359333), dentary with Ml-2 (359334). MNI = 1.

These very limited remains represent an extinct rice rat larger than Undescribed species A. As indicated by Clayton E. Ray's studies (Wing et al., 1968), this form of oryzomyine is known from archaeological or paleontological material from Antigua, Barbuda, and Guadeloupe, as well as Montserrat. Wing (1973) also reported this form of rice rat from an archaeological site on Marie Galante.

cf. Oryzomyini sp.
Large form (distinct species?)

Material.—Trant's, Stratum I: unit 1—femur (359335); unit 2—tibiofibula (359336); unit 3—femur (359337). MNI = 1.

Small form (distinct species?)

Material.—Trant's, Stratum I: unit 2—humerus (359338). Stratum II: unit 5—lower incisor (359339). MNI = 1.

These specimens, mostly fragmentary post-cranial elements, are not from agoutis, guinea pigs, or introduced murid rodents, and seem to be either larger than Undescribed species B or smaller than Undescribed species A. Thus they may possibly represent an additional species or two of extinct rice rat, but additional material is needed to confirm or refute this notion. At present we simply cannot determine the range of variation in the taxa of rice rats from Montserrat. These tantalizing bits, however, hint that the monster-rats of Montserrat may have been much more diverse than previously expected.

One must entertain the possibility that Amerindians were involved in the dispersal of one or more of these species of rodents. Only Undescribed species B is known from pre-archaeological remains, these being from Barbuda. As yet there is no clear evidence that such transport occurred, but Rímoli (1976) and Olson (1982) noted that Amerindians apparently transported various caviomorph rodents from island to island in the Greater Antilles.

Order Rodentia

Family Dasyproctidae

Dasyprocta aguti (Linnaeus, 1766)—agouti

Material.—Trant's, Stratum I: unit 2—auditory bulla (359317). MNI = 0. Radio Antilles, Stratum I: unit 4—upper incisor (359318). MNI = 0.

These specimens are known only from disturbed units, so they cannot be considered as evidence of contemporaneity of agouti and Saladoid peoples on Montserrat. Such probably was the case, however, for agoutis are known from archaeological sites throughout the Lesser Antilles. Agoutis still survive on Montserrat, for Steadman observed two of them on 28 January 1983, at Foxes Bay Bird Sanctuary.

Mammal sp.

Material.—Trant's, Stratum I: unit 1—3 fragments of long bone (359340); unit 2—fragment of long bone (359341). MNI = 0. Radio Antilles, Stratum I: unit 1—fragment of long bone (359342). MNI = 0.

These very limited remains are reminiscent of human bones, but lack diagnostic features.

Vertebrate sp.

Material.—Trant's, Stratum I: unit 1—2 specimens (359343); unit 2—2 specimens (359344); unit 3—2 specimens (359345). Stratum II: unit 4—1 specimen (359346).

MNI = 0. Radio Antilles, Stratum I: unit 4—1 specimen (359347); unit 7—1 specimen (359348); unit 8—2 specimens (359349), 2 specimens (359350). MNI = 0.

These boney scraps cannot be allocated even to a class.

DISCUSSION

The sites at Trant's and Radio Antilles share a number of characteristics. They are located at the coast near mouths of streams, and both have sandy and rocky shores nearby. Four of the five verified sites on Montserrat, including Trant's and Radio Antilles, are situated on Grove Sandy Loam, a Protosol soil (Fig. 2) that Lang (1967) indicates is capable of sustaining drought-resistant crops. (The probable site in the Belham River valley, which has yet to be confirmed on the ground, is also on a Protosol soil.) Not surprisingly, the Saladoid peoples were horticulturists who raised manioc (*Manihot escuelenta* Crantz) and other drought-resistant root crops. Such crops, however, are notoriously deficient in protein. The vertebrate and mollusk remains from the archaeological sites represent the Saladoid people's source of protein. Our discussion of vertebrate remains considers only those taxa recorded from uncontaminated units.

The fish from Trant's and Radio Antilles are from families and genera that occupy a variety of marine environments (Randall, 1968; Fischer, 1978). Coral reefs, either as banks or as fringing reefs, are not common on Montserrat, where deep offshore waters are close to shore. Tunas and mackerals (scombrids) were more abundant in the collection by count, but not MNI, than any other family of fishes. Scombrids, along with the jack, are fish of deep waters. Heavy aboriginal use of scombrids has been reported elsewhere in the West Indies where deep waters are close to shore (Wing and Reitz, 1982). The other families of fishes identified represent primarily deep or shallow coral reef fishes (groupers, snappers, porkfish, grunts, porgies, wrasses, parrotfishes), although some members of these families can also be found over rocky bottoms such as those near Montserrat. Because none of the fish could be identified beyond generic level, inferences about the marine habitats exploited by Saladoid peoples cannot be stated more precisely than that they fished in areas of coral reefs, rocky bottoms, and nearby deep waters.

The fish from Trant's and Radio Antilles indicate the use of at least two fishing methods, following Wing and Reitz (1982). The parrotfishes were probably caught in traps, although they may have been speared or netted. Parrotfishes are not captured by hooks because they feed on corals and associated invertebrates. Tunas and mackerels suggest that handlines were also used. The remaining fish could have been caught by these or other techniques, although a combination of traps and lines can account for the capture of nearly all those identified.

Comparison of the data from Trant's and Radio Antilles might provide information about subtle differences in habitat exploitation and fishing techniques if we had larger samples. Compared to archaeological remains from islands such as Antigua and Barbuda that are nearly surrounded by reefs, fish make up a relatively low portion of the vertebrate faunal remains on Montserrat (Watters, 1982).

Sea turtles occurred in low numbers in both archaeological sites. We are not aware of any regular nesting of sea turtles today on Montserrat, where there are few if any suitable nesting beaches. Thus sea turtles probably have always occurred in lower densities near Montserrat than near flatter islands that have large areas of beach.

As with sea turtles, we cannot yet say how important the iguana was in the diets of Saladoid peoples. Iguanas generally are not a food item among most West Indians today, although Lazell (1973) noted that they are eaten on Guadeloupe. Iguanas are considered excellent eating by many peoples, and are relished in much of Central and South America. Today, iguanas on Montserrat live mainly near the coast, and this may have been true in the past. So they probably were readily available at both Trant's and Radio Antilles, but we need much larger samples to determine their importance in Amerindian diets.

The birds recovered from Trant's are dominated by pigeons and doves, highly edible birds that have been important food items for prehistoric as well as modern West Indian peoples. The gallinules and large passerines were probably eaten also. None of these birds is known for their spectacular plumage, although certain feathers of pigeons and doves are colorfully iridescent and may have been used for some decorative purpose. All of the birds except the gallinule occur today within easy walking distance of Trant's. Most of the species live entirely or mainly in forests, the exception being the ground dove, which prefers open areas, and the water-loving gallinule. It is interesting that the strictly forest-dwelling Bridled Quail-dove was the most common species of bird from the Trant's site; if one were to hunt for pigeons and doves in the Trant's region today, even in the nearby forest, one would procure more Zenaida Doves than any other species. Once again, we need larger samples to determine if these numbers are meaningful.

Few mammals were recovered at Radio Antilles, although the only remains of bats or humans were taken here. All mammals from Trant's are native oryzomyine rodents except for limited remains of a dog. These rodents probably were eaten by Amerindians, whose only other sources of terrestrial mammal flesh were bats, dogs, and agoutis. It seems unlikely that predation by humans could wipe out a native rice rat, unless such predation were accompanied by massive habitat destruction. The predominance of forest birds argues against large-scale cutting or burning of forests by aboriginal peoples, at least on nearby steep slopes. Although solid evidence is lacking, we believe that the extinction of native oryzomyines in Montserrat, as well as elsewhere in the Lesser Antilles, is somehow related to the historic introduction of Old World murid rodents, namely *Rattus* and possibly *Mus.* Only through extensive, well dated excavations will we be able to pinpoint the chronology of extinction of Montserrat's indigenous rodents. Such work is also necessary to determine their taxonomic diversity.

We are fortunate that the excavations on Montserrat were screened through ⅛ in. mesh rather than the ¼ in. mesh more often used by archaeologists. Many of the specimens of fish, birds, and rodents recovered would have passed through ¼ in. mesh. In the future, however, we hope to undertake large-scale excavations at the Trant's site that will incorporate $\frac{1}{16}$ in. mesh screening in areas of higher than normal concentrations of bone. This will allow us to recover a much more diverse fauna. For example, our present sample includes few or no very small fish, frogs, lizards, snakes, birds, or bats, yet there is no reason to believe that some of these small forms were not used by aboriginal peoples or that they are not preserved within the sediments. These time-consuming efforts will give us a much more complete picture of the relationships between prehistoric man and animals on Montserrat.

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MIDDLE EOCENE MARSUPIALS (MAMMALIA) FROM NORTHEASTERN UTAH AND THE MAMMALIAN FAUNA FROM POWDER WASH

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Abstract

Four species of didelphid marsupials—*Peratherium marsupium, Peratherium innominatum, Peradectes chesteri, Armintodelphys dawsoni*—are reported from the Powder Wash locality, upper fossiliferous zone, Green River Formation, Utah. *P. innominatum* is represented by the largest known sample of marsupial remains from a single Eocene horizon, and an upper molar of *Armintodelphys* is described for the first time. A revised list of the fossil mammals from Powder Wash contains 59 species, of which 34 were previously unrecorded and include the first record in the fauna of leptictids, apatemyids, pantolestids, palaeoryctids, mesonychids, perissodactyls, and chiropterans. The fauna, composed mostly of small mammals, is early Bridgerian in age and corresponds most closely with other Bridger A and B faunas.

Introduction

In 1957 J. LeRoy Kay reported the first record of fossil marsupials (*Peratherium innominatum*) from the Uinta Basin and the Green River Formation. The locality, called Powder Springs (Gazin, 1958) or, more commonly, Powder Wash (Dawson, 1968), was first noted by Burke (1935), who reported five mammalian taxa from an upper fossiliferous zone and two from a lower zone. Fossil mammals are rare in the Green River Formation, but, since 1923, field parties from the Carnegie Museum of Natural History led by Kay, Burke, C. C. Black, and M. R. Dawson have recovered one of the richest assemblages of Bridgerian

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microvertebrates, including the marsupials described here, from the upper fossiliferous horizon at Powder Wash. The mammalian fauna from this zone is early Bridgerian (Dawson, 1968) and probably post-Gardnerbuttean in age (see Robinson, 1966; Stucky, 1982; Stucky and Krishtalka, 1983). Only the rodents (Wood, 1962; Dawson, 1968), insectivores (Krishtalka, 1975, 1976*a,* 1976*b*; Lillegraven et al., 1981), condylarths (Gazin, 1968; West, 1979), some of the primates (Gazin, 1958; Szalay, 1969, 1976) and an artiodactyl (Burke, 1969) have been treated systematically. A more complete list of the fossil mammals from the upper fossiliferous zone is presented here. Remains of lower vertebrates from this horizon are extremely numerous, but have never been studied. A preliminary analysis indicates that at least two anguids, two iguanids, and one varanid are present, in addition to an undetermined number of snakes and amphibians.

The lower fossiliferous zone in the Green River Formation at Powder Wash has only produced remains of a primate (*Uintalacus nettingi* Gazin, 1958) and *Lambdotherium* sp., and is apparently Lostcabinian in age (Burke, 1935). Postcranial remains of a large carnivore, and skeletal material of three species of birds (Wetmore, 1926; Kay, 1957) were reported from the lowest levels of the Green River Formation at Powder Wash—beds which may correspond to Burke's lower fossiliferous zone. In the same area, deposits of the Wasatch Formation underlie the Green River Formation and have yielded dental remains of *Phenacodus, Hyracotherium, Coryphodon,* and *Paramys* (Kay, 1957).

Four species of didelphids from the upper fossiliferous zone at Powder Wash are represented by 247 identifiable specimens, most of which are isolated teeth of *Peratherium innominatum.* The other three didelphids are *P. marsupium, Peradectes chesteri,* and *Armintodelphys dawsoni.* The two species of *Peratherium* belong to the Tribe Didelphini, whereas *Peradectes* and *Armintodelphys* are members of the Peradectini. The systematics, evolutionary relationships and occurrences of these species, as well as all North American Paleocene and Eocene didelphines, were treated elsewhere (Krishtalka and Stucky, 1983*a,* 1983*b*) and are not repeated here.

All of the material referred in this paper is in the collections of the Carnegie Museum of Natural History (CM). Other abbreviations in text are: USNM—United States National Museum; UW—University of Wyoming.

SYSTEMATICS

Family Didelphidae Gray, 1821
Subfamily Didelphinae Gray, 1821
Tribe Didelphini Crochet, 1979
Peratherium Aymard, 1850

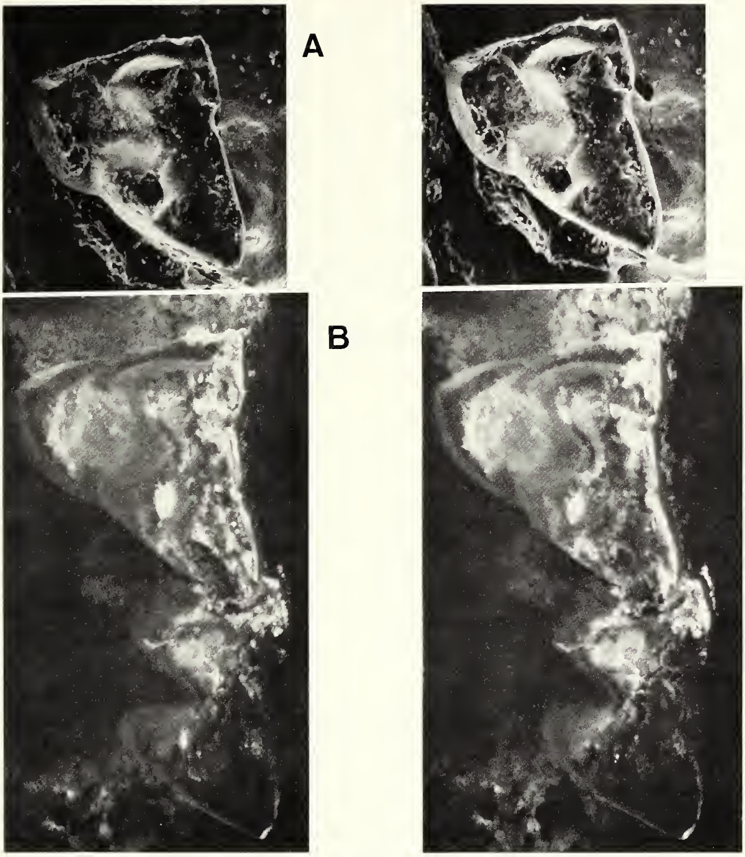


Fig. 1.—*Peratherium marsupium.* (A) CM 41741, LM^1; (B) CM 17314, LM^{2-3}; both approx. ×13.5.

Peratherium marsupium (Troxell, 1923)
(Fig. 1, Table 1)

Referred specimens.—Partial lower jaw with C, P_3–M_3 and alveoli for P_{1-2}—CM 6473; isolated teeth: M_1—42041; M_3—35073; partial maxilla with M^{2-3}—17314; isolated teeth: dP^3—41733; M^1—35072, 35082, 41741; M^2—41740; M^3—35052, 35053, 41738, 41739, 42216; M^4—42215.

Description and discussion.—On CM 6473, a well-preserved lower jaw, the canine is trenchant, recurved, and approximately twice as high as P_3. The four alveoli between C and P_3 account for double-rooted P_1 and P_2, as in the type of *P. marsupium* (Troxell, 1923). There are no

Table 1.—*Dental measurements of* Peratherium marsupium *(CM material) from the upper fossiliferous zone, Green River Formation, Powder Wash, Utah.*

Catalog no.	DP^3		M^1		M^2		M^3		M^4		P$_3$		M$_1$		M$_2$		M$_3$	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
41733	2.2	1.5																
35072			2.7	2.5														
35082			2.6	2.4														
41741			2.5	2.2														
17314					2.6	2.7	2.6											
41740					2.5	2.7												
35052							2.7	3.2										
35053							2.7	3.2										
41738							2.5	3.0										
41739							2.6	3.1										
42216							2.6											
42215									2.1	2.4								
6473											2.0	1.2	2.4	1.4	2.7	1.7	2.9	1.6
42041													2.6	1.4				
35073																	2.8	1.6

diastemata between the antemolar teeth, unlike the condition in *P. innominatum,* where diastemata occur between the lower premolars. As in the type of *P. marsupium,* two mental foramina occur on CM 6473, one below the posterior root of P_1, and the other below M_1, between the two roots. The area of insertion of the digastric muscle extends to below the alveoli for P_2, and there is no indication of symphysial fusion. The mandible is deepest below M_3 on CM 6473 (4.7 mm), and becomes shallower anteriorly.

The upper molars of *P. marsupium* from Powder Wash, like those from other localities (Krishtalka and Stucky, 1983*a*; Setoguchi, 1975) vary in the size and position of the stylar cusps. On M^1, stylar cusp B is the largest and C is doubled; on M^{2-3}, B or C may be largest, and C or D can be doubled; on CM 42216, an M^3, cusps B, C and D are doubled.

The single dP^3 is similar in morphology to one referred to *P. sudrei* (Crochet, 1978, Fig. 169). The crown is triangular, much longer than wide, and has a large metastylar salient, but lacks a stylar shelf labial to the paracone. The paracone, tall and spire-like, is slightly lower than the metacone and smaller at the base. The centrocrista between the two cusps is not dilambdodont. The protocone lies directly lingual to the paracone, and a small parastyle (? stylar cusp A) occurs anterior to the latter. Cusps C and D are moderately developed, ridge-like and subequal. Cusp B is absent.

Peratherium innominatum Simpson, 1928
(Fig. 2, Table 2)

Referred specimens.—Partial lower jaws with: P_2—35076; C, P_3 and alveoli for P_{1-2}—CM 35063; P_{2-3} and alveoli for P_1, M_{1-2}—17315; M_{1-2} and alveoli for P_{1-3}, M_3—17313; M_{2-4}—35064; M_2—35077; isolated teeth: M_1—35038, 35070, 35083, 35084, 41166–41170, 41753–41755, 41763, 41978, 41983–41989, 42044, 42050, 42054, 42062–42064; M_2 or M_3—35065–35068, 35075, 35085, 35086, 41171–41182, 41750–41752, 41764–41773, 41990–41998, 42048, 42049, 42051–42053, 42055–42060; M_4—41183–41185, 41975–41977, 41979–41981, 42043, 42045–42047, 42212, 42213; partial maxillae with: M^{1-2}—42196; M^{2-4}—8749; isolated teeth: DP^3—41186, 41187, 41734, 41761; M^1—35037, 35041, 35044, 35045, 35055, 35079, 35080, 35087, 41188–41199, 41737, 41760, 41761, 42023, 42024, 42029, 42030, 42032–42040, 42192, 42196; M^2—35048–35051, 35057, 35060, 35071, 42001, 42004–42014, 42025–42028, 42031, 42193–42195, 42197–42204; M^3—35046, 35047, 35054, 35056, 35058, 35059, 35061, 35078, 35081, 41774, 41999, 42000, 42002, 42003, 42015–42022, 42205–42209; M^4—35039, 35040, 35043, 41729, 41756–41759, 41762, 42210, 42211, 42214.

Description and discussion.—The lower canine preserved on CM 35063 is identical morphologically to that in *P. marsupium.* Unlike the latter, however, diastemata occur between the lower premolars, which are also two-rooted. The anterior of the two mental foramina occurs below either the diastema between P_1 and P_2 or the posterior root of P_1. The posterior one lies below M_1 or between P_3 and M_1. The

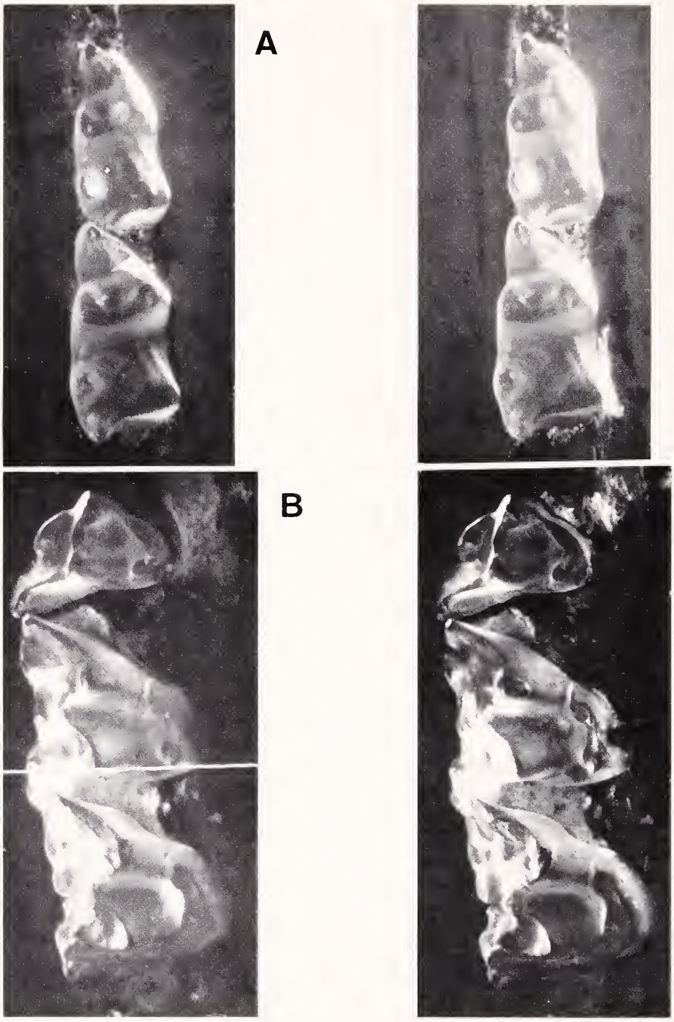


Fig. 2.—*Peratherium innominatum.* (A) CM 17313, RM_{1-2}; (B) CM 8749, LM^{2-4}; both approx. ×13.5.

area for insertion of the digastric muscle extends to below the posterior root of P_3. M_1 is the smallest of the lower molars, with a more anterior paraconid. Isolated M_2s and M_3s cannot be distinguished with certainty. The size of the entoconid on the lower molars varies from being tall and spire-like (most specimens) to almost the size of the hypoconulid.

Table 2.—*Dental measurements of* Peratherium innominatum *from the upper fossiliferous zone, Green River Formation, Powder Wash, Utah (L = length; W = width).*

Tooth and measurement	N	Range	Mean	SD	C.V.
M^1, L	32	1.6–1.9	1.78	0.09	5.1
M^1, W	32	1.4–1.7	1.58	0.09	5.7
M^2, L	36	1.7–1.9	1.82	0.08	4.3
M^2, W	36	1.7–2.0	1.87	0.08	4.4
M^3, L	27	1.7–2.0	1.79	0.10	5.7
M^3, W	27	1.7–2.2	2.03	0.10	5.0
M^4, L	12	1.1–1.5	1.31	0.14	10.7
M^4, W	12	1.9–2.2	2.06	0.12	6.0
M_1, L	27	1.5–1.8	1.68	0.08	4.8
M_1, W	26	0.8–1.1	0.95	0.06	6.3
$M_{2\text{ or }3}$, L	51	1.8–2.0	1.88	0.06	3.2
$M_{2\text{ or }3}$, W	50	0.9–1.2	1.07	0.07	6.5
M_4, L	14	1.7–2.0	1.83	0.11	6.0
M_4, W	14	0.9–1.1	1.02	0.06	5.9

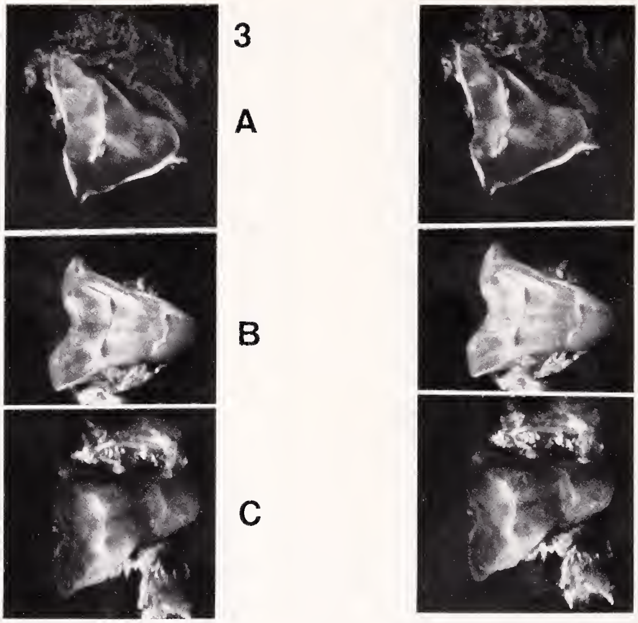
The few lower molars that exhibit the latter end of the range of variation retain the deep, wide notch between the entoconid and hypoconulid—a diagnostic feature that distinguishes *Peratherium* from members of the Peradectini.

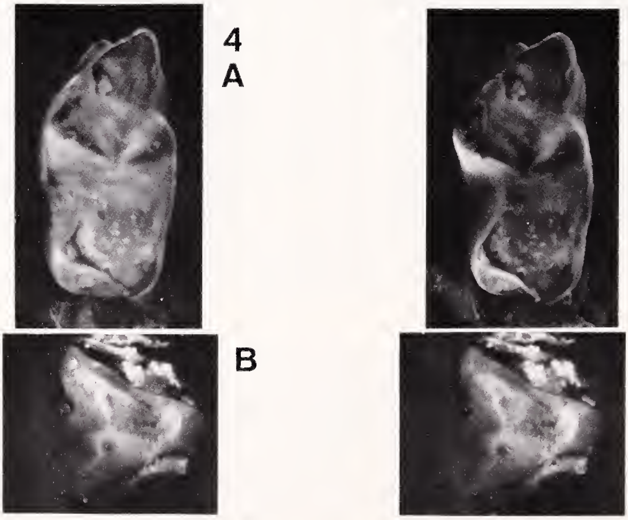
As in *P. marsupium,* but in contrast to *P. knighti,* M^{2-3} of *P. innominatum* invariably have deep ectoflexi. The position and size of the stylar cusps are, on the other hand, extremely variable, and not useful in distinguishing between *Peratherium* and *Herpetotherium* (contra Crochet, 1978, 1979), or among the species of *Peratherium.* On M^1, cusps B and D can be equal and the largest of the stylar cusps, or B can be the largest and doubled. Cusps B, C and D are either cusp-like or developed on a ridge, and C can be doubled or barely distinguishable. On M^{2-3}, cusp B is usually the largest, although B, C and D can be subequal, and on M^2 C and/or D can be doubled. On M^4, A is well-developed, C is higher, ridge-like and sometimes incipiently doubled, and cusps B, D, and E are absent.

DP^3 in *P. innominatum* resembles that in *P. marsupium,* but is smaller and has a more labio-lingually compressed paracone and a stronger centrocrista.

Tribe Peradectini Crochet, 1979
Peradectes Matthew and Granger, 1921
Peradectes chesteri (Gazin, 1962)
(Fig. 3)

Referred specimens.—M_3—42136; DP^3—41743; M^1—41747; M^2—41725, 41736, 42042, 42217; M^3—41726, 41730, 41735, 41744–41746, 41748; M^4—42218.


3
A
B
C


4
A
B

Description and discussion.—The single lower molar, an M_3 (CM 42136; L = 1.4, W = 0.8), has subequal entoconid and hypoconulid and a weak entoconid notch—diagnostic features of the Peradectini. The M_3 closely resembles that in the type (USNM 19199) and referred material (UW 984) of *P. chesteri* (see Krishtalka and Stucky, 1983*b*, Fig. 5) in having an occlusally narrow talonid and in lacking the labial emargination between the talonid and trigonid.

As in other species of *Peradectes,* the upper molars are not dilambdodont. In *P. chesteri,* they are progressively more transverse from M^1 to M^3, and lack all stylar cusps except B; M^3 has a highly compressed protocone and a deep ectoflexus. In these features *P. chesteri* is intermediate morphologically between the early Wasatchian *P. protinnominatus* and the Oligocene *P. minutus.*

CM 41743, a DP^3 (L = 1.2, W = 1.1), is referred to *P. chesteri* on the basis of its smaller size and morphological distinction from DP^3 of *Peratherium.* Unlike the latter, the paracone and metacone are subequal and the metastylar salient is less elongate, so that the crown is more nearly equilateral in occlusal view.

Measurements.—CM 41747 (M^1), L = 1.4, W = 1.1; CM 42042 (M^2), L = 1.5, W = 1.6; CM 41744 (M^3), L = 1.2, W = 1.7; CM 41748 (M^3), L = 1.3, W = 1.7; CM 41730 (M^3), L = 1.3, W = 1.7; CM 41735 (M^3), L = 1.4, W = 1.7; CM 42218 (M^4), L = 0.9, W = 1.7.

Armintodelphys Krishtalka and Stucky, 1983*a*
Armintodelphys dawsoni Krishtalka and Stucky, 1983*a*
(Fig. 4)

Referred specimens.—M_3—41742; M_4—41982; M^2—41749.

Description and discussion.—The M_3 (CM 41742; L = 1.5, W = 0.8) and M_4 (CM 41982; L = 1.6, W = 0.7) agree in size and morphology with those in the type of *A. dawsoni* from the Wind River Formation. As is diagnostic of this genus, the entoconid is much smaller than the hypoconulid. The lower molars also differ from those of *P. chesteri* in retaining the labial emargination between the trigonid and talonid. The talonid of M_4, previously unknown in *A. dawsoni,* is longer than the trigonid, as in *A. blacki.*

CM 41749, an M^2 (L = 1.4, W = 1.65), is the first upper molar re-

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Fig. 3.—*Peradectes chesteri.* (A) CM 41747, LM^1; (B) CM 42042, RM^2; (C) CM 41735, RM^3; all approx. ×14.

Fig. 4.—*Armintodelphys dawsoni.* (A) CM 41742, LM_3, approx. ×20; (B) CM 41749, RM^2, approx. ×14.

ferred to *Armintodelphys.* Among known North American early Tertiary marsupials, it resembles M^2 in other Peradectini (*Peradectes, Mimoperadectes*) and differs from all Didelphini in lacking dilambdodonty and a posteriorly expanded protocone, and in having subequal paracone and metacone. However, unlike M^2 in *Peradectes* and *Mimoperadectes,* CM 41749 has expanded, flaring stylar salients, an enlarged stylar cusp C that is equal in size to B, and a weaker protocone. Its size is consistent with that of the lower molars of *A. dawsoni,* the only other peradectinine in the Powder Wash fauna. The crown is equilateral rather than transverse and, as such, most closely resembles M^2 in *P. protinnominatus* and *P. elegans* (M^2 is unknown in *P. pauli*) among known species of *Peradectes.* This record extends the range of *A. dawsoni* into the late early Bridgerian (see below).

COMPOSITION AND AGE OF THE POWDER WASH FAUNA

A review of the CM collection from Powder Wash indicates that at least 59 species of mammals are represented (Table 3), of which 34 were previously unreported and mark the first noted occurrence in this fauna of leptictids, apatemyids, pantolestids, palaeoryctids, mesonychids, perissodactyls, and chiropterans. The occurrence of *H. vassaciense* represents the third known record of *Hyracotherium* from the Bridgerian (Robinson, 1966; Stucky, 1982); the isolated upper molars lack the mesostyle that is diagnostic of *Orohippus* (Kitts, 1956, 1957). *Aethomylos* and *Cryptolestes* were previously known only from Uintan localities in California (Novacek, 1976). At least three new mammalian species are represented by isolated teeth; formal recognition of these taxa will occur in future studies.

Large mammals are rare in the fauna, and significantly, uintatheres, brontotheres, taeniodonts, phenacodonts, pantodonts, oxyaenids, and large artiodactyls are absent. Approximately 95% of the dental remains represent fossil small mammals, especially marsupials, primates, insectivores, and rodents. This atypical composition, likely due to an ecological and depositional bias, makes precise biostratigraphic correlation difficult. As other workers have concluded, the fauna is early Bridgerian in age. This is implied by the co-occurrence of *Palaeictops bridgeri, Talpavus nitidus, Pantolestes, Nyctitherium,* the two species of *Centetodon, Omomys, Smilodectes, Anaptomorphus, Uintanius, Helaletes, Hyrachyus, Trogosus, Antiacodon,* and *Sciuravus.* Assignment of the fauna to one of the three subdivisions of the early Bridgerian (Gardnerbuttean, Bridger A, Bridger B) is less certain. The absence of typical Gardnerbuttean genera such as *Coryphodon, Bunophorus, Didymictis* and *Esthonyx* is not reliable evidence of a post-Gardnerbuttean age considering the bias against the preservation of large mammals.

Table 3.—*Mammalian fauna from the upper fossiliferous zone, Green River Formation, Powder Wash, Utah. Citations refer to previous identifications of taxa from this locality.*

Order Marsupicarnivora
- *Peratherium marsupium*
- *Peratherium innominatum* (Kay, 1957)
- *Peradectes chesteri*
- *Armintodelphys dawsoni*

Order Leptictida
- *Palaeictops bridgeri*

Order Cimolesta
- *Apatemys* sp., cf. *A. rodens*
- *Apatemys* sp., cf. *A. bellus*
- *Apatemys* sp., cf. *A. bellulus*
- *Pantolestes* sp., cf. *P. longicaudus*
- palaeoryctine sp.

Order Creodonta
- *Sinopa grangeri*
- *Sinopa minor* (Kay, 1957)
- *Tritemnodon* sp., cf. *T. gracilis*
- *Tritemnodon* sp., cf. *T. whitiae*
- *Limnocyon* sp., cf. *L. verus*
- ?*Proviverroides* sp.

Order Carnivora
- *Viverravus minutus* (Kay, 1957)
- *Viverravus gracilis*
- *Viverravus sicarius*
- *Miacis* sp., cf. *M. parvivorus*
- *Uintacyon* sp., cf. *U. major*
- ?*Oodectes* sp.
- miacid n. gen., n. sp.

Order Insectivora
- *Scenopagus edenensis* (Krishtalka, 1976*a*)
- *Scenopagus priscus* (Krishtalka, 1976*a*)
- *Talpavus nitidus* (Krishtalka, 1976*a*)
- *Talpavus* sp., cf. *T. nitidus* (Krishtalka, 1976*a*)
- *Nyctitherium serotinum* (Kay, 1957; Krishtalka, 1976*b*)
- *Centetodon pulcher*
- *Centetodon bembicophagus* (Krishtalka, 1975; Lillegraven et al., 1981)
- "*Eoryctes*" (McKenna, MS; Novacek, 1977)
- *Cryptolestes* sp.
- *Aethomylos simplicidens*

Order Chiroptera
- cf. *Ageina* sp.

Table 3.—*Continued.*

- Order Primates
  - *Uintasorex* sp., cf. *U. parvulus* (Gazin, 1958; Szalay, 1969)
  - *Microsyops* sp.
  - *Utahia kayi* (Gazin, 1958)
  - *Anaptomorphus aemulus*
  - *Omomys carteri* (Gazin, 1958)
  - *Omomys lloydi* (Gazin, 1958)
  - *Uintanius ameghini*
  - *Smilodectes gracilis* (Gazin, 1958)
  - *Notharctus* sp., cf. *N. tenebrosus*
- Order Tillodontia
  - *Trogosus* sp. (Kay, 1957)
- Order Condylarthra
  - *Hyopsodus paulus* (Gazin, 1968; West, 1979)
  - *Hyopsodus minusculus* (Kay, 1957; Gazin, 1968; West, 1979)
- Order Perissodactyla
  - *Hyracotherium vassaciense*
  - *Helaletes nanus*
  - *Hyrachyus modestus*
- Order Artiodactyla
  - *Antiacodon pygmaeus* (Burke, 1969)
  - diacodexine n. sp.
  - homacodontine n. sp.
- Order Acreodi
  - mesonychid sp.
- Order Rodentia (Dawson, 1968)
  - *Paramys* near *P. delicatus*
  - *Pseudotomus* near *P. robustus*
  - *Microparamys minutus*
  - *Sciuravus eucristadens*
  - sciuravid sp.
  - *Pauromys* sp.

The same holds true for the absence of large mammals that are characteristic members of Bridger A and Bridger B faunas. Most of the small mammals in the fauna are also not helpful in determining a precise age; three species are restricted to Powder Wash; many are known from Wasatchian and Bridgerian horizons, or throughout the Bridgerian; and many are poorly documented and the subject of taxonomic contention.

The only small mammals of possible biostratigraphic utility are: (1) *Omomys carteri* and *Smilodectes gracilis,* which are most common in Bridger A and B faunas (Gazin, 1958, 1976; McGrew and Sullivan, 1970; West, 1973), but which are also represented by single specimens from Gardnerbuttean levels in the Huerfano Formation (Gingerich, 1979; Stucky, 1982); (2) *Notharctus tenebrosus, Anaptomorphus aemulus,* and *Microparamys minutus,* which are restricted to Bridger B horizons (Dawson, 1968; Szalay, 1976; Gingerich, 1979); and (3) the species of *Paramys, Pseudotomus, Sciuravus,* and sciuravid, which are closest morphologically to species from Bridger B, C, and D (Dawson, 1968). Also possibly useful is the absence of *Knightomys* and *Shoshonius,* common elements of Gardnerbuttean faunas.

Among the larger mammals, the three species of perissodactyls and *Antiacodon pygmaeus* are common in Gardnerbuttean horizons in the Wind River and Huerfano formations, but *H. nanus, H. modestus,* and *A. pygmaeus* also occur in Bridger A and B faunas. The carnivores and creodonts, which have not been studied in systematic detail since Matthew's (1909, 1915) reviews, currently are too muddled taxonomically to be of precise biostratigraphic utility.

Taken together, the co-occurrence of the species of rodents and some of the primates (*O. carteri, S. gracilis, A. aemulus, N. tenebrosus*), and the absence of *Knightomys* and *Shoshonius* imply a post-Gardnerbuttean, early Bridgerian age for the Powder Wash fauna from the upper fossiliferous zone.

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POTTERY FROM CURRIDABAT AND CONCEPCIÓN IN THE CENTRAL HIGHLANDS OF COSTA RICA

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Abstract

Data from part of the Hartman Collections at Carnegie Museum of Natural History is used to produce a stylistic analysis of the alligator motif on burial urns of the Curridabat Phase and to establish interrelationships between the Highlands and the Atlantic Watershed as is evidenced in the pottery.

Introduction

The Hartman collection in Carnegie Museum of Natural History is well known to students of Costa Rican archaeology. It is not only a large and varied collection, but contains material which Hartman excavated according to exacting standards thus providing excellent provenience data (Rowe, 1959). Such information is often missing in the large collections of Costa Rican artifacts made under less than ideal circumstances. The Hartman collection, made when Carl Hartman served as Curator of Archaeology and Ethnology at Carnegie Museum of Natural History (1903–1908), is valuable, therefore, in providing basic contextual information on the material. The collection can be used to provide information and answers to problems relevant to current archaeological work in Costa Rica. For example, excavations of 1903 at the Las Huacas burial ground in the Nicoya Peninsula by Hartman (1907*a*) provided data for a stylistic seriation of stone pendants by Fonseca in 1978 (Fonseca and Scaglion, 1978). This analysis can be utilized by others for the purpose of comparison with similar, non-provenienced material.

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This article concerns the pottery from two small cemetery sites in the Cartego Valley of the Central Highlands excavated by Hartman in 1903. The provenience data on this material, which Hartman named Curridabat and Concepción, is, unfortunately, not as complete as that at Las Huacas. Because the sites were in productive coffee plantations at the time, Hartman's usual excavation procedures were greatly inhibited. Hartman left Carnegie in 1908 without publishing the complete results of the Curridabat and Concepción excavations. Efforts to recover his excavation notes have been unsuccessful. The Hartman collections in Sweden are now at the Etnografiska Museet. Through the cooperation of this museum efforts were made to locate information in their collections and a search was also made of the National Archives, the Royal Swedish Academy of Sciences, and major libraries in Stockholm. Unfortunately, no information on Curridabat and Concepción was discovered.

Some information about the excavation was provided, however, in an article of 1907 which is primarily devoted to a discussion of the alligator motif on some of the pottery (Hartman, 1907*b*).

The material from Curridabat and Concepción is important in the prehistory of Costa Rica as it has long formed the basis of the Curridabat phase of the Central Highlands (A.D. 400–900). The entire pottery complex has never been published; in fact, the published material has been restricted to a few of the pottery types actually present in the collection from these sites. A more complete description of the variety of pottery recovered is essential for an understanding of the Curridabat Phase.

While the complete description of the Curridabat and Concepción pottery is to be found in Skirboll (1981), the following issues will be discussed here: First, the analysis of one important motif appearing at these and other sites of this general period is undertaken in the hope that it will establish a framework for the relative dating of similar excavated material. Second, the relationship between the Central Highlands and the Atlantic Watershed during the Curridabat phase based on the variety of pottery found at these sites in comparison with pottery from sites in the Atlantic Watershed is discussed.

EXCAVATIONS

In excavations at both Curridabat and Concepción, Hartman discovered the pottery in two groups which appear to have had separate functions. First he recovered the tripod vases which had apparently been deliberately broken over the burials. The burials themselves were encountered lower in the excavations indicated by the second functional class of pottery—the small bowls and jars, some containing residues of offerings placed in the graves with dead. Due to the soil conditions, no traces of human remains were found (Hartman, 1907*b*). Although this is scanty provenience information, it has been enough to suggest that these burials were similar to others of the period in the Atlantic Watershed area in which tripod vases were broken over or near the burials (Skinner, 1926; Snarskis, 1978).

TRIPOD JARS

The large tripod jars, sometimes called floreros, form the largest cohesive group of ceramics at both sites numbering 411 specimens (Curridabat: 278; Concepción: 133). Of these, only 19 are whole vessels having been completely or partially reconstructed. The great majority were broken at the time of their burial. The very ornately decorated legs of these vessels interested Hartman, and he spent a good bit of energy attempting to match them to the vessel bodies and reconstruct them. What attracted him to these specimens in particular was the variety of zoomorphic and anthropomorphic figures decorating them. The most prevalent motif in the collection from both sites is the alligator or iguana figure appearing on the legs. Hartman's article of 1907*b* is a preliminary stylistic analysis of this alligator figure. In it, he suggested certain relationships within the material as well as to outside data. The number and variety of alligator figures make it a natural subject for stylistic seriation. While Hartman made some suggestions regarding the direction which stylistic change appeared to follow in the material, a completed seriation of this motif had never been made. The primary aim of this study has been to seriate the alligator figure. In the course of the work several hypotheses regarding the significance of the motif and its appearance at Curridabat and Concepción developed. These will be discussed below.

A few explanatory comments are in order regarding the description of this motif as an alligator. There has been some discussion in the literature about whether the "alligator god" of Central America was indeed an alligator or another animal such as an iguana (Helms, 1977). Dr. C. J. McCoy, Jr., Curator of Reptiles at Carnegie Museum of Natural History, examined the alligator motifs on the Curridabat and Concepción material and concluded that although they were crocodilian, they appeared to combine elements of several types and could not be assigned to a genus. They are highly schematicized animal figures with various alligator-like attributes, but possess iguana-like attributes as well. The possible significance of the schematization of the figure will be discussed below. The term alligator is used here because it is familiar to those interested in Central American archaeology, but the use of the term does not suggest that the animal being depicted is intended to represent a real alligator; in fact, it is possible that it is not intended to look like a specific living animal.

The stylistic analysis of the alligator required that study be concentrated on the vessel legs. Since these were broken off their original bodies, it was not possible to associate the seriation of the legs with the bodies. In order to discover changes in vessel bodies across time, a separate seriation of body forms was undertaken. A complete description of these forms and their seriation can be found in Skirboll (1981). All vessels were made in two parts—necks and bodies were made in separate sections and then joined. The tripod legs, which could be either solid or hollow, were added to a finished body form. Hollow legs are more numerous at both sites. There are 150 hollow and 28 solid legs at Curridabat, and 95 hollow and 8 solid legs at Concepción. In spite of their small numbers, solid legs proved to be of importance in the seriation. It has been suggested by Aguilar (1976) in regard to the Highlands and by Snarskis (1978) in reference to the Atlantic Watershed that solid legs on tripod vessels of the florero type are early in Period V, being prevalent in the Pavas Phase in the Central Highlands and in the El Bosque Phase in the Atlantic Watershed.

There are distinct differences in the motifs on solid and hollow legs. None of the solid legs carry the alligator motif (see Fig. 1). All are decorated instead with a variety of zoomorphic or anthropomorphic figures or with highly schematicized motifs which may be called adornos. Solid legs are generally smaller and thinner than hollow ones and tend to lack the outward curve at the bottom seen in the hollow legs.

Two vessels with solid legs could be identified as a named Pavas Phase type—Molino Acanalado (Aguilar, 1976:76). These vessels (see Fig. 2), as well as other solid legs were useful as anchors to the early end of the seriation.

The great majority of the tripod legs are hollow, a form of construction which permitted a larger leg to be formed than was possible with solid construction. Often a slit was cut into the side of the hollow leg and several small clay pellets were inserted to serve as rattles. Only 19 of the hollow legs carry zoo or anthropomorphic figures which are like those decorating solid legs (see Fig. 3). By far the most common motif on them is the alligator with a total of 175 legs bearing this motif at both sites.

The alligator figures were produced in a large range of techniques. In some examples the bodies of the animals are highly schematic, almost abstract, while in others they are somewhat naturalistic. The scales are undoubtedly a very important element in depicting the figure. They were never omitted on an alligator figure although other features such as eyes and mouths might be. They were made in several ways. In some figures each scale was an individually formed pellet, uniform in size and attached to the animal's back in a careful line (see Fig. 4C). Some, however, were carelessly made, uneven in size, and attached in

Fig. 1.—Solid tripod legs from Costa Rican pottery.

an irregular fashion. In some cases shortcuts were taken, and ridges of clay represent lines of scales. This was much easier and faster than making individual pellets (Fig. 4A). It was obvious to Hartman that a final step in a simplification of elements of the figure occurred when

Fig. 2.—Solid leg vessel of Molino Acanalado type.

three ridges of clay were the only elements left on the alligator after all other animal features were omitted (Hartman, 1907*b*). The figure at this point was simplified to the extent that it no longer looked anything like a real alligator. Hartman was correct in his assumption that the simplest alligators, made up of three plain, unadorned ridges of clay were the latest to be produced. They consistently represented the recent end of the seriation in tests.

Fig. 3.—Hollow zoomorphic tripod legs from Costa Rican pottery.

Method of Analysis

The technique chosen for the seriation was nonmetric multidimensional scaling. This technique was selected because of several advantages it provides over other seriation procedures. In a multidimensional approach more than one dimension of relationship can be detected. Thus, a time dimension can be separated from other dimensions if they exist. Furthermore, it is a technique which can fail to produce a seriation if one does not exist in the data. The program used to produce the scaling was MINISSA I (Lingoes, 1973). This program provides for solutions in one to 10 dimensions. The dimensionality

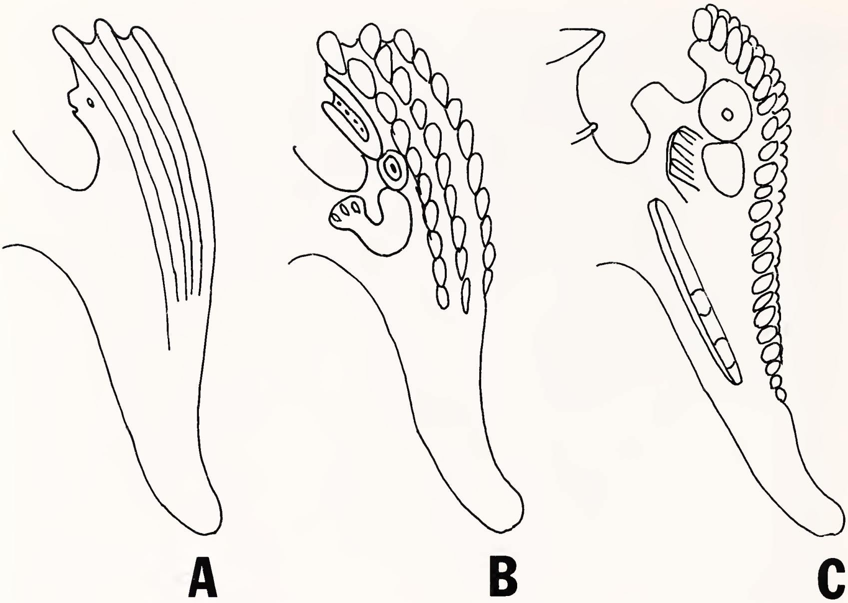

Fig. 4.—Variation in alligator motif styles from Costa Rican pottery.

selected depends on several factors chief among them being interpretability. For this seriation, two or three dimensional solutions generally produced good fits and were readily interpretable.

To prepare the data for seriation, the presence or absence of 57 attributes relating to the legs and their motifs were coded. Twenty-three of these related to the size, shape, and surface treatment of the leg itself, and 34 referred to the alligator motif. For a complete listing of attributes, see Skirboll (1981). Data from both hollow and solid legs were included in the tests in the hope that the earlier, solid legs would provide the early end of the seriation. Motif attributes for solid legs were not coded, but these specimens were included on the basis of the 23 attributes of size and surface treatment which were available for them.

The Seriation

Five separate tests were ultimately run using these data. The first, Run A (Fig. 5), included data from Concepción using both hollow and solid legs. On the right side of the chart are all the solid legs (identified by the number "1") followed by the earliest hollow legs bearing alligators ("2") and other animal motifs ("3"). The first alligator motif, labeled "2," is one in which the animal has two rows of uniform appliqued scales. This is a very highly schematicized group with some specialized characteristics which will be described below. It is named Two Row. These are followed in time by a group with three rows of

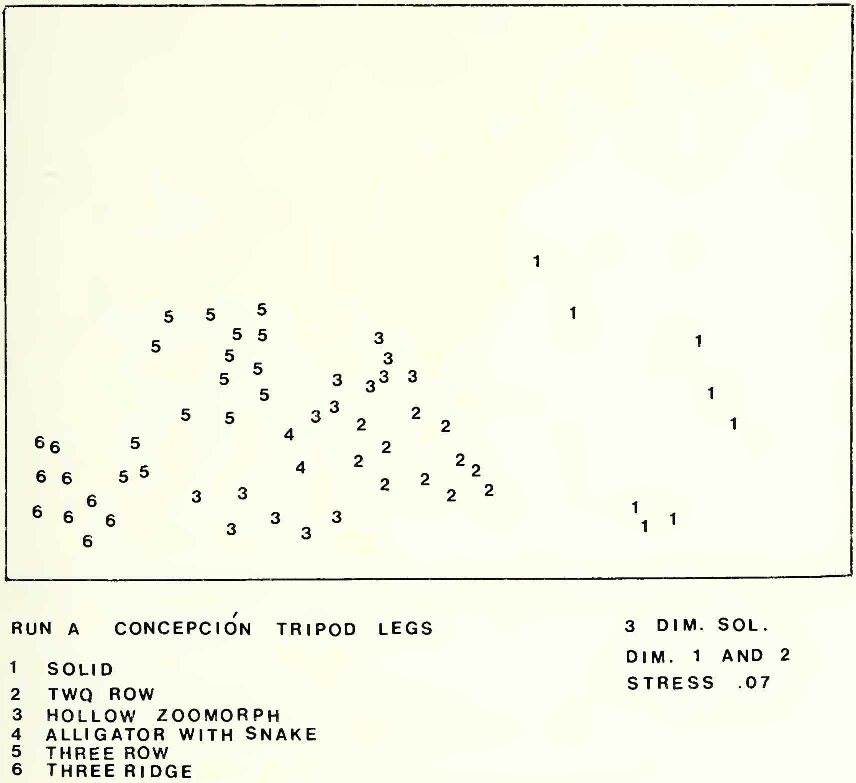

Fig. 5.—Seriation of Concepción tripod legs.

scales ("5"). These alligators have relatively naturalistic modeling and generally have individually appliqued scales, although they are not as regular or well made as those in the Two Row group. This group is named Three Row. These, in turn, are followed by the highly simplified group in which the animal is represented by three ridges of clay representing scales and is no longer recognizable as an alligator ("6"). These have been named Three Ridge. There are two clues to the direction of time in this result. The first is the appearance of solid legs, which generally occur earlier archaeologically in the Highland/Atlantic Watershed zone, on one end of the scale; and the second is the rather obvious evolution from the three rows of scales to the three ridges of clay representing scales at the opposite end of the seriation.

The second test, Run B (Fig. 6), also from Concepción, looks only at the alligator motif. All the solid legs and hollow legs with anthro-

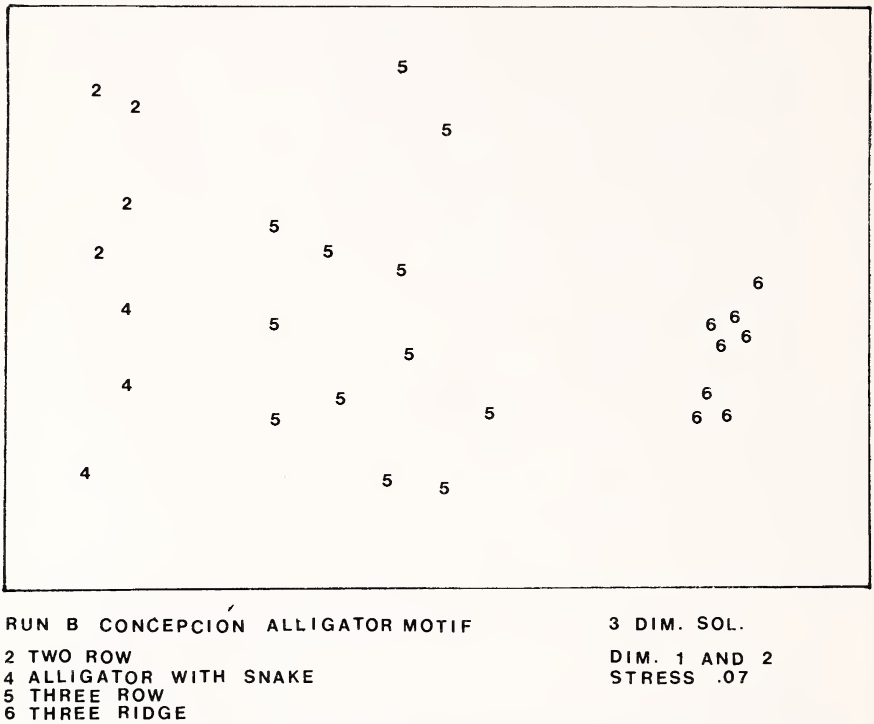

Fig. 6.—Seriation of alligator motif—Concepción.

pomorphic motifs have been removed. The early side of the scaling is at the left of the chart with the Two Row alligators ("2"), and a small group which is called "Alligators with Snake" ("4"). The Three Row motifs ("5") are followed by the Three Ridge alligators ("6"). Thus the ordering of the three styles of alligator is the same in Figs. 5 and 6.

The third test, Run C (Fig. 7), is a test run on the data from Curridabat. Here the time progression is quite clear from solid legs ("1") to Two Row alligators ("2"), to Three Row alligators ("5"). In this case it was possible to identify a group of Three Row alligators which are transitional to Three Ridge ("5+"), and finally the Three Ridge style ("6"). See Fig. 9 for these transitional motifs.

Run D (Fig. 8) is a closeup of alligator legs only from Curridabat, and this again shows the relationships seen previously. Here it was possible to identify two examples ("2+") which are transitional from Two Row to Three Row styles and also those transitional from Three Row to Three Ridge. See Fig. 9 for transitions.

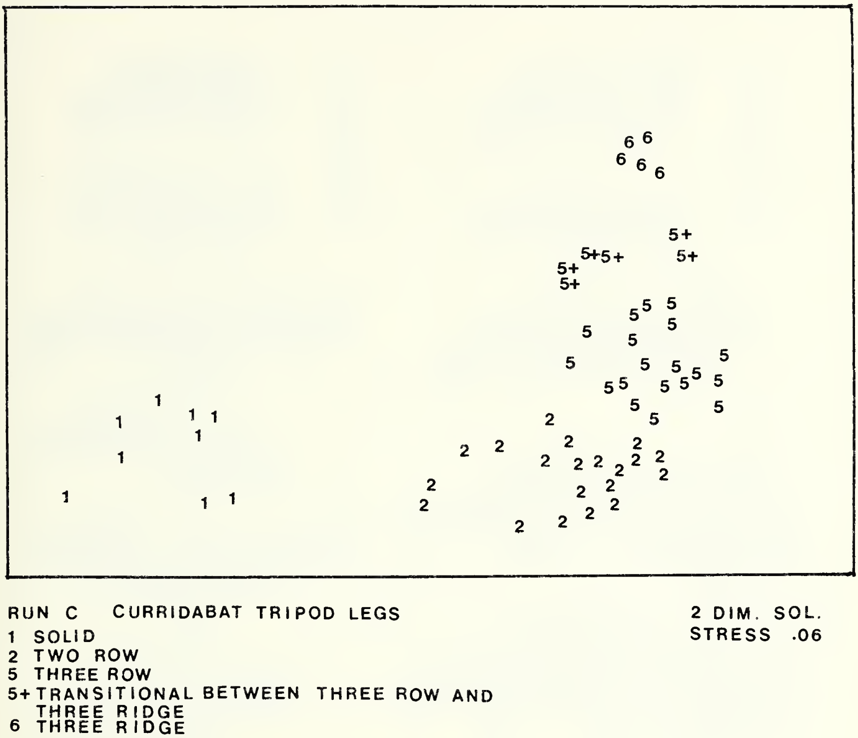

Fig. 7.—Seriation of Curridabat tripod legs.

Run E (Fig. 10) is a test of all legs and motifs from both sites combined. This test was made primarily to examine the possibility of one of the sites being earlier than the other. Here the same progression from solid legs with zoomorphs to hollow legs with zoomorphs can be seen. These are followed by Two Row to Three Row to Three Ridge styles all appearing in the same order and time at both sites indicating that the sites are roughly contemporary.

Based on these results the following order of events appears likely: Solid legs on tripod vessels were locally decorated with a variety of animal and human-like figures. Many of the animals are identifiable birds and mammals. When hollow legs were introduced, they were decorated at first with the animal motifs which had been the local tradition. Soon after, however, the alligator motif appears. When it does, it is a very sophisticated and schematic design quite unlike the naturalistic approach seen in prior animal forms on pottery. It possesses

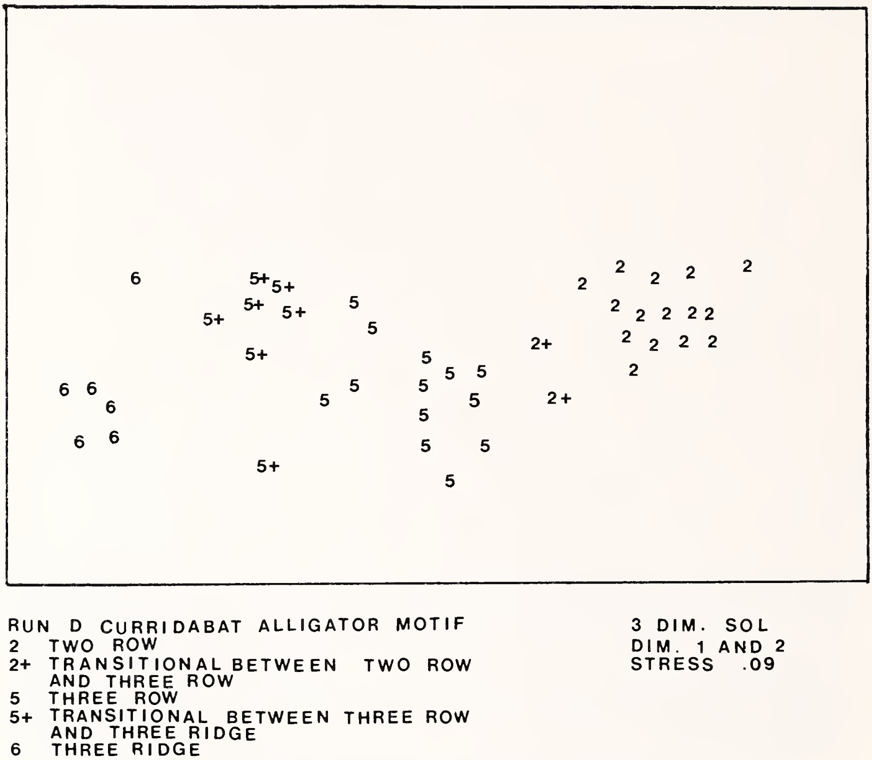

Fig. 8.—Seriation of alligator motif—Curridabat.

generally crocodilian attributes among which the scale is always emphasized, but it cannot be identified as to genus. In design elements, it is unlike the animals of current popularity which are solid, three dimensional figures. The alligator design has open spaces incorporated into the figure giving it an open quality. It lacks the three dimensional, sculptural look of the zoomorphs on solid and early hollow legs. It has a somewhat two dimensional, linear quality instead. One of the outstanding features of the early alligators is the two even rows of scales. Certain other decorative elements are also found only in Two Row style. These include snouts which curve upward and, in some cases, meet the scale element arching over the animal's head. The scale element consists of two rows of uniform, appliqued pellets attached to a supporting bar (Fig. 11). Eyes are generally made of two circles of clay, one inside the other. These eye motifs may appear at various locations on the animal in addition to the normal position on the head. Two

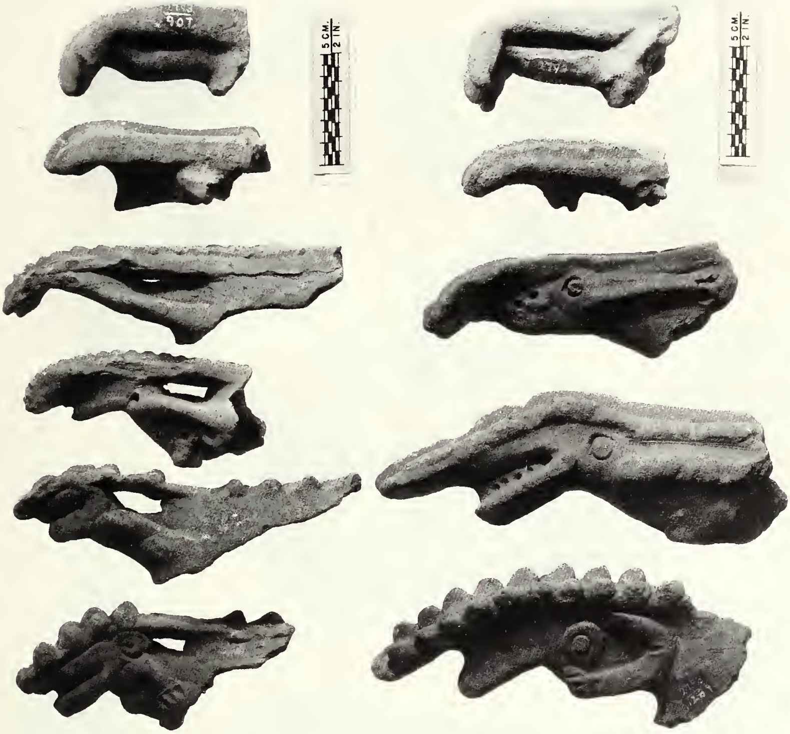

Fig. 9.—Three ridge style alligators from Costa Rican pottery.

Row alligators may also have a rather enigmatic figure associated with them. The figure, usually a head, may represent a monkey or snake or other animal. There is often also a hand-like figure which projects from the alligator's body. Overall, Two Row alligators have a decorative appearance totally unlike the zoomorphs made prior to its introduction. The highly schematic nature of this variety suggests that far from representing an inaccurate attempt at an actual alligator figure, it functioned as a part of a well-understood symbol system involving the alligator, but also including other symbols. The upturned snout, the eye motifs, the hand-like projection and the animal head projection are all evidence of abbreviated symbolic forms. While the alligator as an animal retains importance, it is more important as a symbol within the social system than as a real, living animal.

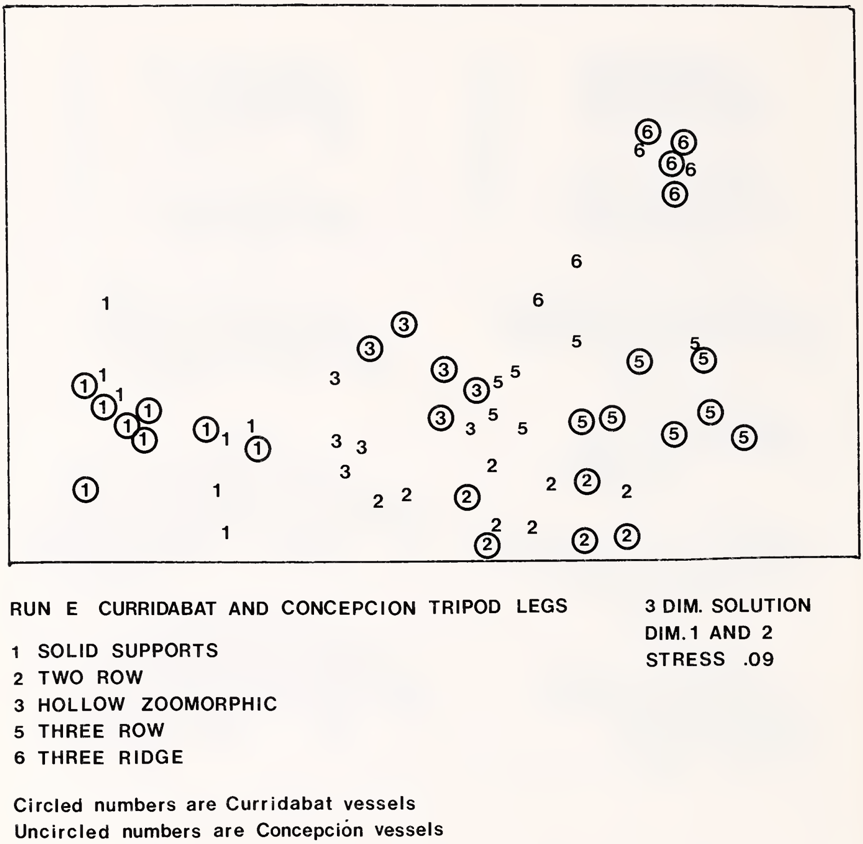

Fig. 10.—Seriation of Curridabat and Concepción tripod legs.

These early Two Row figures are the most highly stylized. They are quite carefully made with great attention to regularity in size and shape of appliqued sections, especially the scales. The later Three Row alligators lose these qualities. They are rounder, solid figures similar to the earlier zoomorphs on solid legs. Open spaces within the figure become smaller and finally disappear. The two rows of scales become three rows, and each scale is less regular in size and shape than on earlier Two Row figures. Through time, Three Row figures become more and more simplified and abbreviated until, as in the Three Ridge style, they are unrecognizable as alligators. The final Three Ridge figures consist of three simple ridges of clay representing rows of scales down the figure's back. They are once again highly schematicized, but now

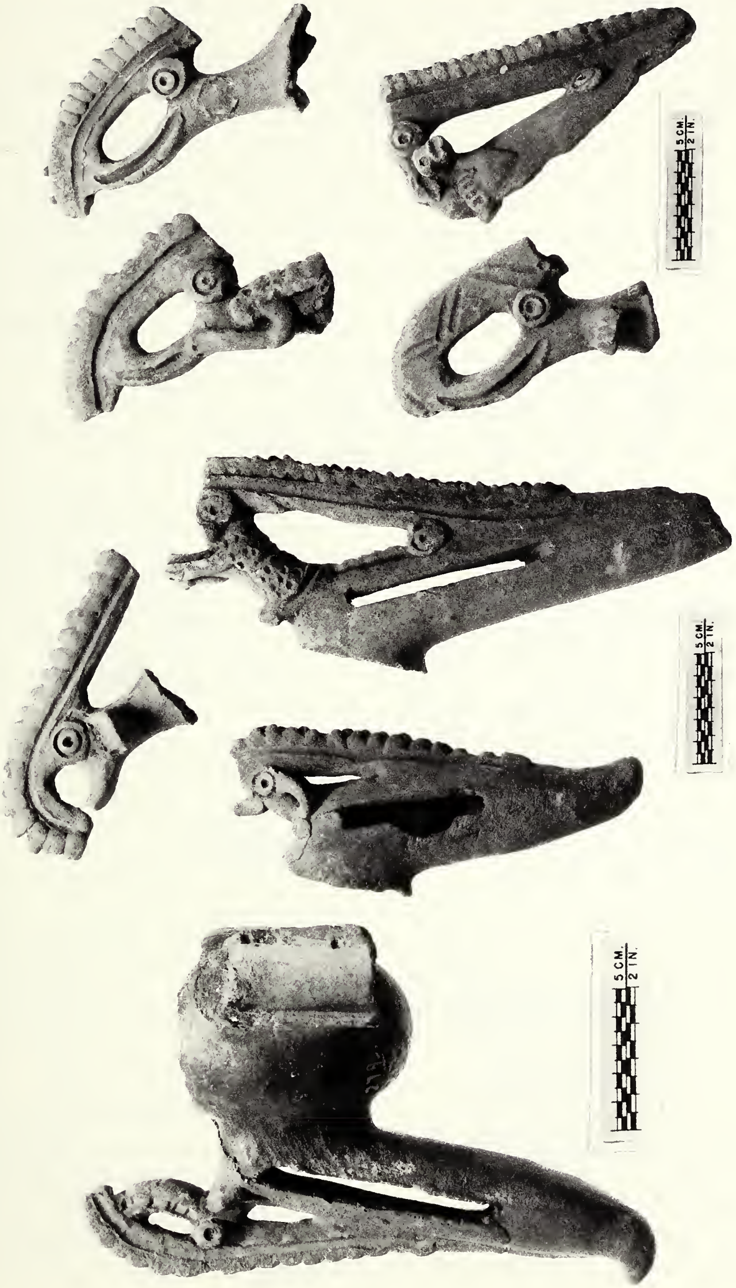

Fig. 11.—Two row style alligators from Costa Rican pottery.

in an entirely different way than the Two Row style. See seriation chart, Fig. 12.

The order suggested by the seriation remains to be proven by excavation. If it is accurate, and Two Row alligators are earliest, we find little evidence within the Highlands/Atlantic Watershed for the origin of the motif. It has been suggested by Snarskis (personal communication) that a very early version of the Two Row alligator appears in the Ticoban tripods of the El Bosque Phase in the Atlantic Watershed. These forms exhibit open, looped tripod legs which could be antecedent to the Two Row style. If looped-leg tripods are directly antecedent to Two Row alligators, it is another expression of close cultural sharing between the Highlands and the Eastern area as early as the El Bosque Phase. Further research is required to substantiate this possibility and to push back the early end of the alligator motif seriation.

The alligator motif has attracted much speculation throughout the literature on Costa Rica, Panama, and indeed throughout Central America.

Hartman suggested that the motif was related to the alligator designs on Panamanian ceramics from the Cocle Period (1907*b*). His assessment was based entirely on stylistic similarities because chronological information was lacking at the time. We know now that the Cocle Period was contemporary with the Curridabat Phase. This is not to suggest that either the pottery itself or its motif ideas were directly imported from Panama. The pottery is certainly locally made. The paste used in alligator leg tripods is identical to that of other locally made wares of the time. It is possible, however, that the alligator motif found in the Central Highlands/Atlantic Watershed may be related to similar motifs in Panama. There is reason to believe that cultural exchange between these areas was occurring as elite oriented gold objects from Panama and Colombia begin to appear in Costa Rica around this time (Snarskis, 1982). Such valued objects must have been the possessions of powerful individuals or groups in an increasingly complex political system in Costa Rica. It seems reasonable that motifs symbolizing elite power would also be adapted in some form by emerging leaders in Costa Rica. Whether Hartman was correct that the alligator motif originated in Panama is less important than understanding its significance in the society.

Interpreting the significance of this symbol is far from simple, and it must be remembered, as Linares has cautioned, "Difficult as it may be to discuss motivation in the arts of contemporary primitive peoples, this problem is compounded when we are dealing with art forms that existed a thousand years ago, among people whose belief systems are unknown to us." (Linares, 1977). With this in mind, Linares goes on to interpret the animal motifs on Panamanian ceramics on the basis

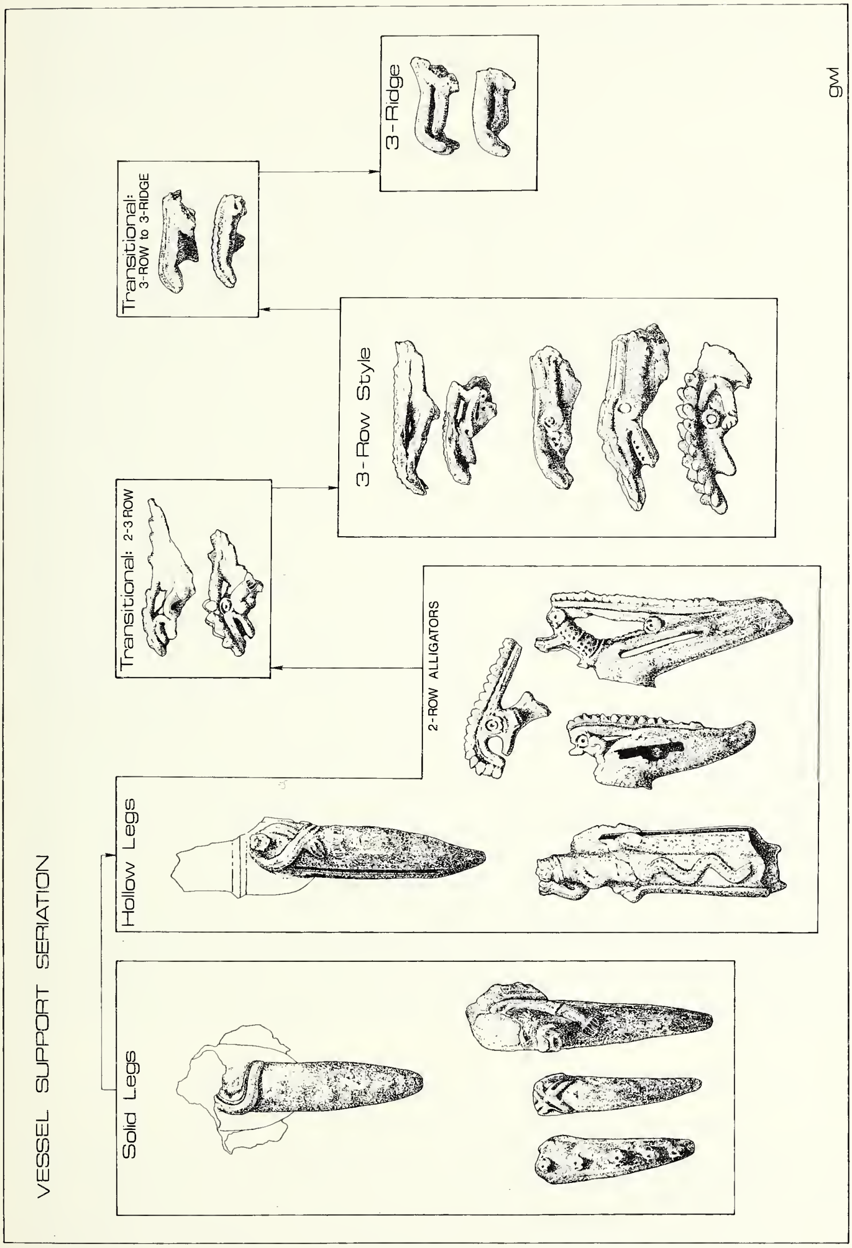

Fig. 12.—Vessel support seriation for Costa Rican pottery.

of the behavioral characteristics of the animals depicted. She suggests that animals which are poisonous, dangerous, or predatory are often the subjects in Panamanian art. Crocodiles and felines are among them because of these characteristics. She attributes the portrayal of these powerful and dangerous animals in the art forms of the local groups to the transference of their aggressive attributes to humans and to human social and political life.

Helms (1977, 1979) has also approached the question of interpretation with regard to the "crested crocodile" or alligator motif in Panamanian art. In her view the animal depicted is actually an iguana, and it represents chiefship in Panama. She reaches this conclusion through studies of modern Cuna mythology and of archaeological art forms of Panama. Her view that the iguana indicates chiefdom level social integration is not inconsistent with Linares' suggestions. Crocodilians and felines may be important because of their predatory characteristics; and these attributes may serve to identify the aggressive strength and power of human warriors or chiefs. This motif does appear in Panama undeniably associated with many aspects of a chief level social system. We may assume tentatively that the alligator theme in Costa Rica has the same meaning there that the alligator/iguana has in Panama. Similar social and political events were occurring in Costa Rica at roughly the same time as chiefs with a large measure of local power were appearing in Panama. There is evidence in Central Highlands and Atlantic Watershed zones after A.D. 700 (Period V) for social change. According to Snarskis (1982) house forms, ceramics and other artifacts show a distinct change. The appearance of the alligator figure on burial urns also represents a change. It is being suggested here that in the Highland/Atlantic Watershed Zone the alligator motif was associated with the kind of power manifested by a chiefly lineage. Far too little is known about the Curridabat Phase in the Central Highlands to permit any final conclusions to be drawn about the extent and nature of societal complexity at this time. The suggestion that the appearance of the alligator motif here represents social change should be considered as a working hypothesis. It is to be hoped that field research will be directed toward a more complete knowledge of the social and political systems in this area.

RELATIONSHIPS WITH THE ATLANTIC WATERSHED IN THE POTTERY OF CURRIDABAT AND CONCEPCIÓN

A valuable aspect of the pottery from these sites is the information it contains on the cultural relationships between the Central Highlands and the Atlantic Watershed during the Curridabat Phase. Tripod burial urns such as those discussed in the preceding section are commonly found in the Atlantic Watershed region. There can be no doubt that they represent burial practices there which were similar in many ways to those in the Central Highlands. In addition to tripod urns, two other large groups of pottery found at Curridabat and Concepción can be presented as evidence of the interrelationship between the two areas.

Curridabat Sandy Applique Bowls

Hartman (1907*b*) published photographs of a few examples of this and related pottery. In the 1920's Lothrop studied the Curridabat pottery as well as pottery from the Atlantic Watershed. He recognized clear similarities between what he named Curridabat A, the small ollas and tecomates from the Highlands and similar pottery from the Atlantic Watershed which he named Curridabat B. Relationships were determined on purely stylistic grounds, but it is now recognized that the material is contemporary. Snarskis (1978), as a result of his work in the Atlantic Watershed, has given the descriptive name La Selva Sandy Applique to the Curridabat B pottery. Because both Curridabat A and B are basically the same sand tempered paste and share a great number of traits of form and motif, the Type A pottery is named Curridabat Sandy Applique here. This name preserves the interregional relationship as well as the descriptive and historical name.

As Lothrop described the Curridabat Sandy Applique bowls, they are characterized by two basic forms—a simple olla with a rolled or everted lip and a small tecomate. The ollas are especially notable for several beads of clay around the widest circumference and between the widest circumference and the neck (Fig. 13). They are sometimes further decorated with appliqued animal figures, and are slipped or painted with orange, red, or maroon slip applied in zones. Often one color is applied above the shoulder bead and another below it. Insides of bowls are uniformly slipped in orange. Adornments include animal figures made up of appliqued pieces of clay forming snakes, frogs, woodpeckers, kinkajous, and a reptilian figure. Many also have abstract designs created by incision, punctation, and reed stamping, and by the application of small dots of clay in geometric shapes, such as zigzags, chevrons, triangles, and rectangles. As Snarskis (1978) describes the paste and motifs of the La Selva Sandy Applique bowls, and as they are illustrated, they are identical to these.

Red-Orange Incised Group

The second group of pottery includes a very diverse number of pottery types which has been named Red-Orange Incised based on the red to red-orange to purple slip and incised geometric decoration they all share. This group, in turn, contains five temporary subgroups placed together on the basis of shared features (see Table 1).

The largest of the subgroups, Concepción Red, features the typical

Fig. 13.—Curridabat sandy applique bowls.

red-orange slip, incised motifs, and negative painting. The paste is quite similar to that of Curridabat Sandy Applique. It is very rough with abundant temper and has a gritty surface when unpolished. Many of the small tripod bowls form animal effigies. Effigies are formed by the placement of small adornos on the body of the vessel (Fig. 14) to represent the animal's head and tail. The vessel legs then become the animal's legs. Incised decorations often consist of rows of triangles

Table 1.—*Red-orange incised pottery groups from sites in Costa Rica.*

Pottery group	Curridabat	Concepción
Concepción red	17	14
Maroon and orange		4
White flecked	2	
Fine purple	1	1
Brown incised	1	
Scroll incised	1	
Total	22	19

Fig. 14.—Red-orange incised group pottery from Costa Rica.

filled with crosshatching. This group is the same as that pottery named Zoila Red in the Atlantic Watershed by Snarskis (1978) and Red Incised by Kennedy (1976). It also shares attributes with pottery types of the Nicoya area such as Guinea Incised and Zelaya Bichrome (Baudez, 1967).

The balance of the Red-Orange Incised groups each contains very few specimens which have been given temporary descriptive names. Their exact relationship to Concepción Red is unclear as they may represent chronological changes in the Red-Orange Incised group, or they may belong to separate contemporary pottery groups. They are described in Skirboll (1981).

Miscellaneous Pottery Groups

In addition to these major groups of pottery, links to the Atlantic Watershed in pottery appearing in small numbers at Curridabat and Concepción can be seen in such types as Congo Punctate, Lajas-Yacuare, and Tuis Fino. Also, there are a few examples of pottery which are generally associated with the Cartego Phase (Period VI). The most abundant of these is a group related to the La Cabana pottery of the Atlantic Watershed. These consist of small vessels in the form of human effigy heads, and bowls with elaborate appliqued decoration. These often take the form of strips of clay with numerous punctations such as those illustrated in Aguilar for the Cartego Phase of the Central Highlands (Aguilar, 1976). Similar pottery is named Stone Cist Ware by Lothrop (1926) and is illustrated both by Lothrop (1926) and Hartman (1901). Other later pottery types include Bere Red, Irazú Yellow Line, and Cartego Red Line. These later pottery types, appearing in sites which are traditionally considered to be between A.D. 500–800, may be an indication that the sites are multicomponent. However, since the later material is in small quantities (in the case of Cartego Red Line and Irazú Yellow Line, one example of each), it is more likely that they represent the beginning of the use of later forms at the conclusion of the Curridabat Phase. Since Curridabat and Concepción contain small amounts of late Pavas and Cartego pottery, they must encompass the entire Curridabat Phase.

CONCLUSIONS

Based on the data from these two sites alone, there is ample evidence of a very high level of social exchange between people of the Highlands and the Atlantic Watershed during the Curridabat Phase. There are, of course, similar kinds of information on such exchange from other archaeological sites and collections. With the evidence now at hand from all sources, there is an emerging picture of intense cultural exchange between these two areas. There has been a trend in recent years to acknowledge these interrelationships by including them in a single archaeological zone. Doris Stone included the Central Highlands in the Atlantic Watershed Zone in 1977 (Stone, 1977), and the two areas were discussed together as the Highland-Atlantic Watershed Region recently by Snarskis (Snarskis, 1982).

This has been a brief example of utilization of museum collections in a way relevant to current archaeological interests. In this case, the material contained limited provenience data, but still provided enough useful information to produce an in-depth stylistic analysis of a pottery motif, and also evidence of the interrelationships between two geographic areas. It is hoped that this example will stimulate further use of museum holdings such as the Hartman collections which have not been thoroughly studied in the past.

ACKNOWLEDGMENTS

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RESULTS OF THE ALCOA FOUNDATION SURINAME EXPEDITIONS. VIII. COMPARATIVE ULTRASTRUCTURE OF GASTRIC MUCOSAE IN FOUR GENERA OF BATS (MAMMALIA : CHIROPTERA), WITH COMMENTS ON GASTRIC EVOLUTION

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Abstract

Ultrastructure of gastric mucosa was studied comparatively in six species representing four microchiropteran genera, *Pteronotus parnellii, Phyllostomus hastatus, P. elongatus, Carollia perspicillata, Artibeus lituratus,* and *A. concolor,* which have different diets. Overall, the ultrastructural comparisons were shown to have systematic value as well as value for determination of evolutionary patterns at the cellular and tissue levels. Generic differences were found in numbers and types of entero-endocrine cells; a glucagon-producing A cell was the only type common to all four genera. Generally, entero-endocrine cell types could be correlated with both diet and systematics and the specific composition of cell types could be explained in terms of potential interactions with other cell types within individual species. Intergeneric ultrastructural differences also were found among chief cells and their secretory products and among mucous neck cells. The chief cell differences were related to diet and it was clear that stenodermatine chief cells are functionally divergent and, therefore, might be useful to an understanding of evolution of cell types. Interfamilial histochemical analyses of mucous neck cell product appeared to loosely match diet (insectivore-omnivore versus strict frugivore), whereas ultrastructural features of these cells were more nearly indicative of systematic relationships among

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the bats. Regardless of staining similarities, the phyllostomids collectively were more similar to one another than any one was to the mormoopid, *Pteronotus.* Acid-producing parietal (=oxyntic) cells also varied considerably among the genera; degree of intracellular secretory canalization and apparent average levels of activity of fasted animals differed in correlation with diet in the sense that the frugivorous species had the largest and most active cells. An hypothesis is offered to explain the evolution of the specialized gastric mucosa in *Artibeus,* which is considered representative of the frugivorous stenodermatines. High HCl production without significant buffering from mucous neck cells is discussed by calling attention to the abundant and apparently watery parotid salivary gland secretions in *Artibeus.*

Introduction

The digestive tract of mammals is highly diversified in both gross and microscopic anatomy. Stomachs of primates, rodents, and bats have been studied in detail and it can be stated that in each of these orders both gross and histological anatomy are 1) correlated with diet and 2) likely to be reflective of systematic relationships (Dearden, 1969; Schultz, 1965; Forman, 1972; Chivers and Hladik, 1980). Species of Chiroptera, particularly the Phyllostomidae, have attracted special attention because of the extreme diversification in their feeding habits and because many species appear to have somewhat restricted, if not fully obligate, diets (for example, Gardner, 1977). Indeed, bats as a group comprise a most attractive mammalian model for study of evolution of complex structure in conjunction with exploitation of nutrient resources because contemporaneous extant species probably represent all of the historical dietary regimes (Phillips et al., 1977; Gardner, 1977).

In a series of previous investigations, Park and Hall (1951), Kolb (1954), Rouk (1968, 1973), Rouk and Glass (1970), Schultz (1965), Hart (1971), Swarup et al. (1971), and Forman (1971*a,* 1971*b*, 1972, 1973, 1974*a,* 1974*b*) have reported on histological and some general histochemical characteristics of gastric mucosa, small intestine, and gut-associated lymphoid tissue in many different species of bats. Insofar as the stomach is concerned, these studies have demonstrated clearly a number of diet-associated evolutionary trends in gastric structure. The gastric mucosa has been shown to vary significantly in height (which apparently translates into total numbers of cells), in relative proportions of differentiated cell types, and in mucin histochemistry (for example, Hart, 1971; Forman, 1972; Forman et al., 1979). In addition to these epithelial patterns, Forman (1972) also has detailed a variety of differences, including interspecific differences in the organizational patterns of gastric musculature.

As a result of extensive recent field studies in Suriname, we have had an opportunity to investigate for the first time the comparative ultrastructure of gastric mucosa in several related species of bats. Nearly all of our prior knowledge of fine structure of gastric epithelial cells not surprisingly has derived from intensive experimental studies of common laboratory species. Insofar as we know, no previous attempt has been made with any group of mammalian species to correlate patterns of homologous cell ultrastructure with diet or systematic relationships. However, because many of the biochemical techniques and consequent discoveries about function of cells in the gastric mucosa date from the last decade, the foundation data for a comparative, systematic analysis heretofore were unavailable. Indeed, until very recently an insectivorous vespertilionid species, *Myotis lucifugus,* was the only chiropteran for which even general gastric ultrastructural data were available (Ito and Winchester, 1963). Now, a number of significant ultrastructural differences between chief cells in phyllostomines (*Tonatia, Trachops,* and *Phyllostomus*) and stenodermatines (*Artibeus, Ametrida,* and *Chiroderma*) have been documented by Phillips and Studholme (1982).

For the present paper we selected an insectivorous mormoopid, *Pteronotus parnellii,* and five phyllostomids—two largely "animalivorous" species, *Phyllostomus hastatus* and *P. elongatus*; an "omnivore," *Carollia perspicillata*; and two "frugivores," *Artibeus concolor* and *A. lituratus.* The dietary habits of these phyllostomids are imperfectly known but both species of *Phyllostomus* feed on small vertebrates, insects, and fruit and possibly pollen and nectar (Gardner, 1977). *Carollia perspicillata* apparently feeds primarily on fruit, although in one study insects were reported to have accounted for up to 13% of the contents of 272 stomachs (Fleming et al., 1972). Regardless of the role of insects in its diet, *Carollia perspicillata* is extremely efficient at consuming fruit. According to Herbst (1982), this species can absorb 53% of the energy in *Chlorophora tinctoria*: this includes 71% of the soluble matter; 60% of the lipids; 95% of the total carbohydrates; and only 6% of the total nitrogen. The two species of *Artibeus* clearly consume large amounts of fruit and are primarily frugivores (see Gardner, 1977), but the possibility exists that at least during some times of the year *A. lituratus* also feeds on insects (Fleming et al., 1972).

We proposed to address the following series of previously unexplored questions. 1) How are reported histological differences represented at the ultrastructural level? 2) Does ultrastructure of fully differentiated (morphologically) cells vary significantly among species? 3) Can ultrastructural differences be related to histochemical differences? 4) Can ultrastructural data be used in conjunction with histology and histochemistry to develop an understanding of evolution of chiropteran stomachs? We also sought to use our data to develop insights into chiropteran evolution at the cellular level. At present, virtually nothing is known about how "new cell types" originate or to what extent, or how, cellular function can be modified among closely related species.

METHODS AND MATERIALS

Specimens used in this study were collected in the immediate vicinity of Rudi Kappelvliegveld, Brokopondo, Suriname (see specimens examined section). Vouchers of all but the specimens of *Carollia* are deposited in the collections of the Carnegie Museum of Natural History (CM). Each of the bats was captured in a mist net at night (1700–2400 hrs) while feeding; subsequently, each was kept in a cloth bag and fasted until between 0900 and 1200 hrs. The bats then were anaesthetized with 0.25 cc sodium pentabarbital (50 mg/ml) and a polyethylene tube was inserted into the stomach *via* the mouth and esophagus. Approximately 1 cc of fixative (at ambient temperature) was injected into digestive tract lumina by means of a syringe attached to the tubing. Following a period of approximately 8 min, during which time the fixative was passively absorbed by the digestive tract, an incision was made into the abdomen and the stomach removed. The stomach then was cut into samples representing the cardiac zone, the fundus, and the pylorus. Only samples from two areas of the fundus were used for the present study (Fig. 1). Because each of the embedded tissue blocks actually analyzed by transmission electron microscopy was very small (1 by 1 mm), we relied on earlier light microscopic histological studies (for example, Forman, 1972) to ascertain whether or not our samples actually were representative of the fundic gland.

The fixation protocol was developed specifically for field projects involving transmission electron microscopy (Phillips, 1984). The primary fixative (based on Kalt and Tandler, 1971) consisted of 3% glutaraldehyde, 2% formaldehyde (made fresh each day from paraformaldehyde powder), 1% acrolein, 2.5% dimethyl sulfoxide (DMSO), and 1 mM $CaCl_2$ in an 0.05 M cacodylate buffer at pH 7.2 with 0.1 M sucrose. All tissues were stored in primary fixative for 20 hrs at ambient temperature (30–40°C). The fixative then was replaced with 0.05 M cacodylate buffer (pH 7.2) with 0.1 M sucrose. While in the field, tissues were left in this buffer, unrefrigerated, for up to 10 days. When refrigeration was available, the tissues were placed in fresh buffer with 3% glutaraldehyde and stored at 4°C. For processing, tissues were washed for one hr in 0.05 M cacodylate buffer (pH 7.2) with 0.1 M sucrose and post-fixed for one hr in 1% OsO_4 with cacodylate buffer and sucrose. Tissues then were dehydrated in an EtOH series and embedded in Epon 812. Thick sections (0.5 μm) were stained with toluidine blue and studied with an Olympus Vanox photomicroscope with Nomarski Interference-Contrast Optics. Thin sections were post-stained with uranyl acetate (saturated solution in 50% EtOH) and lead citrate (Reynolds, 1963) and examined and photographed with a Philips 201 transmission electron microscope (TEM) operated at 60KV.

RESULTS

General light microscopic comparisons of "thick" sections stained with toluidine blue were undertaken as a preliminary step to ultrastructural analysis. Epon-embedded "thick" sections offered a considerable advantage over material embedded in paraffin because cell boundaries and cell types could be examined with much greater resolution than otherwise (see Fig. 2).

The gastric mucosa in all four genera of bats had essentially the same organizational pattern but differed greatly in relative numbers of particular cell types. Such differences are demonstrated in Fig. 2, in which three representative gastric mucosae can be compared directly. In both *Pteronotus* and *Phyllostomus,* the gastric epithelium was exceptionally thick and characterized principally by deep gastric pits and numerous

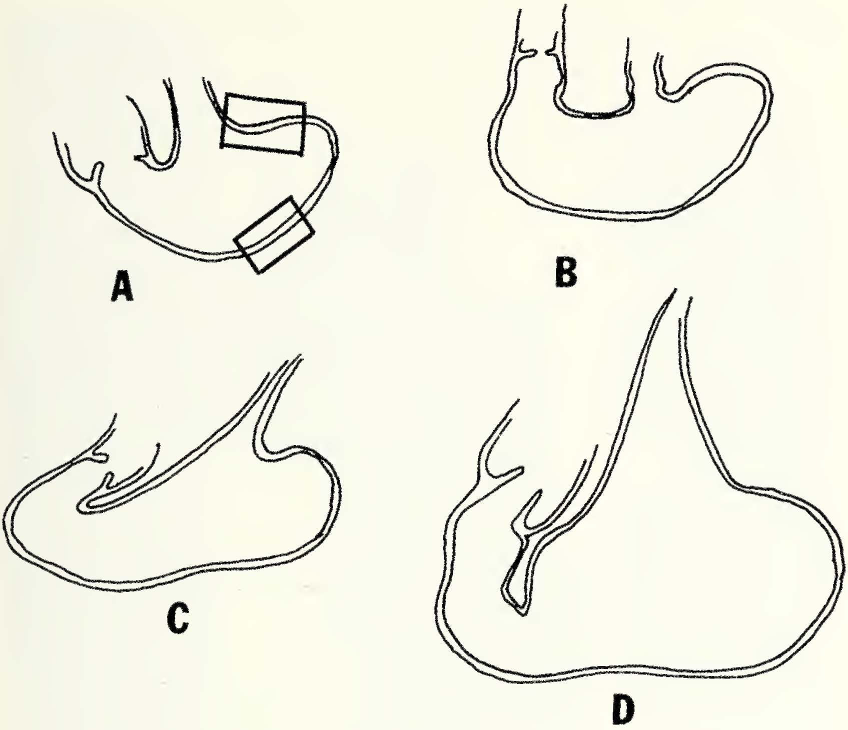

Fig. 1.—Diagramatic comparisons of stomachs from *Pteronotus* (A), *Phyllostomus* (B), *Carollia* (C), and *Artibeus* (D). The rectangular outlines on drawing "A" illustrate typical locations from which tissue was excised for TEM analysis. Modified from Forman, 1972.

mucous neck cells filled with heavily stained apical granules (Fig. 2). The parietal (=oxyntic) cells occupied a zone in the lower one-third of each gastric gland and chief cells always were clustered at the proximal-most terminus of each gland (Fig. 2). The two species of *Artibeus* (*A. concolor* and *A. lituratus*) represented a substantial contrast in that their gastric epithelium was significantly thinner than in *Pteronotus* or *Phyllostomus.* With thick sections it was obvious that this difference in thickness primarily resulted from shallow (nearly non-existent) gastric pits and the virtual absence of mucous neck cells (Fig. 2) in both species of *Artibeus.* Indeed, extremely large parietal cells proved to be the major volumetric component of gastric glands in *Artibeus* (Fig. 2). *Carollia perspicillata,* an omnivorous phyllostomid, occupied an intermediate position between *Phyllostomus* on the one hand and *Arti-*

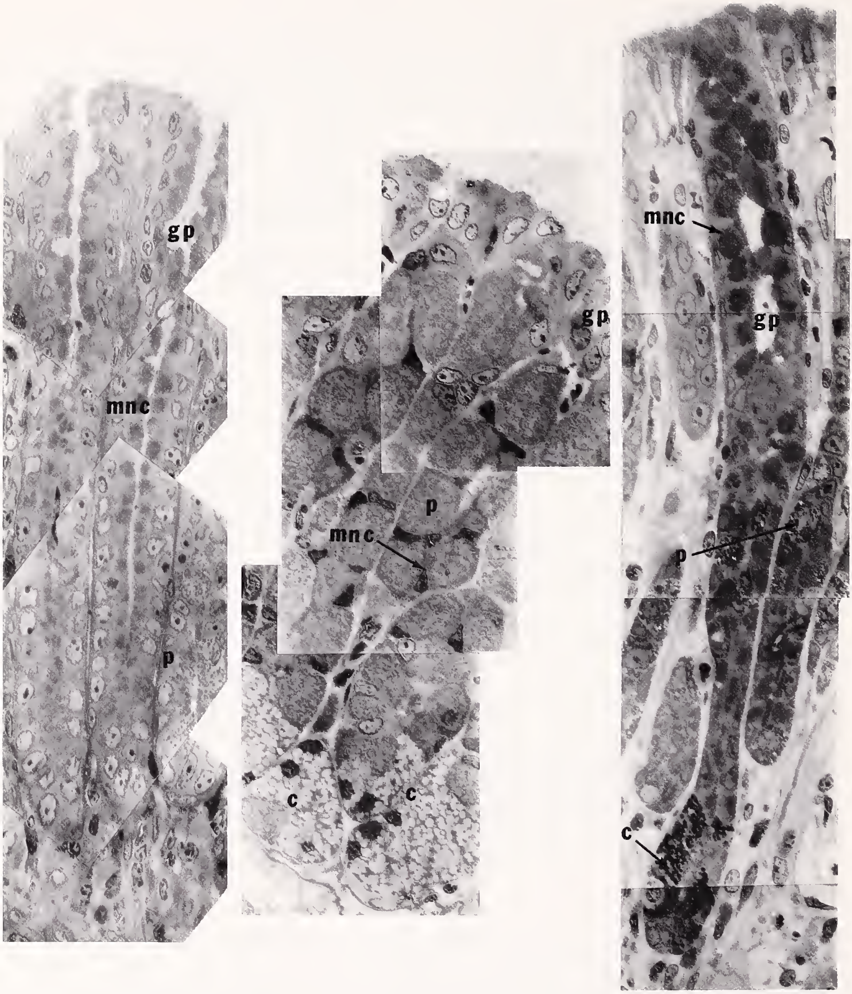

Fig. 2.—Light microscopic photomosaics of fundic tissue from *Pteronotus parnellii* (left), *Arbibeus concolor* (center), and *Phyllostomus hastatus* (right). Note the differences in thickness, gastric pits (gp), mucous neck cells (mnc), parietal (p), and chief cells (c). All these mosaics are the same magnification; 290×.

beus on the other. In *Carollia* the parietal cells were abundant but not extremely large as in *Artibeus* and the mucous neck cells were larger and more abundant than in the stenodermatine frugivores.

With transmission electron microscopy we were able to identify in the four genera at least 10 different types of gastric cells. With the exception of minor differences in mucous neck cells in *A. lituratus* and *A. concolor,* specific differences were not found between either the two species of *Artibeus* or the two of *Phyllostomus* and in the following ultrastructural accounts we have not distinguished between congeners. In all six species we found cells that could be classified either as immature or as "undifferentiated" in the sense that they possessed a generalized cytoplasm and did not fully correspond to any of the familiar, mature cell types. Mature chief cells, parietal cells, mucous neck cells, and mucous surface epithelial cells, all could be distinguished readily at the TEM level in each of the six species. Additionally, entero-endocrine cells (="argentaffin" cells) also were easily recognizable as a general category but their ultrastructural features, particularly the size, shape, and appearance of their secretory product, differed greatly and, thus, no two genera were exactly the same when compared in terms of their entero-endocrine cell populations. Among all of these various cell types we found that our field protocol resulted in generally good TEM fixation with the exception of the entero-endocrine cells, which frequently appeared to have disrupted areas within their cytoplasm. Detailed ultrastructural comparisons of each of the cell types follow.

Entero-endocrine Cells

Several distinctive types of entero-endocrine cells could be identified by previously published ultrastructural criteria (see Grube and Forssmann, 1979, for a detailed summary). Secretory granule size and ultrastructural appearance (that is, halo or no halo, electron dense or flocculant contents, and shape) were the criteria that we found to be most useful. We assumed from experience that our fixation procedures did not introduce any new artifacts that would invalidate the criteria of Grube and Forssmann (1979). Usually (but not always), it was extremely difficult to ascertain with certainty whether or not particular cells were of the "open" (that is, luminal contact) or "closed" type because TEM-level examination provides limited opportunities for three-dimensional analysis of relatively uncommon cell types. Additionally, it also was difficult to determine with precision the physical relationships between entero-endocrine cells and other cell types and such data are offered here with the caveat that total spatial relationships could not always be determined.

None of the four genera was exactly the same; entero-endocrine A cells were the only cell type common to all (Table 1). In *Pteronotus, Phyllostomus,* and *Carollia,* the entero-endocrine cells always were positioned among chief and parietal cells and restricted to the basal one-third of the gastric gland, whereas in *Artibeus* entero-endocrine

Table 1.—*Entero-endocrine cell types in the gastric mucosa in four genera of bats. Identification and categorization based on Grube and Forssmann (1979).*

Species	Cell type	Granules (size in nm)	Amines	Peptides
Pteronotus	ECL	332 (261–370)	Histamine Serotonin?	?
	X	414 (248–466)		?
	A	212 (186–248)		Glucagon Glicentin
	D	356 (285–399)		Somatostatin
Phyllostomus	A	237 (217–261)		Glucagon Glicentin
	D	366 (326–413)		Somatostatin
	ECn(?)	434	Serotonin	
Carollia	A	215 (152–261)		Glucagon Glicentin
	D(?)	391 (261–478)		Somatostatin
Artibeus	A	233 (261–279)		Glucagon Glicentin
	D_1(H)	160		VIP

cells also were found among the parietal cells comprising the upper one-third of each gland, immediately below the overlying mucous surface epithelial cells.

Mature A cells in all four genera were characterized by the presence of spherical, electron-dense secretory granules averaging 240 nm in diameter (Figs. 3–6). Many of the A cell granules had an electron lucent zone that imparted a distinct but narrow halo effect between the granule membrane and the electron-dense core (Fig. 3). Typically, the A cell cytoplasm contained virtually no granular endoplasmic reticulum (GER), but ribonucleoprotein (RNP) particles usually were abundant in the form of polyribosomes (Figs. 3, 6). The A cell cytoplasm in both *Phyllostomus* and *Artibeus* contained conspicuous spherical bodies filled with combinations of small amounts of electron-dense material on a flocculent background (Fig. 3). The apparent absence of a limiting plasma membrane around these bodies suggested that the inclusions were lipid. Immature A cells were a surprisingly common feature in both *Phyllostomus* and *Pteronotus* (Fig. 4); these cells differed from

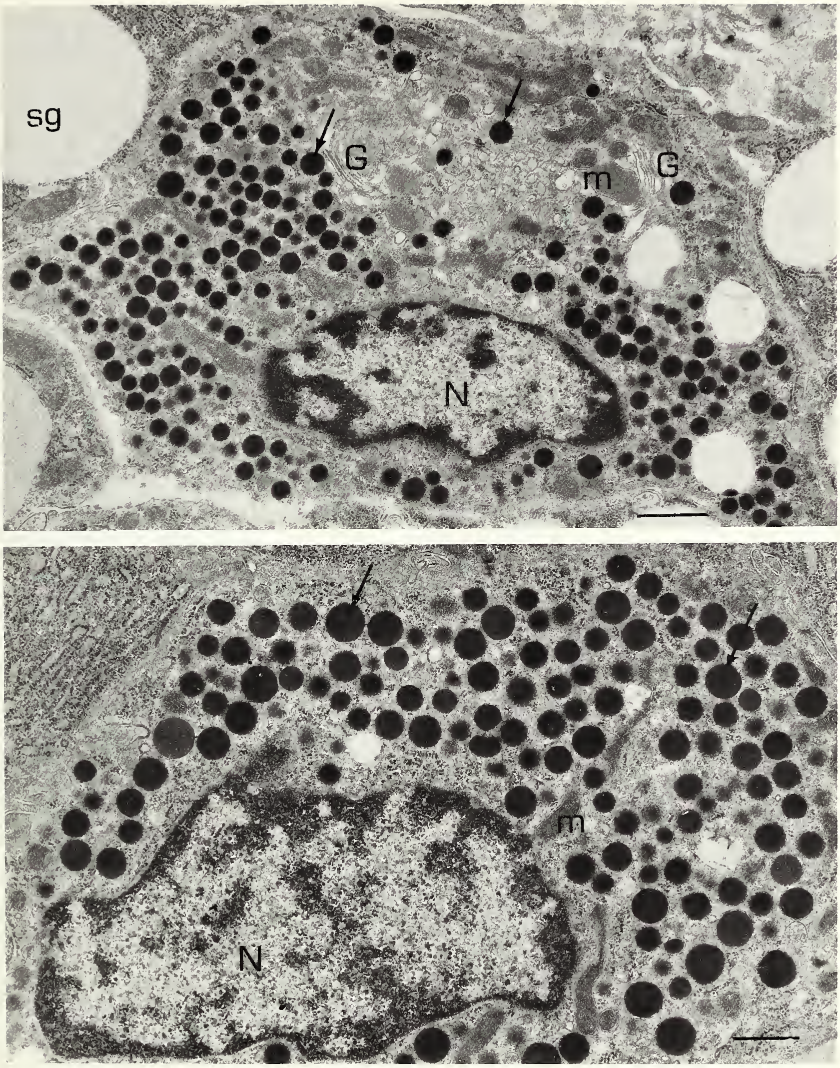

Fig. 3.—Top: An entero-endocrine A cell in *Artibeus concolor* (CM 63791). Bottom: An X cell in *Pteronotus* (CM 63972). Abbreviations are: N, nucleus; G, Golgi complex; m, mitochondria; sg, chief cell secretory granules; arrows, mature entero-endocrine granules. Scale bars equal: top, 0.7 μm; bottom, 0.5 μm.

Fig. 4.—An apparent entero-endocrine D cell in *Pteronotus* (CM 63972). Note the extensive Golgi complex (G), associated small electron dense granules (arrows), and mature secretory product (sg). Other abbreviations are: N, nucleus; m, mitochondria. Scale bar equals 0.5 μm.

mature cells in having extremely large and more euchromatic nuclei and in having peripheral strands of GER but few secretory granules within the cytoplasm.

In addition to A cells, *Pteronotus* also had D and ECL entero-endocrine cells as well as a fourth cell type that we tentatively have identified as an "X" cell. The D cells were characterized by abundant mature product as well as electron dense granules that we judged to be immature because they often were associated with the Golgi complexes (Fig. 4). The ECL cells were characterized by cytoplasm containing relatively large (332 nm), pale granules with small amounts of material either dispersed or condensed into electron-dense cores (Fig. 5). The "X" cell type ultrastructurally was similar to the A cells but differed in that the spherical electron-dense product was significantly ($P \leq 0.01$) larger (414 as compared to 212 nm) in diameter (Fig. 3; Table 1).

None of the phyllostomids had either ECL or X entero-endocrine cells, at least in the samples examined by us. In both *Phyllostomus,* the A cells were accompanied by D cells and, rarely, a type of ECn cell. The D cells were distinguished by their large (366 nm) spherical granules of intermediate electron density (Fig. 5), whereas the ECn cells contained a large (about 434 nm), elongate, electron dense secretory product. The exact size of the granules in the latter cell type was difficult to determine because only longitudinal measurements (long axis) were of diagnostic value. In *Carollia* we found an unusual entero-endocrine cell that we tentatively have identified as a type of D cell (Table 1). As can be seen in Fig. 6, the secretory product in this cell type is somewhat similar to that found in *Phyllostomus* D cells with the exception that in *Carollia* the granules were polymorphic and more nearly elongate than spherical.

No examples of ECn or D cells were found in either species of *Artibeus.* Instead, we identified yet another entero-endocrine cell type, probably a D_1 (or H) cell, with extremely small (160 nm) electron dense granules (Fig. 5). Overall, our specimens of *Artibeus* were conspicuously different from the other genera in that both the A and D_1 cells were extremely scarce. We found only four entero-endocrine cell profiles among approximately 500 cellular profiles examined.

Chief Cells

The gastric chief cells, which in mammals are known to secrete the proteolytic proenzyme, pepsinogen, differed ultrastructurally among the four genera (Figs. 7–8). The most obvious consistent differences among these homologous cells were: 1) the appearance of the fixed mature secretory granules; and 2) relative amounts of heterochromatin within nuclei. In all specimens the chief cells occupied the basal-most

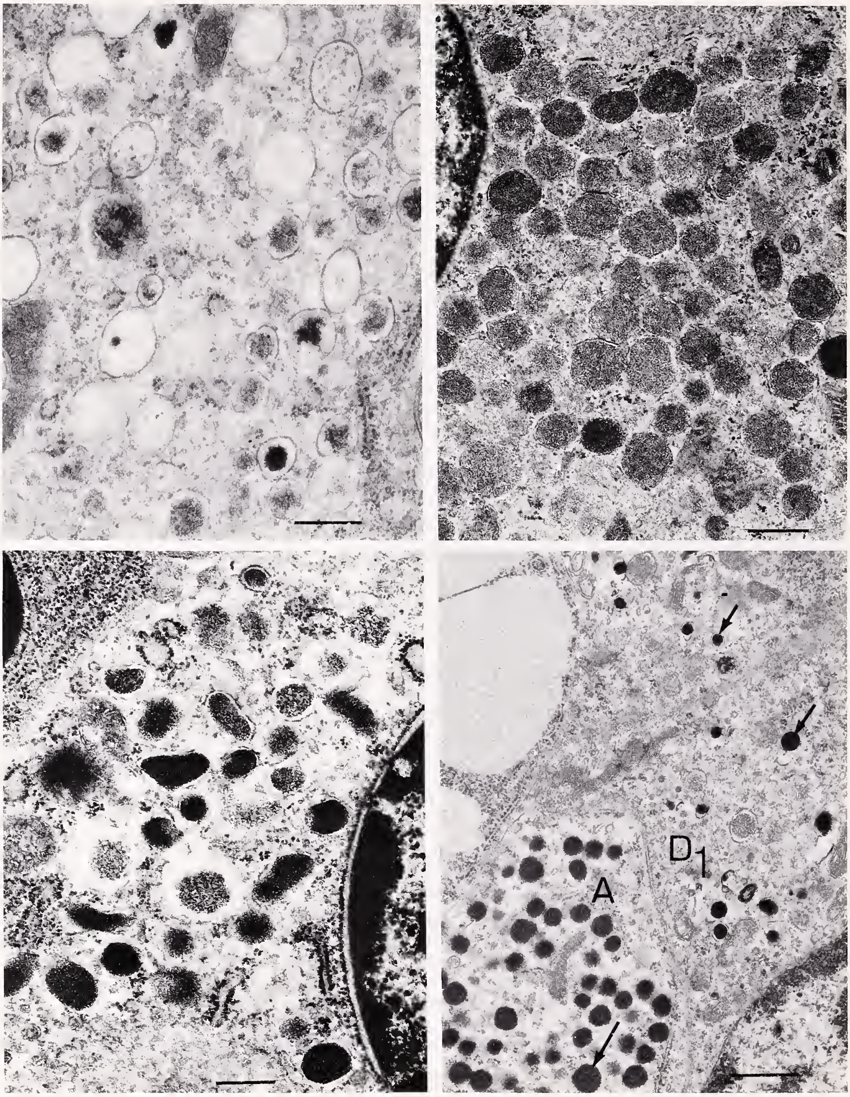

Fig. 5.—Top left: Secretory granules in the cytoplasm of an ECL entero-endocrine cell in *Pteronotus* (CM 63972). Scale bar equals 0.4 μm. Top right: Secretory product in an entero-endocrine D cell in *Phyllostomus hastatus* (CM 64035). Scale bar equals 0.4 μm. Lower left: ECn cell in *P. hastatus* (CM 64035). Scale bar equals 0.4 μm. Lower right: Entero-endocrine A cell (A) and adjacent D_1 cell in *A. concolor* (CM 63791). Compare the sizes of the secretory products (arrows). Scale bar equals 0.5 μm.

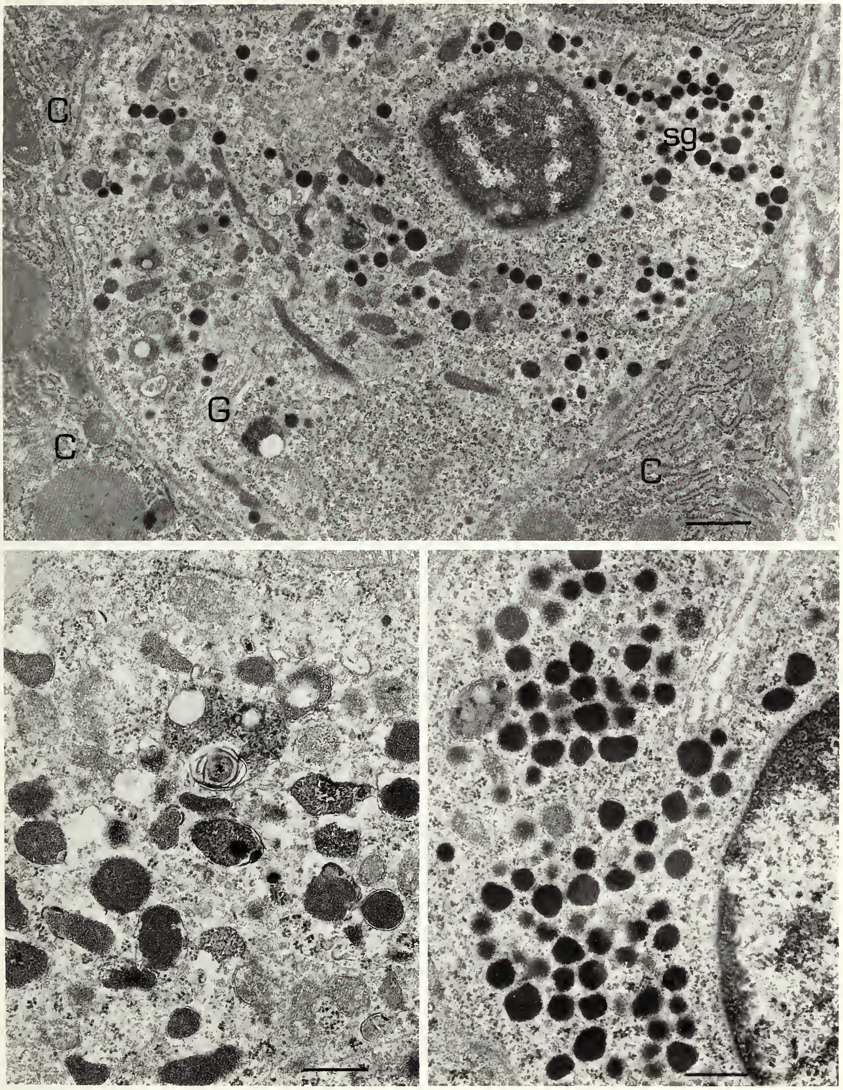

Fig. 6.—Top: Survey view of an entero-endocrine A cell in *Carollia* (CJP 3631). Note how this cell is positioned among chief cells (c). Abbreviations are: sg, secretory granules; G, Golgi complex. Scale bar equals 0.5 μm. Lower left: Secretory granules in an entero-endocrine D cell in *Carollia* (CJP 3631). Compare with D cells in Figs. 4, 5. Scale bar equals 0.4 μm. Lower right: Higher magnification view of A cell secretory granules in *Carollia* (CJP 3631). Scale bar equals 0.4 μm.

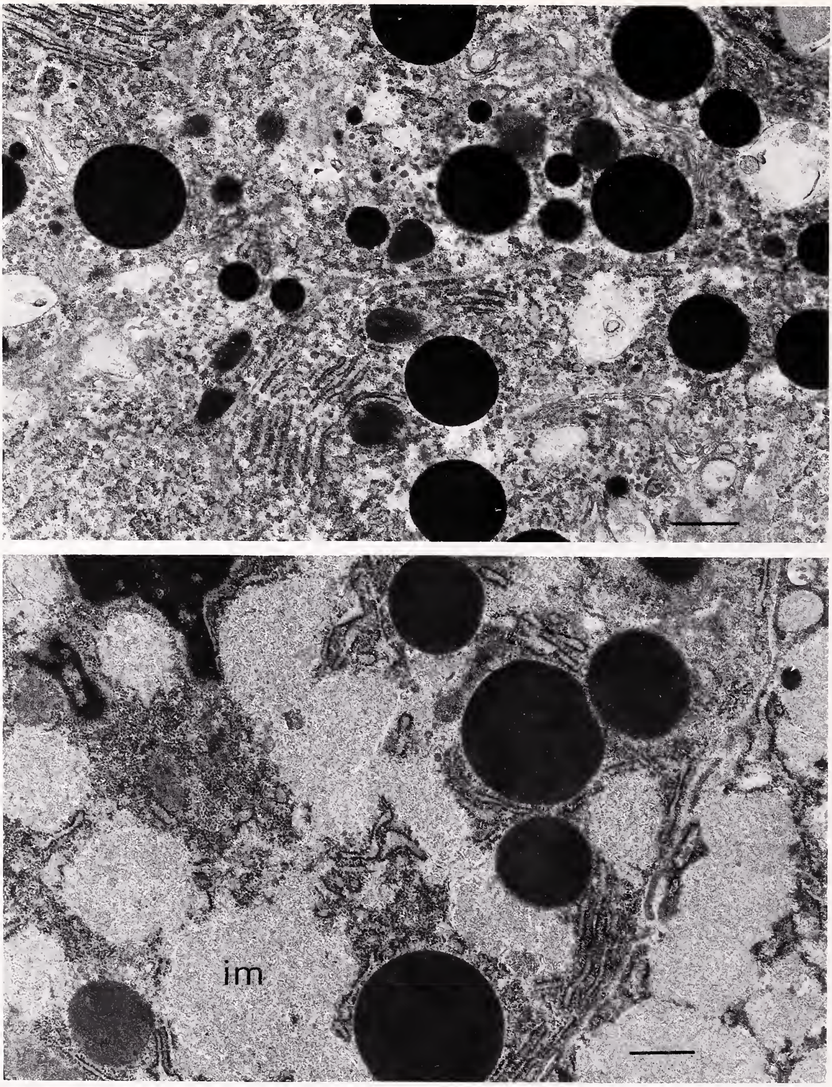

Fig. 7.—Top: Chief cell in *Pteronotus* (CM 63972). Note the extreme electron density of the mature secretory product. Scale bar equals 0.8 μm. Bottom: Chief cell in *Phyllostomus hastatus* (CM 64035). Note the electron dense mature product and flocculent, coalesced appearance of the immature product (im). Scale bar equals 0.5 μm.

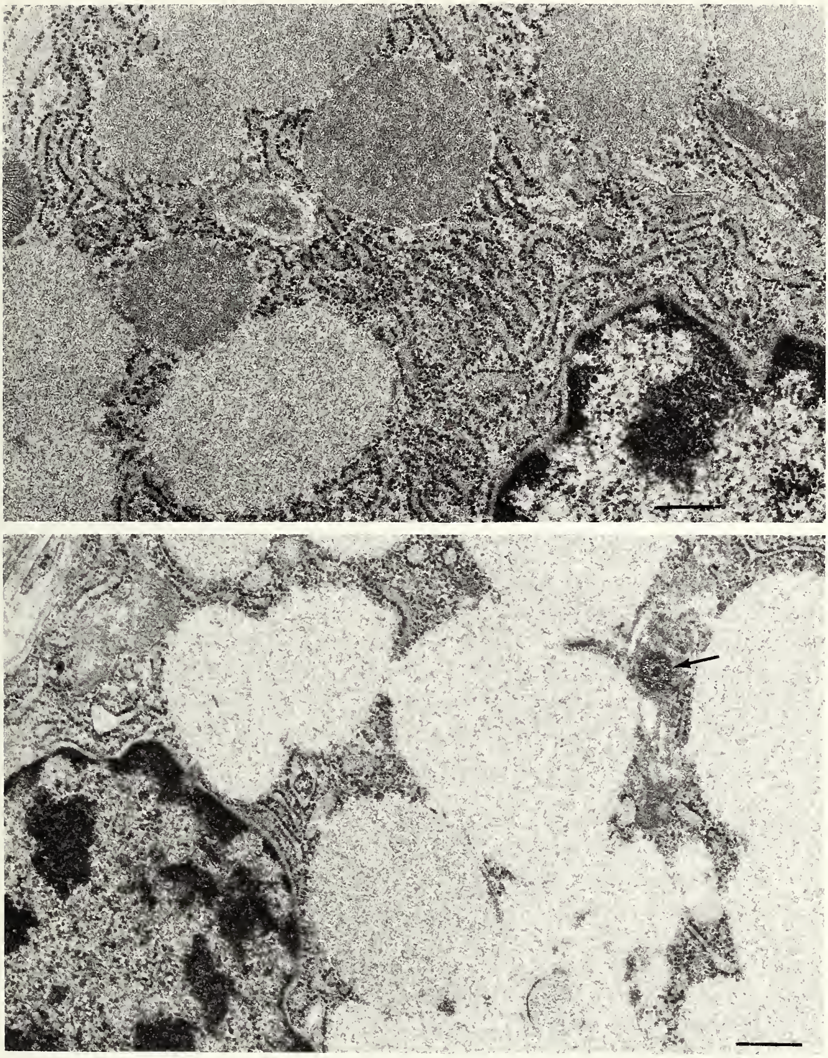

Fig. 8.—Top: Chief cell in *Carollia* (CJP 3631). Scale bar equals 0.4 μm. Bottom: Chief cell in *Artibeus concolor* (CM 63791). Note the centriole in this cell (arrow). Scale bar equals 0.4 μm.

zone of the gastric gland (Fig. 2) and gave the appearance of being clustered in groups although individual parietal cells frequently were located within the clusters in all four genera. Published autoradiographic analyses of secretory cell processes in laboratory animals (for example, Palade, 1975) were used by us to distinguish between the mature and immature chief cell secretory product. We assumed for the following analysis that mature product in aldehyde-fixed cells would appear to be more condensed, and would occupy the apical cytoplasm near the luminal plasma membrane, whereas immature product would have a more "swollen" appearance and would be located in physical proximity of the forming-face of the Golgi complex.

In both *Pteronotus* and *Phyllostomus* the mature chief cell product was classically "zymogenic" (that is, discrete, spherical, electron-dense granules). Immature product, usually in proximity of large Golgi complexes, had a pale, flocculent appearance, tended to be irregular in outline and, in some instances, the TEM image suggested that individual granules had coalesced with each other (Fig. 7). In *Carollia,* the mature chief cell product was not nearly as electron dense as in the two previous genera, however, the immature product essentially was the same (Figs. 7, 8) as in *Pteronotus* and *Phyllostomus.* The chief cells in *Artibeus* proved to be the most extreme; virtually all product found within the cytoplasm was in the form of pale, swollen, coalesced secretory granules with flocculent or finely granular contents (Fig. 8). Disrupted limiting membrane commonly was associated with both mature and immature secretory granules in *Artibeus* chief cells. Other chief cell membranes (such as GER and the plasmalemma) always were intact. The nuclei of these chief cells always were highly irregular in outline, restricted to the basal periphery of the cell, and contained decidedly more heterochromatin than did homologous chief cells in the other three genera (Fig. 2).

Parietal (*Oxyntic*) *Cells*

Secretion of hydrogen ions is the major function of gastric parietal cells. The secretory process involves extraordinarily dynamic cytoplasmic features including intracellular secretory canaliculi with extensive microvilli (Schofield et al., 1979). The transient nature of parietal cell ultrastructure poses some potential problems in making static comparisons between individuals and species but we found that data from experiments on rodents (for example, Ito and Schofield, 1978) allowed us to recognize and distinguish among actively secreting and inhibited cells. Comparisons in the following paragraphs therefore are based on cells judged to be in corresponding phases of the secretory cycle.

Parietal cells in all four genera differed to the extent that tissue specimens from each genus easily could be identified taxonomically on the basis of ultrastructure of their parietal cells (Fig. 9). Parietal cells in both specimens of *Pteronotus* typically were characterized by abundant mitochondrial profiles, numerous spherical vesicles, a few isolated profiles of secretory intracellular canaliculi, and complexly infolded lateral cell margins (Figs. 9, 10, 11). Although we presume that the infolded membrane along the cell margins (Fig. 10) actually was continuous with what appeared to be isolated canaliculi, we obtained no direct confirmation. Three especially obvious and consistent features of parietal cells in *Pteronotus* were: 1) many cells possessed images of dividing mitochondria (Fig. 11); 2) the intracellular canaliculi usually had an "occluded" appearance and contained electron dense zones (Fig. 10); and 3) the microvilli of the intracellular canaliculi typically were pleimorphic and lacked bundles of filaments (compare Figs. 10 and 13). The free margins of the parietal cells (that is, the surface not in contact with other cells) were characterized by a thin basal lamina and dense bundles of collagen surrounding the gastric gland. In summary, the abundant parietal cells in *Pteronotus* always had ultrastructural features associated with a very low level of secretory activity (Ito and Schofield, 1978). Indeed, essentially all of the hundreds of cell profiles that we examined in both specimens of *Pteronotus* contained so few vesicles and so little canaliculi that HCl production must have been extremely low at the time of fixation.

In *Phyllostomus hastatus* and *P. elongatus* the abundant parietal cells differed dramatically from those found in *Pteronotus* (Figs. 9, 12). In both species of *Phyllostomus* the typical parietal cell contained an extensive amount of intracellular secretory canaliculi that coursed throughout the cytoplasm (Fig. 12). The microvilli of these secretory canaliculi had a more organized appearance than in *Pteronotus* and, unlike *Pteronotus,* in *Phyllostomus* these microvilli contained bundles of filaments (Fig. 12). In the most active parietal cells in *Phyllostomus,* the secretory canaliculi occupied approximately 25% of the cell volume and very little free cytoplasm with polyribosomes or GER could be found in either active or reorganizing parietal cells. Unlike *Pteronotus,* in which smooth membrane took the form of vesicles, in *Phyllostomus* much of the smooth membrane was organized as elongate tubules (Figs. 11, 12). The free margins of parietal cells in *Phyllostomus* were characterized by a thin basal lamina, sparse collagen fibers, and smooth muscle cells. In summary, the average parietal cell in our specimens of *Phyllostomus* contained ultrastructural features consistent with those found in actively secreting and reorganizing cells (Ito and Schofield, 1978).

Carollia differed from *Phyllostomus* most obviously in that the typical parietal cells (regardless of activity level) contained a considerably greater volume of free cytoplasm with polyribosomes and scattered

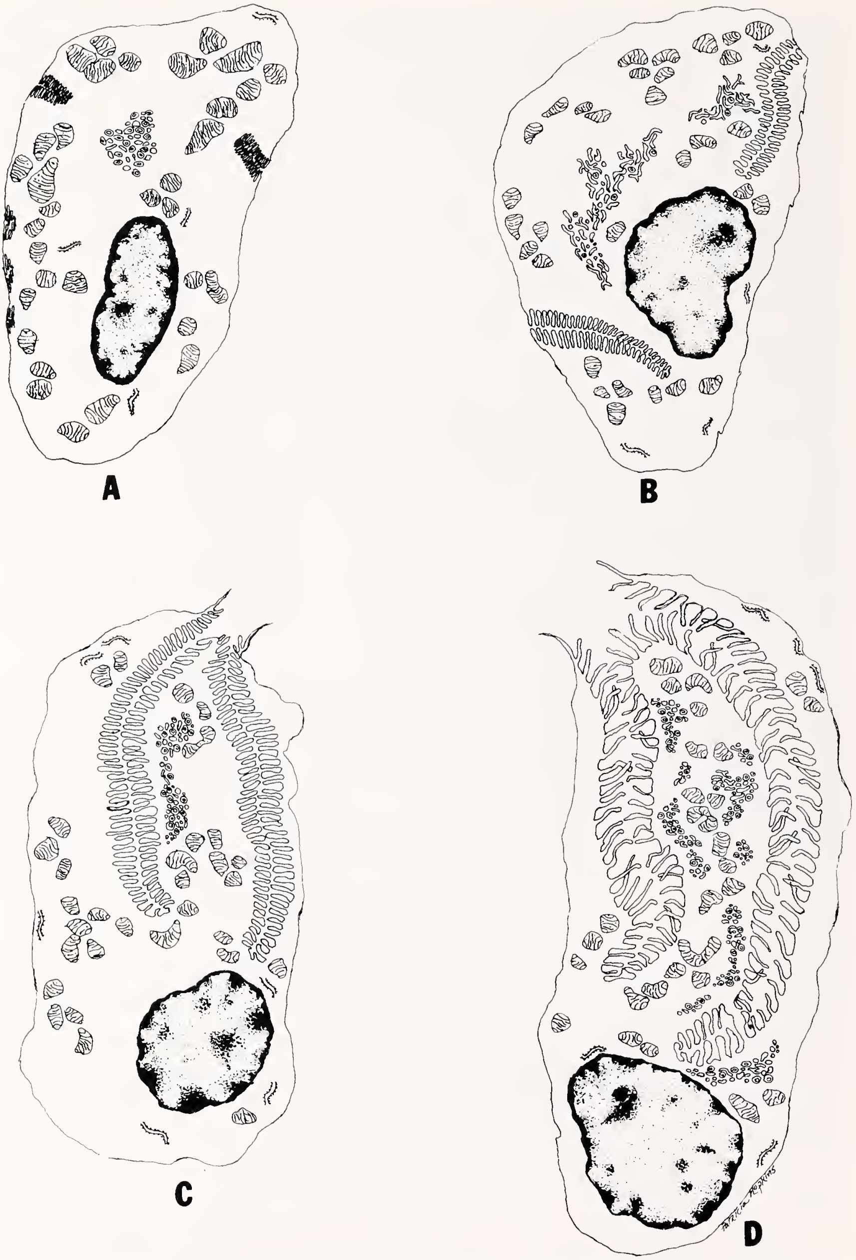

Fig. 9.—Diagramatic comparisons of typical parietal cell profiles in *Pteronotus* (A), *Phyllostomus* (B), *Carollia* (C), and *Artibeus* (D). Note the obvious differences in relative amounts of intracellular secretory canaliculi (compare with Figs. 10–15).

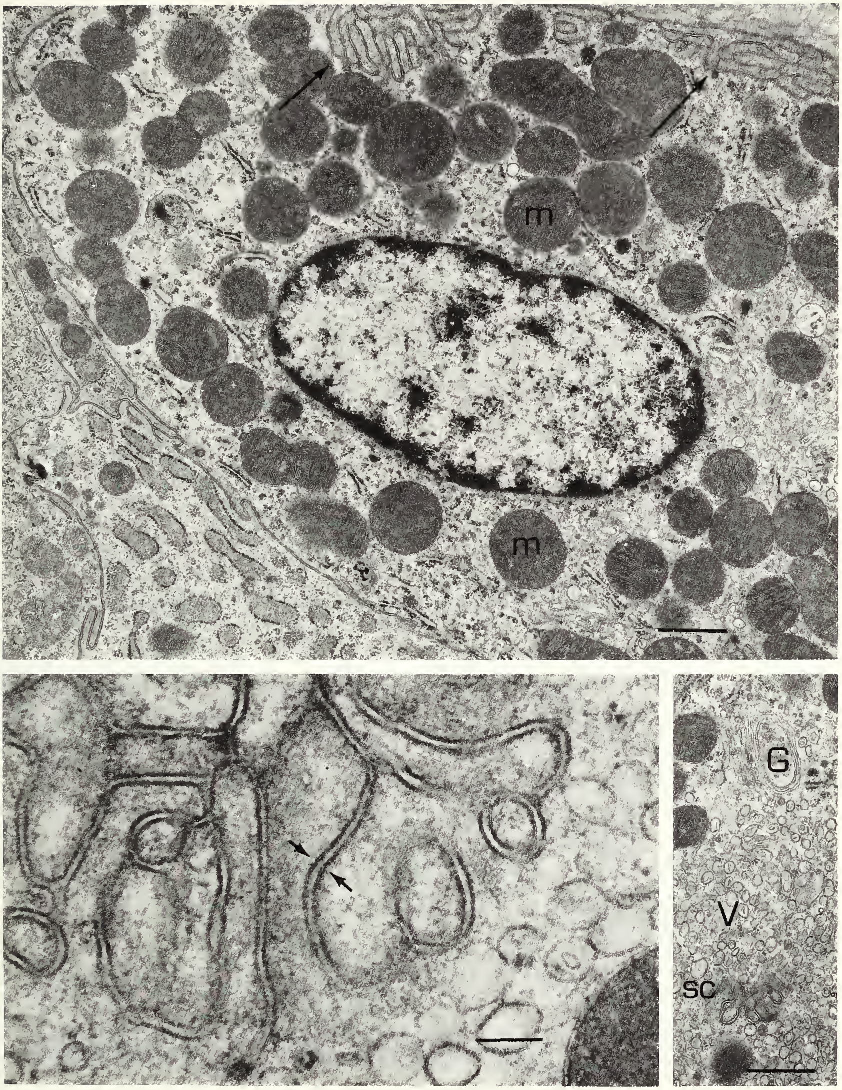

Fig. 10.—Top: Survey of typically inactive parietal cell in *Pteronotus* (CM 63972). Note the large, abundant mitochondrial profiles (m), and infolded plasma membrane along the cell border (arrows). Scale bar equals 0.5 μm. Lower left: High magnification view of "closed" intracellular secretory canaliculus in *Pteronotus.* Compare the nearly occluded membrane (arrows) to the profiles shown in *Artibeus* (Fig. 15). Scale bar equals 0.13 μm. Lower right: Survey of Golgi complex (G) and numerous vesicles (v) in active parietal cell in *Pteronotus.* Note the small, closed profile of an intracellular secretory canaliculus. Scale bar equals 0.5 μm.

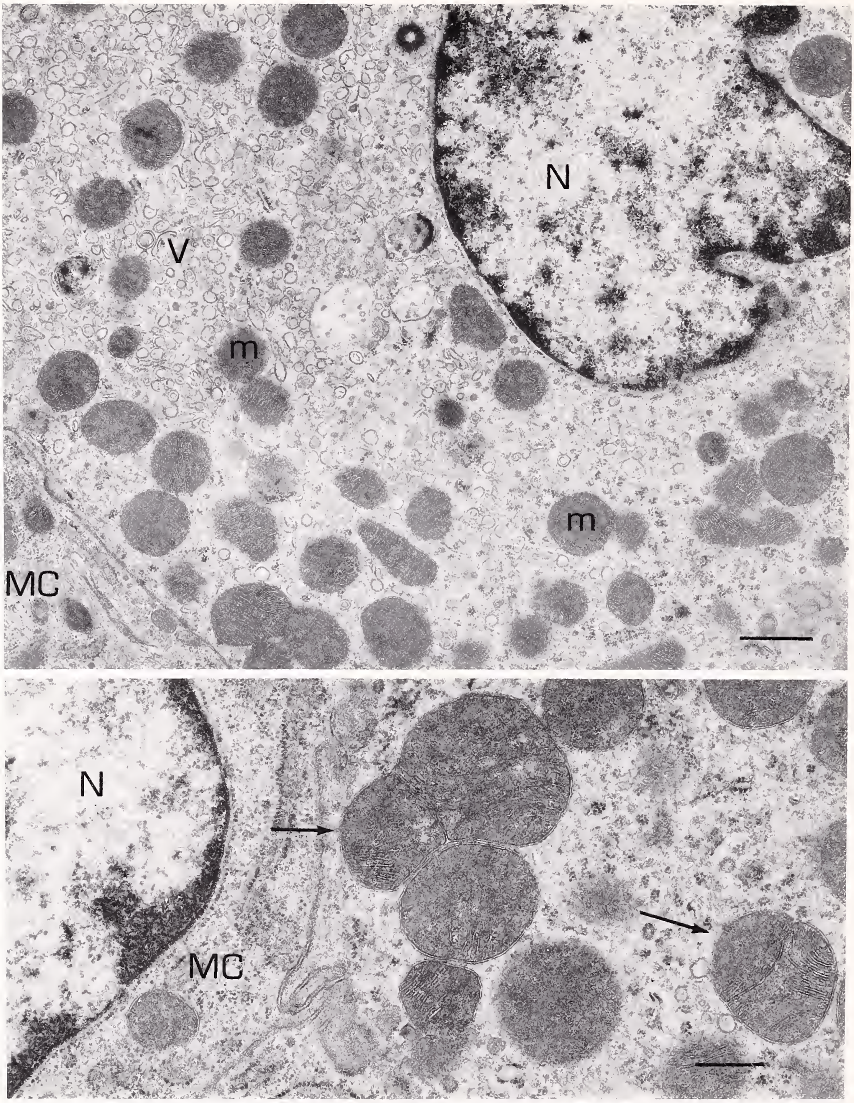

Fig. 11.—Top: Survey of parietal cell in active synthesis (*Pteronotus*, CM 63972) for comparison with the more common appearance shown in Fig. 10. Scale bar equals 0.5 μm. Bottom: Dividing mitochondria (arrows) were found commonly in *Pteronotus* parietal cells in all stages. Scale bar equals 0.4 μm. Abbreviations are: v, vesicles; m, mitochondria; MC, mucous cell cytoplasm; N, nucleus.

GER profiles (Figs. 9, 13). Tubular profiles of smooth membrane always were relatively less abundant, or less densely packed, than in *Phyllostomus* and numerous discoid profiles, not seen in either species of *Phyllostomus,* were common in parietal cells of *Carollia* (Fig. 13). Regardless of these consistent and distinctive differences, the general activity level of parietal cells in *Carollia* essentially was the same as in *Phyllostomus* and, thus, the volume of intracellular secretory canaliculi and the ultrastructural appearance of the microvilli in the two genera differed little (Figs. 12, 13). In addition to mature parietal cells, one of our specimens of *Carollia* (CJP 3621) was interesting in that we found numerous cells that we judged to be "immature" parietal cells. These particular cells had all of the features usually associated with parietal cells (including at least some intracellular canaliculi, vesicles, and tubular membrane profiles) but in the overview were characterized by considerably more free cytoplasm, GER, and more obvious Golgi complexes than were in the more typical parietal cells.

In *Carollia,* free margins of the parietal cells differed greatly from *Pteronotus* and *Phyllostomus.* In the former, the parietal cell free margins appeared to be in intimate contact with a dense zone of elastin (Fig. 13) that made the thin basal lamina nearly impossible to detect. Beyond the elastic fibers, which appeared to be interlaced with collagen, we generally found abundant smooth muscle cells. In summary, parietal cells in our specimens of *Carollia* exhibited features consistent with an active secretory state but could be distinguished from those of *Phyllostomus* by having a much greater area of free cytoplasm per cell.

Both species of *Artibeus, A. lituratus* and *A. concolor,* were distinctive in that the parietal cells were significantly larger and more active than in any of the other species examined (Figs. 9, 14, 15). In these frugivores, even the least active parietal cells had ultrastructural features associated with actively secreting cells in *Phyllostomus* and *Carollia* (compare Figs. 12–14). The most highly active cells (Fig. 14) matched the ultrastructure of parietal cells deliberately stimulated with exogenous chemicals during experimental procedures described in literature (for example, Ito and Schofield, 1978). The majority of the parietal cells in both species contained greatly swollen intracellular canaliculi such as that illustrated in Fig. 14. As can be seen in this typical example, the expanded luminal surface had only a relatively few microvilli. Another usual feature of cells in this active state was the zone of highly concentrated tubular and vesicular membrane profiles shown in Fig. 14. Such zones usually lacked other cytoplasmic constituents except for coated vesicles (Fig. 15).

The least active parietal cells in stomachs of *Artibeus* were most similar in their ultrastructure to parietal cells in *Carollia* (Figs. 13, 14).

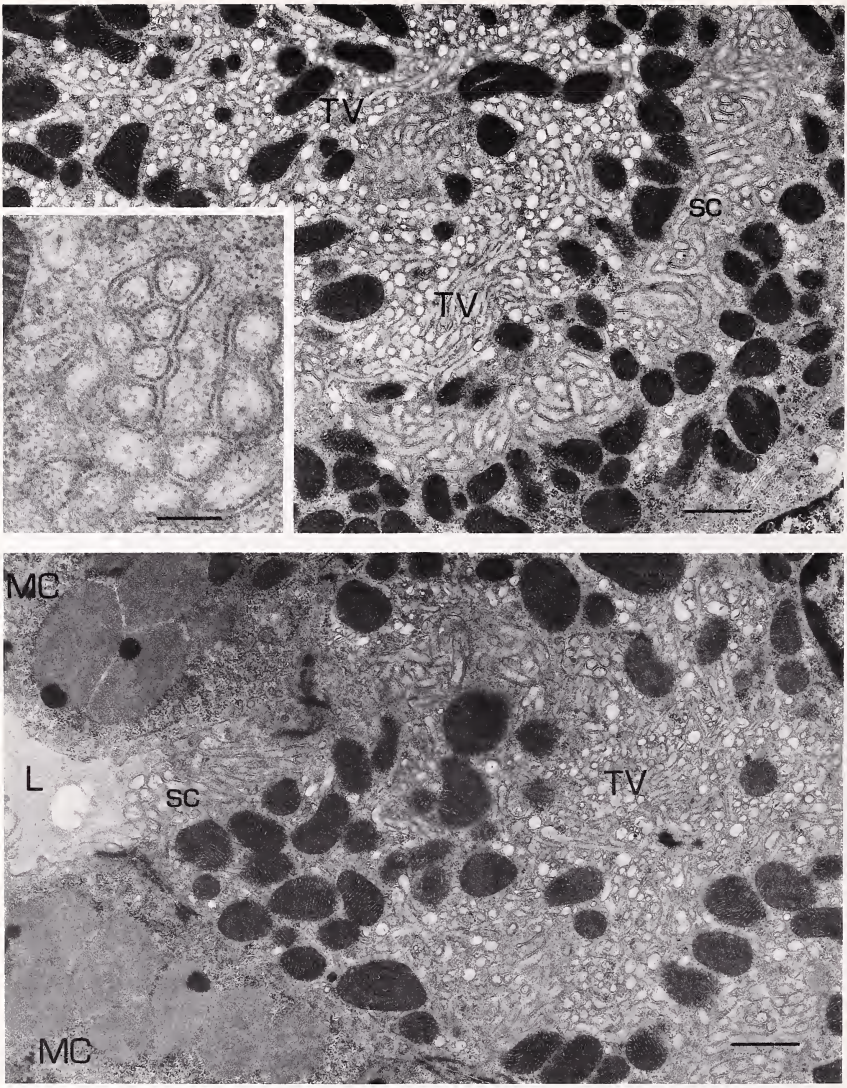

Fig. 12.—Top: Survey of an active parietal cell in *Phyllostomus hastatus* (CM 64035). Note the extensive tubulo-vesicular profiles (TV) and intracellular secretory canaliculi (SC). Scale bar equals 0.5 μm. Inset: High magnification of secretory canaliculus. Scale bar equals 0.23 μm. Bottom: Actively secreting parietal cell (*P. hastatus,* CM 64035), with two adjacent mucous neck cells (MC). Scale bar equals 0.5 μm. Abbreviations are: sg, mucous secretory granule; L, lumen.

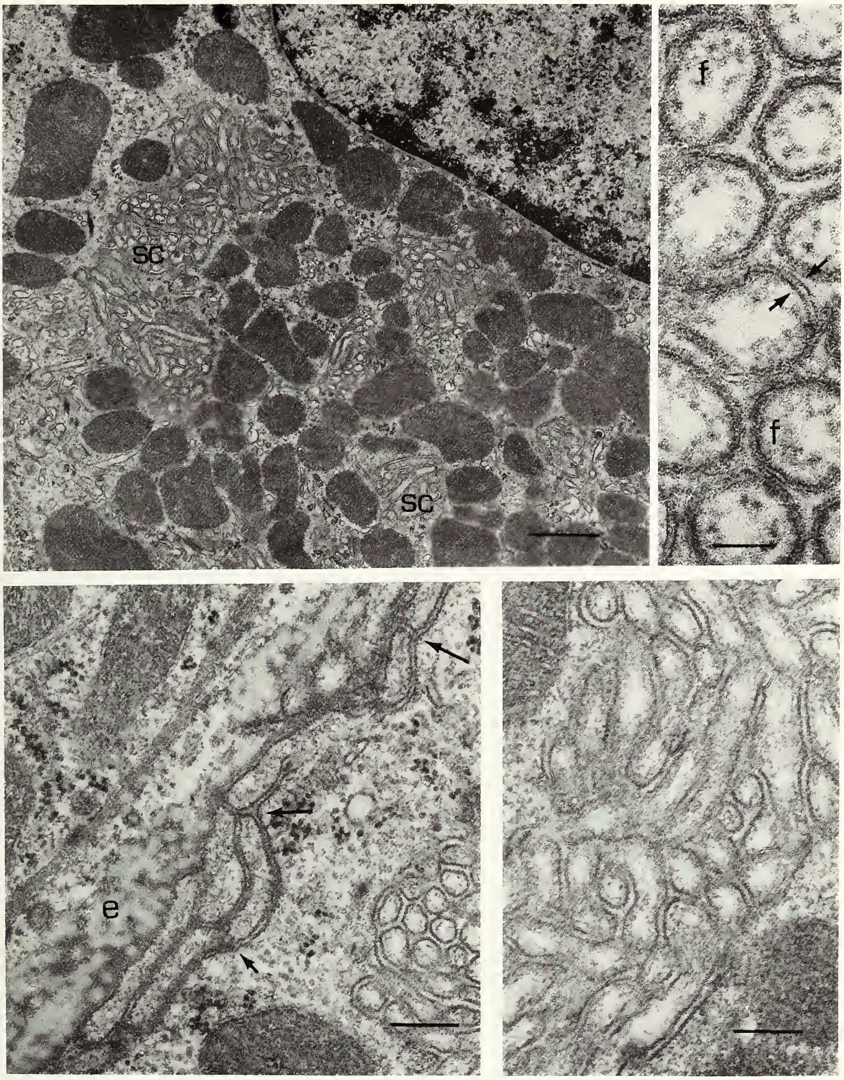

Fig. 13.—Upper left: Typical parietal cell in *Carollia* (CJP 3631). Note the extensive intracellular secretory canaliculi (SC), which are more "open" than in *Phyllostomus* (Fig. 12) or *Pteronotus* (Fig. 10). Scale bar equals 0.5 μm. Upper right: High magnification cross-section through microvilli of a secretory canaliculus in *Carollia*. Note the typically thick appearance of the unit membrane (arrows) and filaments (f) within the microvilli. Scale bar equals 0.18 μm. Lower left: Elastin (e) and infolded membrane (arrows) of a free margin of a *Carollia* parietal cell. Scale bar equals 0.5 μm. Lower right: Intracellular secretory canaliculus in an active parietal cell (*Carollia*). Scale bar equals 0.2 μm.

The most obvious difference, however, was in the appearance of intracellular secretory canaliculi. In *Artibeus* the intracellular canaliculi in even the least active cells always had an "open" rather than partially occluded configuration found in all of the other species (compare Figs. 10, 12, 13, and 15).

The free margins of the parietal cells in *Artibeus* differed from all the other species in our sample by lacking a close association with dense bundles of either collagenous and elastic fibers (compare Figs. 13–14). Associations between parietal cell free margins and nerve terminals also were seen more commonly in *Artibeus* than in the other species (Fig. 14).

Mucous Cells

Among the species examined, *Pteronotus* and *Phyllostomus* had the largest and by far the most numerous mucous surface cells lining the deep gastric pits and mucous neck cells, which sometimes occupied more than one half of each gastric gland (Fig. 2). The large volume of mucus produced in the stomachs of these bats was clearly indicated at the TEM level. Histochemical analysis by Forman (1972) previously has demonstrated that the cellular product, in addition to being abundant in both species, consists of acid, neutral, and sulfonated mucins. In *Carollia* and *Artibeus* we found significantly smaller and fewer mucous cells. *Artibeus* had by far the fewest and smallest-sized mucous neck cells; histochemically these cells produce the least variety of mucoid products (Forman, 1972). Interspecific chemical differences among the products produced by these homologous cells was reflected at the ultrastructural level in that a variety of secretory product morphologies was evident (Figs. 16–18).

Three ultrastructurally distinct mucoid products were found in *Pteronotus* (Fig. 16). The mucous neck cells were moderate in size and an irregularly-shaped euchromatic nucleus typically was located in the basal third of the cell (Fig. 2). The mitochondrial profiles were small and ovoid and located mostly in the basal half of the cells. Large, well-developed Golgi complexes and an extensive GER system consisting of many distended profiles also was found in the cytoplasm. The secretory product morphology found in *Pteronotus* mucous neck cells consisted of spherical granules with a moderately electron dense matrix with an electron dense core (Fig. 16). The mucous cells of the gastric pits had two different products. In the most common a reticulated matrix had one or more small electron dense clumps and the granules were more nearly elongate in shape (Fig. 16). In the second, the product was spherical with a reticulated matrix (Fig. 16). These two products never were found in the same cell, suggesting that either the two types

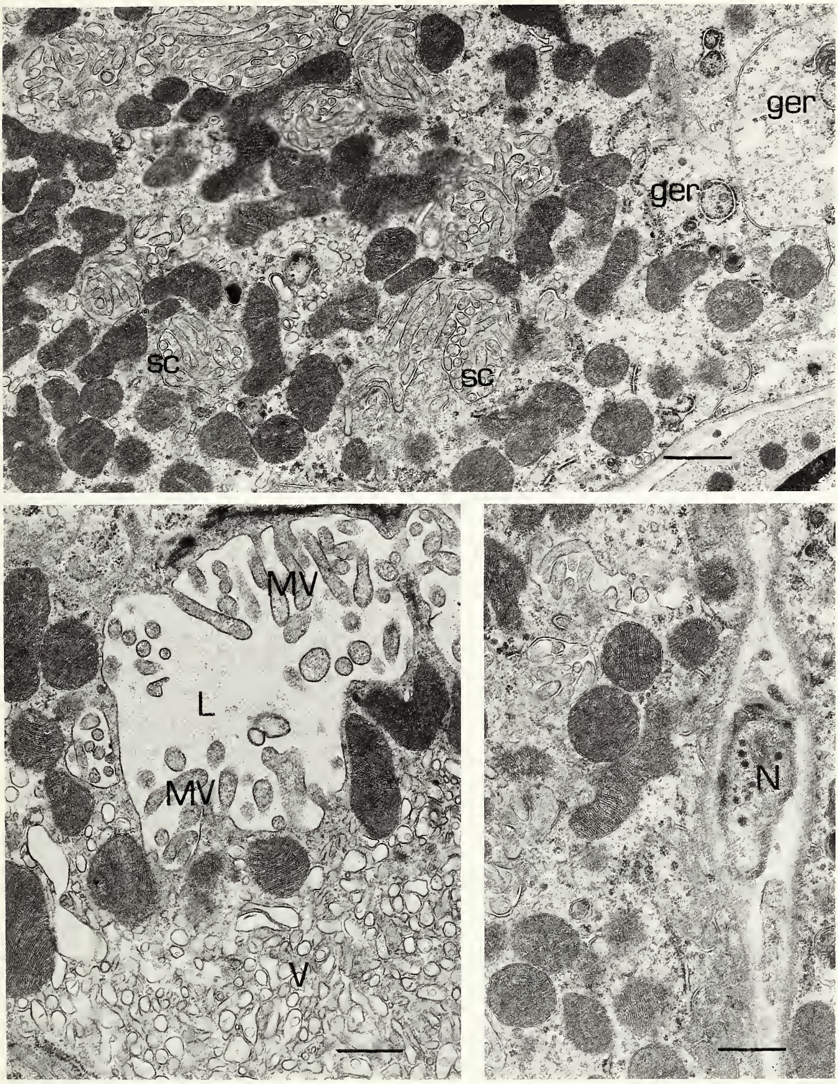

Fig. 14.—Top: Typical parietal cell ultrastructure in *Artibeus concolor* (CM 63791). Note the extensive, open intracellular secretory canaliculi (SC) and unusual granular endoplasmic reticulum (ger). Scale bar equals 0.5 μm. Lower left: Extremely active parietal cell in *A. concolor*. Note the sparse microvilli (mv), open lumen (L), and abundant vesicles (v) suggesting that this cell was in a late secretory-early synthesis phase. Scale bar equals 0.5 μm. Lower right: Innervation (N) of the parietal cell region of the gastric glands in *A. concolor* (CM 63791). Scale bar equals 0.5 μm.

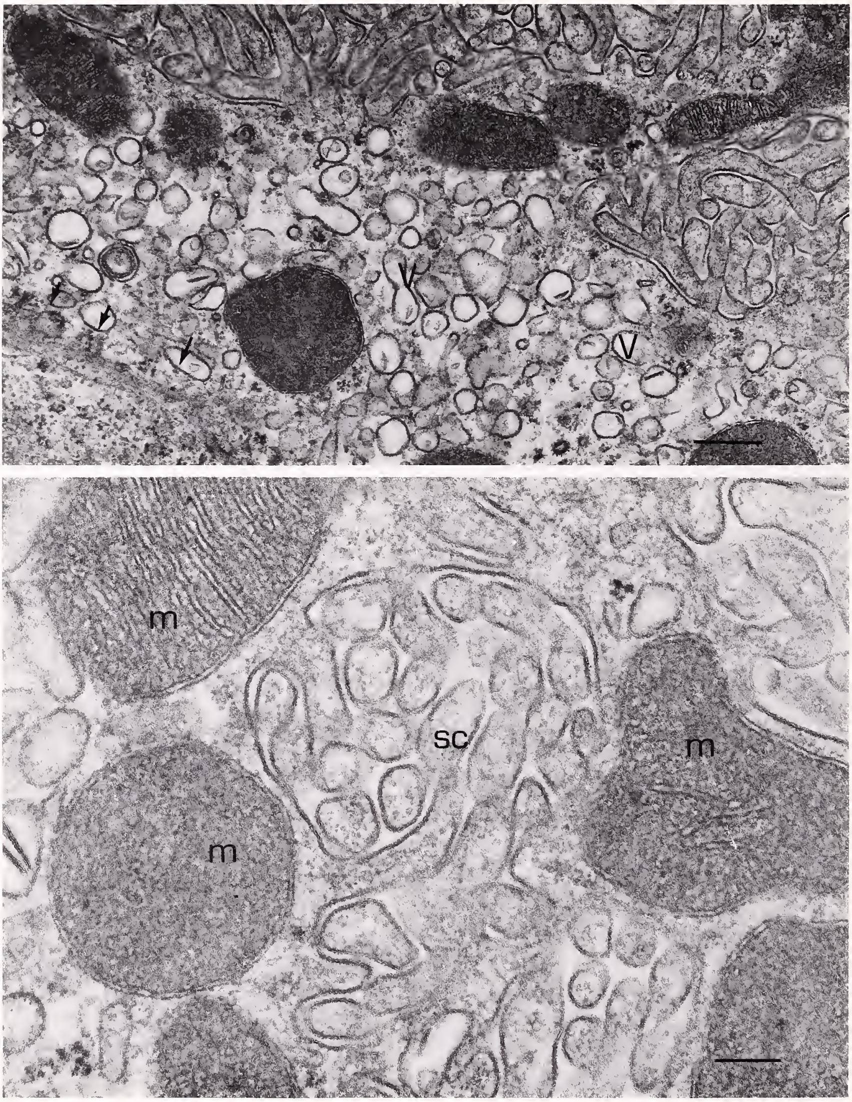

Fig. 15.—Top: Cytoplasmic zone of vesicles (v) in a parietal cell from *A. concolor* (CM 63791). Note the abrupt change in cytoplasm (arrows). Scale bar equals 0.26 μm. Bottom: High magnification view of a typical secretory canaliculus (SC) and surrounding mitochondria (m) in a parietal cell (*A. concolor*, CM 63791). Scale bar equals 0.13 μm.

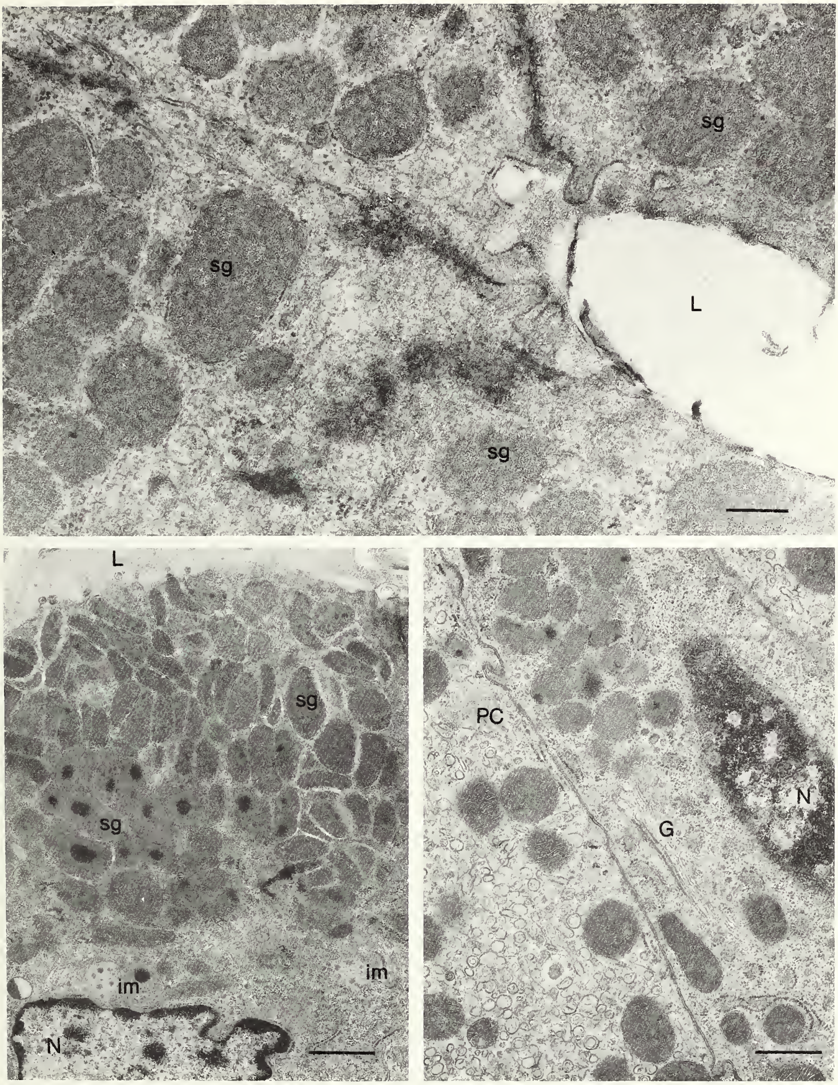

Fig. 16.—Top: Typical secretory granule morphology (sg) of mucous cells deep in the gastric pit (*Pteronotus*, CM 63972). Scale bar equals 0.27 μm. Lower left: Secretory granule morphology near the surface of the gastric mucosa in *Pteronotus* (CM 63972). Scale bar equals 0.89 μm. Lower right: Typical mucous neck cell in *Pteronotus* (CM 36972). Scale bar equals 0.5 μm. Abbreviations are: L, lumen; im, immature mucous granule; N, nucleus; PC, parietal cell; G, Golgi complex.

of mucous cells are present in *Pteronotus* or, alternatively, that mucous neck cells produce different products at different stages of the differentiation process. Mucous cell exfoliation was common in the gastric pits (Fig. 17).

In *Phyllostomus* the mucous cells were similar to those in *Pteronotus* in several general aspects. The major difference, however, was in secretory product morphology. In *Phyllostomus* two different morphologies were identified and found in different mucous cells. In cells lining the gastric pits the granules had a dense homogeneous matrix, whereas in the mucous neck cells the granules had a pale matrix and an electron dense spot positioned at the edge of the granule (Fig. 18).

The ultrastructure of mucous neck cells in *Carollia* was strikingly distinct from that of the two previous species (Fig. 17). The nuclei were more elongate and appeared to be more heterochromatic and the mitochondrial profiles were more numerous and more evenly distributed in the cell cytoplasm. The GER in *Carollia* mucous neck cells had distended cisternae filled with a dense material similar to some of the material seen in the secretory product. Extensive Golgi complexes were yet another distinguishing feature of mucous neck cells in this genus (Fig. 17). Although the general ultrastructure was distinctive, the secretory product itself was similar to that found in both *Phyllostomus* and *Artibeus.* However, unlike *Phyllostomus,* only one type of product was found in *Carollia.* Although variable within a given cell, the secretory product in *Carollia* usually consisted of spherical granules with a pale background, a moderately electron dense zone, and an extremely dense core (Fig. 17). Gastric pits were extremely shallow and lined by surface epithelium.

The mucous neck cells in *Artibeus* were sparse and when located were found to be wedged among parietal cells (Figs. 2, 18). The nucleus typically was heterochromatic, small, and located at the basal margin of the cell. Mitochondrial profiles were small and elongate. The GER system was the least prominent of all species studied and Golgi complexes were observed with less frequency than in other mucous neck cells. Only one type of secretory morphology was found in *Artibeus*; the spherical granules generally resembled those in mucous neck cells in *Carollia* but lacked the electron dense core (Figs. 17, 18).

DISCUSSION

In a series of previous comparative histological and histochemical investigations, Forman (1971*a,* 1971*b,* 1972, 1973, 1974*a,* 1974*b*) demonstrated a variety of significant differences among digestive tracts of microchiropteran bats. Insofar as the stomach is concerned, these differences fell into several categories including: 1) relative size and shape; 2) musculature; 3) presence or absence of and relative numbers

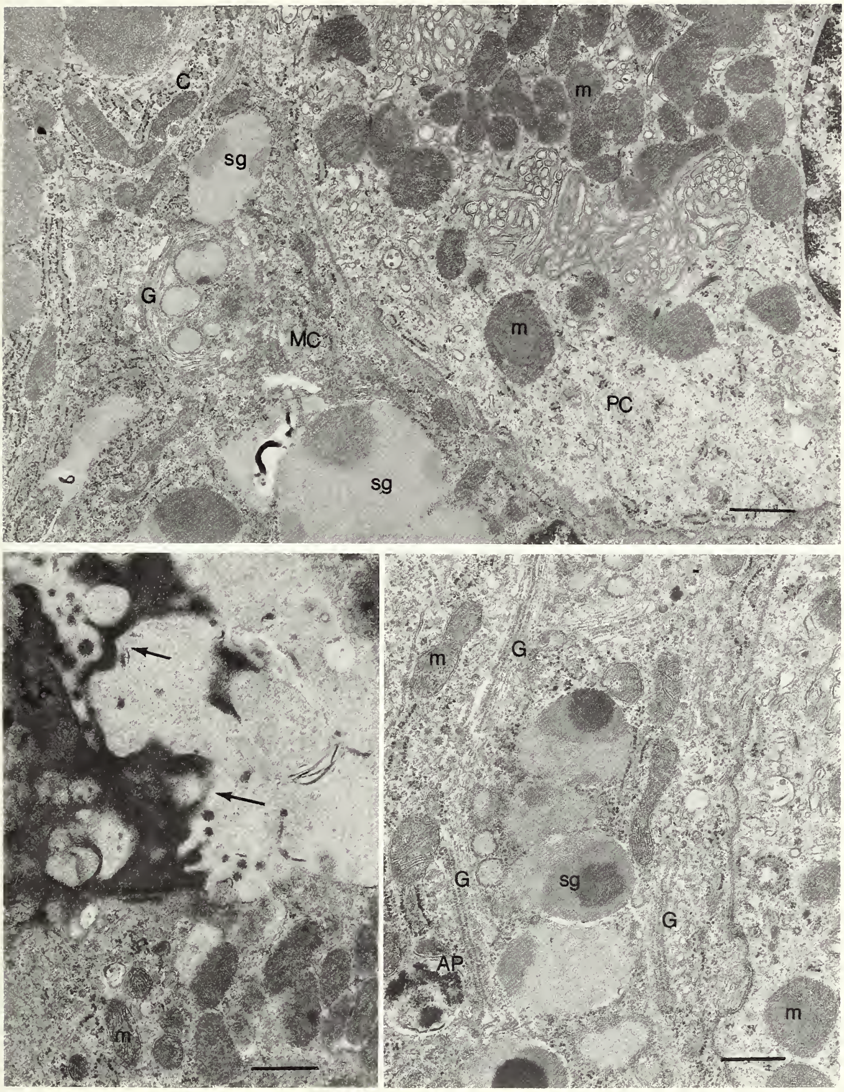

Fig. 17.—Top: Survey of a mucous neck cell (MC) positioned among chief cells (C) and parietal cells (PC) in *Carollia* (CJP 3631). Scale bar equals 0.5 μm. Lower left: Exfoliation of a dead mucous cell (arrows) into the lumen (L) of a gastric pit in *Pteronotus* (CM 63972). Scale bar equals 0.5 μm. Lower right: Extensive Golgi complex (G) in a mucous neck cell in *Carollia* (CJP 3631). Scale bar equals 0.4 μm. Abbreviations are: sg, secretory granules; m, mitochondria; AP, autophagic vesicle.

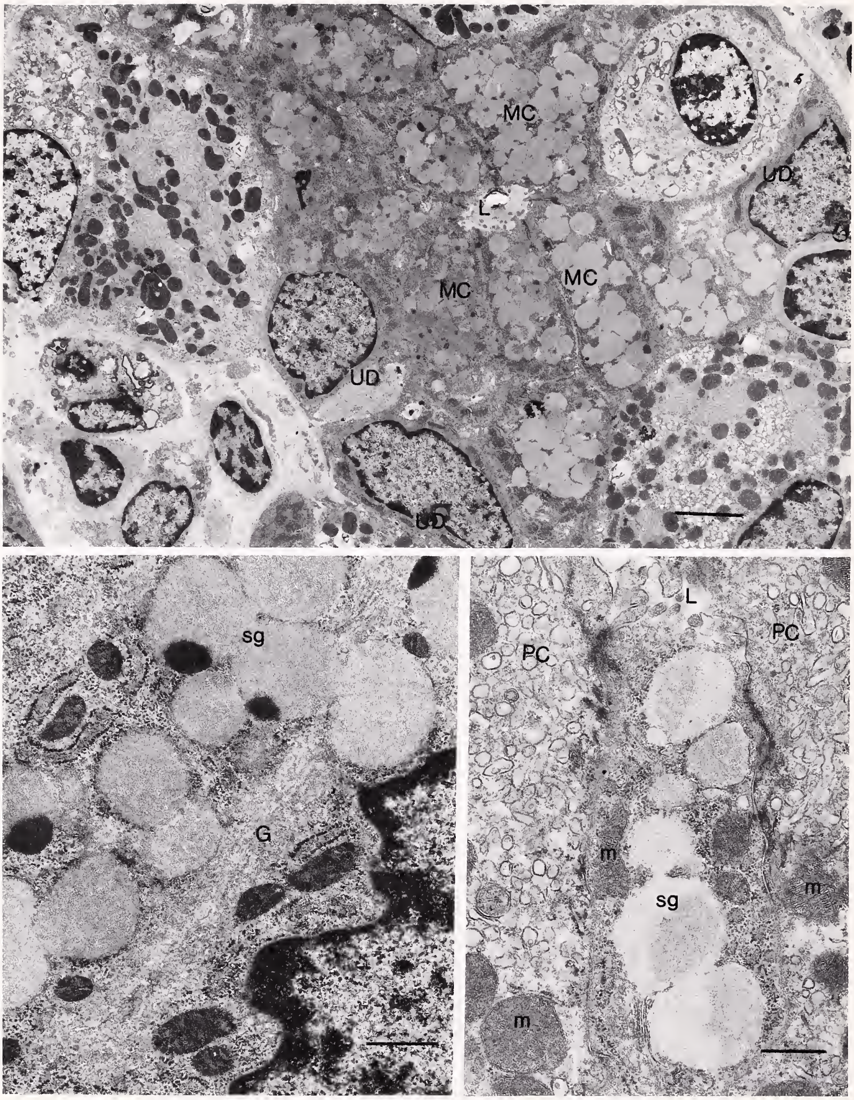

Fig. 18.—Top: Survey view of mucous cells (MC) in *Phyllostomus hastatus* (CM 64035). Note the morphologically undifferentiated cells (UD) at the periphery of the gastric pit. Scale bar equals 2 μm. Lower left: Mucous neck cell secretory granules (sg) in *P. hastatus* (CM 64035). Scale bar equals 0.4 μm. Lower right: Mucous neck cell secretory granules (sg) in *A. concolor* (CM 63791). Scale bar equals 0.5 μm. Abbreviations are: G, Golgi complex; PC, parietal cell; M, mitochondria; L, lumen.

of cells of particular types; and 4) histochemical staining reactions of specific secretory cells. Forman (1972) demonstrated that these differences related in a general way to chiropteran systematics and, by extension, to respective dietary habits.

From an evolutionary point-of-view, the chiropteran stomach is an exceptional example of the extent to which a complex internal organ can undergo adaptive changes. With this in mind, we asked a series of basic, previously unexplored questions about the relationships between interspecific gastric differences and ultrastructure of presumably homologous cells.

Although comparative gastric histology provides data on cell "type," relative numbers of cells of particular "types," and structural pattern (that is, distributional organization of cells) and correlates to some extent with microchiropteran systematics, cellular ultrastructure presents special problems. Therefore, it is important for us to emphasize at the outset of this discussion that we do not view cells as static structures. Indeed, the exact extent to which the ultrastructure of a cell reflects its functional state as opposed to being a fixed and direct consequence of its operational genic constitutent is presently unknown. In our view, the implication of many of the recent studies in molecular biology is that ultrastructure is more nearly a combination of functional state and cellular response to an artificially introduced fixation chemistry than it is a structural pattern directly determined by genes. Consequently, in making our comparisons of ultrastructure we did not assume a priori that ultrastructural differences are themselves the direct result of selection. Instead, because all of our material was fixed in the same way, we assumed when comparing ultrastructure that we probably indirectly were comparing "functions" rather than directly-selected structural differences.

In part, our analysis depended on our ability to recognize and compare homologous, fully differentiated (in a morphological sense) cells. Some criteria for comparing homologous cells have been proposed and discussed in considerable detail by Rieger and Tyler (1979). Fortunately, mammalian gastric epithelium is fairly consistent insofar as cell "types" are concerned and, therefore, not much doubt exists as to whether or not particular cell types (such as parietal or mucous neck cells) are homologous. In regard to this, one possible problem area is that of entero-endocrine cells, which are complex and which we identified on the basis of ultrastructural characteristics of secretory product. As mentioned previously, we followed Grube and Forssmann (1979) but the reader should bear in mind that these cells are less certainly recognizable than are parietal, chief, and mucous neck cells.

The question of differentiation—in a morphological sense—is yet another matter. Most cells in the gastric mucosa have a limited life and, thus, are replaced by progenitor cells at some rate, which is unknown for bats. In making our comparisons we carefully avoided those few cells that clearly either were dividing or which were "generalized" in the sense that their ultrastructural morphology lacked cytoplasmic features associated with known types of mature gastric cells. Presumably such cells were "immature" at time of fixation.

Overall, our ultrastructural data conformed well to earlier histological and histochemical studies of Forman (for example, 1972) in that in instances where light microscopic histological differences were reported, we also found ultrastructural differences. This in itself is significant because it means that comparative ultrastructure is a different but parallel data set to histology.

Although representative of two different families, we found that *Pteronotus* and *Phyllostomus* were similar in a number of features. For example, both have deep gastric mucosa, large numbers of mucous neck cells that secrete a complex mucoid product, small parietal cells, abundant chief cells, and a variety of relatively abundant entero-endocrine cells. *Carollia,* an omnivore, resembles *Phyllostomus* more nearly than it resembles either *Pteronotus* or *Artibeus.* The main difference is that *Carollia* has a lower gastric mucosa (that is, shallower gastric pits) and fewer mucous neck cells than does *Phyllostomus.* In conjunction with this difference in cell number, the mucoid product in *Carollia* neck cells apparently lacks a sulfonated component, at least to judge from the absence of toluidine blue metachromasia (Forman, 1972). In the two stenodermatine species, *Artibeus concolor* and *A. lituratus,* the gastric mucosa is low, gastric pits essentially lacking, and both species are characterized by having extremely large parietal cells and very few mucous neck cells. In summary, therefore, our results paralleled earlier studies by demonstrating microscopic differences that appear to match our concept of systematic relationships and in falling into a series of specific categories: 1) tissue thickness (that is, cell number); 2) proportionate abundance of particular cell types; and 3) possible chemical differences among cell secretory products or activities.

Entero-endocrine Cells

The comparative ultrastructure of entero-endocrine cells was striking in that many interspecific differences were readily apparent (Table 1). We have assumed, of course, that random samples taken from two areas of the fundus would be representative insofar as the entero-endocrine cells are concerned. Many questions remain to be answered about the function(s) of mammalian entero-endocrine cells, but a series of studies over the past fifteen years have provided considerable data about the relationships between ultrastructural morphology and product (for example, Forssmann et al., 1969; Grube and Forssmann, 1979). In tissues prepared for standard histology and studied at the light microscopic level, Forman (1972) was able only to recognize entero-endocrine cells collectively as "argentaffin" cells. This in itself underscores the value of an ultrastructural analysis, which allows for recognition of specific types of entero-endocrine cells.

The presence of A cells in all four of our species was determined by the appearance of the product, which is small (220 nm) and electron dense, and by the cells apparently having a "closed type" of morphology (Grube and Forssmann, 1979). Presumably these entero-endocrine cells secrete glucagon in bats as they do in a wide variety of other mammals (Moody et al., 1978; Unger et al., 1978). If so, the greater abundance of A cells in both *Pteronotus* and *Phyllostomus* is noteworthy because experimentally glucagon has been shown to inhibit both basal and stimulated gastric acid secretion while stimulating glucose-6-phosphate dehydrogenase activity in undifferentiated mucous neck cells and stimulating mucous secretion from the surface epithelial cells (Wilson et al., 1972; Konturek et al., 1975; Stachura et al., 1981). Both *Pteronotus* and *Phyllostomus* are characterized by extremely numerous, active mucous neck, gastric pit, and surface epithelial cells and, thus, abundant A cells correlate with the abundance of these possible target cells.

The A cells in both *Carollia* and *Artibeus* are not nearly as abundant as in either of the other two genera. Quantitative data on numbers of A cells are unavailable and would be difficult to obtain without using immunoreactivity, which generally requires fresh tissue and, thus, is difficult when investigating wild species. It is worth noting, however, that at the light microscopic level, Forman (1972) was unable to find any "argentaffin" cells in *Artibeus,* which certainly suggests that all types of entero-endocrine cells are rare in these frugivores. This is particularly noteworthy when one considers the relatively larger volume that can be surveyed with light microscopy as compared to transmission electron microscopy.

The low number of glucagon-secreting A cells in the gastric mucosa of *Artibeus* is interesting in view of the fact that mucous neck cells also are extremely sparse, small in size, and located in narrow spaces between large and extremely active parietal cells (Figs. 2, 18). It is tempting to speculate that the paucity of mucous neck cells and scarcity of A cells are in some way related and that a "decrease" in real numbers of these cells was a special feature of the evolution of the stomachs of frugivorous stenodermatines. One difficulty in advancing this hypothesis is that we only can assume that decrease in cell numbers within a given volume is equivalent to a decrease in volume of secreted product per unit time. The possibility exists that a few cells can synthesize proteins and assemble and secrete product at a higher rate or over longer periods and ultimately compensate for low cell numbers.

Pteronotus, Carollia, and *Phyllostomus* have in common a second cell type, which we have identified on ultrastructural grounds as a somatostatin-producing D cell (Hokfelt et al., 1975; Grube and Forssmann, 1979). Somatostatin is a labile, adsorbable peptide that in general has inhibitory effects on adjacent secretory cells. In particular, somatostatin has been shown to have a neurotransmitter-like action that inhibits release of gastric acid as well as endocrine release of glucagon (Kusumoto et al., 1979). In *Pteronotus, Carollia,* and *Phyllostomus,* a feedback relationship possibly exists between the A and D cells, which often are in physical proximity of each other. Once again, *Artibeus* is noteworthy because of the apparent absence of D cells and the low number of A cells. In *Artibeus* the abundant parietal cells appear to be hyperactive (our data and that of Forman, 1972). The absence of somatostatin-producing D cells in *Artibeus* thus "fits" well with high parietal cell activity. The low number of glucagon-producing A cells and low number of mucous neck cells in *Artibeus* also is reasonable in terms of the inhibitory role of somatostatin (Kusumoto et al., 1979).

A trend toward sacculation of the fundic caecum is apparent in the frugivorous stenodermatines (Forman, 1971*a,* 1972). This structural pattern correlates with a reduction in thickness of the muscular wall within this portion of the stomach (Forman, 1972). An additional aspect of this evolutionary trend is raised by the presence in *Artibeus* of entero-endocrine cells that conform ultrastructurally to D_1 (H) cells by virtue of having small (160 nm), electron dense secretory product (Grube and Forssmann, 1979). The presence of this particular cell type in a frugivore, but not in the other species that we studied, is significant because vasoactive intestinal peptide (VIP) is the secretory product associated with D_1 cells (Table 1). Recently, VIP has been shown in vitro to be a particularly potent peptide that can cause rapid, dose-dependent relaxation of gastric smooth muscle (Bitar and Makhlouf, 1982). The correlation between the presence of VIP-secretory cells and sacculation of frugivore stomachs not only provides a possible clue for an evolutionary mechanism but also provides a foundation for specific immunological experimentation to search for the presence or absence of VIP in the gastric mucosa of bats in general.

Among the species that we studied, *Pteronotus* occupied a unique position in having both ECL and X entero-endocrine cells, neither of which was found in the phyllostomids. The X cell product is unknown but ECL cells produce histamine and possibly serotonin (Grube and Forssmann, 1979). Histamine is of interest because in addition to stimulating acid secretion and vasodilating submucosal arterioles, it recently has been shown capable of evoking an electrical response in chief cells (Ayalon et al., 1982) and eliciting feeding-related drinking (Kraly, 1983). Although we have not yet found ECL cells in any of the phyllostomids, we did find abundant histamine-producing mast cells in the gastric mucosa of *Phyllostomus* (but not in the other species). The question thus arises as to whether or not different cell types accomplish similar tasks in different species and, thus, serve as functional analogs. If this were to prove to be the case, then an already complex situation would become even more so.

The reported role of gastric histamine in induction of drinking behavior (Kraly, 1983) raises a number of interesting questions about the integration of the digestive tract and excretory system. Studier et al. (1983*b*) recently reported that renal morphology in a selected group of Neotropical bats could be correlated with diet and secondarily related to environmental dehydration pressure. The results of this study together with those discussed by Geluso (1980), demonstrate that kidneys of insectivorous and largely animalivorous bats such as *Pteronotus* and *Phyllostomus* have a sub-divided medulla, whereas species that feed primarily on fruit lack this morphological feature. Presumably kidneys of *Pteronotus* and *Phyllostomus* have a better urine-concentrating capacity and, thus, reflect the importance of water conservation to bats in these genera (Studier et al., 1983*b*). Abundant histamine-producing cells in the gastric mucosa of both *Pteronotus* and *Phyllostomus* seems to further substantiate the significance of water intake during feeding in these bats. On the other hand, the apparent absence of histamine-producing gastric ECL and mast cells in both *Carollia* and *Artibeus* suggests that induction of drinking behavior during feeding is less important to these bats. Not only is this explanation substantiated by kidney morphology (Studier et al., 1983*b*) but also by the remarkable report of Herbst (1982) who found that *Carollia perspicillata* could absorb 50% of water in fruits of *Chlorophora tinctoria.* According to Herbst (1982), *C. perspicillata* can absorb enough water from ingested fruit to survive for ". . . long periods without drinking."

Although *Pteronotus* and *Phyllostomus* both have a variety of relatively abundant entero-endocrine cells, the overall interspecific pattern (Table 1) is strongly suggestive of familial differences. The cell types found in the phyllostomids show distinctive similarities that separate these species from our representative mormoopid, *Pteronotus.* A testable hypothesis from our data is that insectivorous-animalivorous bats in general will be found to have the greatest variety and abundance of gastric entero-endocrine cells but that actual compostion of the endocrine cell population will be reflective of systematic relationships.

Lastly, another question of interest is: How do the entero-endocrine cells in microchiropterans compare to those of species in other orders?

Unfortunately, this question, which ultimately will be essential to our understanding of evolutionary patterns, cannot now be answered satisfactorily because data on entero-endocrine cells, although extensive, have been obtained non-systematically. If our specimens of bats are any indication, one might predict that group-specific patterns eventually will emerge.

Gastric Chief Cells

The interspecific ultrastructural differences that we documented among gastric chief cells suggests that either the product(s) or secretory process (or both), differ in relationship to diet and is reflective of systematics. Although ultrastructure in itself ordinarily does not reveal very much about the actual chemical nature of an intracellular product, consistent differences among tissues processed in the same way certainly are indicative of intracellular molecular differences that in turn have had a differential interaction with the fixatives used (Simson et al., 1978; Phillips and Studholme, 1982). The "zymogenic" appearance of secretory product found in chief cells of fasted *Pteronotus* and *Phyllostomus* is not unlike the product of homologous cells in a wide variety of other mammalian species, including an insectivorous vespertilionid bat, *Myotis lucifugus* (Ito and Winchester, 1963). In addition to these species, similar product also is found in carnivorous-insectivorous species of two other phyllostomid genera, *Tonatia* and *Trachops* (Phillips and Studholme, 1982).

The chief cell product in *Artibeus* is extremely distinctive in having an almost mucous-like ultrastructural appearance. Apparently, this appearance is characteristic of the stenodermatine chief cells because previously we also found and described essentially the same ultrastructure in *Ametrida* and *Chiroderma* (Phillips and Studholme, 1982). The swollen, coalesced secretory granules and disrupted limiting membranes found in stenodermatine chief cells probably are not representative of the morphology of living cells and, furthermore, are not obvious in formalin-fixed specimens studied only with standard histology. The TEM similarities of stenodermatine chief cells to many types of epithelial mucous cells are not indicative of the presence of mucins because chief cells in *Artibeus* are negative to histochemical procedures used for demonstration of mucins (Forman, 1972; Phillips and Studholme, 1982). Previously (Phillips and Studholme, 1982), we suggested that chief cells in *Artibeus* and other stenodermatines have some chemical characteristic that causes them to undergo an osmotic response to our trialdehyde fixation procedure. This would result in intracellular hydration and consequent swelling of stored secretory product, which also is what happens in some types of mucous-producing cells under similar circumstances (Simson et al., 1978). In another experiment, Lee et al. (1982) have shown that glutaraldehyde contributes to fixative osmolarity and that buffers can affect cell volume thus confirming that hydration phenomena can be the direct consequence of procedure.

A recent study of isolated chief cells by Gibert and Hersey (1982) lends substantial support to our hypothesis. They found that chief cells from laboratory rabbits normally had electron dense product, whereas when placed in hyperosmolar solution the cells ultrastructurally resembled chief cells that we have found in stenodermatines. Under hyperosmolar conditions the cultured rabbit chief cells secreted pepsinogen significantly more gradually over a longer period of time and the effect of hyperosmolarity was enhanced in combination with a secretagogue (Gibert and Hersey, 1982). In a related investigation, Case and Clausen (1973) demonstrated that in pancreatic acinar cells hyperosmolarity accelerated the release of labeled calcium (^{45}Ca), suggesting that osmotic changes altered membrane permeability to Ca^{++}. Insofar as our present comparative study is concerned, of special relevance is the observation of Gibert and Hersey (1982): "Whatever [the] mechanism [by which] hyperosmolarity acts . . . in chief cells, it is clear that some preconditioning of the cells determines the extent to which they are susceptible to hyperosmotically-induced exocytosis . . . ." One implication of the foregoing data to our investigation is that stenodermatine chief cells have some characteristic predisposition that makes them different from homologous chief cells of all other studied species of bats. Secondly, response to hyperosmolarity might mean that the stenodermatine chief cells secrete their product in response to a different set of stimuli than do chief cells in the other species. This in itself correlates with the obvious scarcity of entero-endocrine cells in the stenodermatines. Thirdly, the ultrastructural differences in intracellular morphology of secretory granules might not mean that the granules themselves differ chemically but only that they are produced and secreted at a different rate.

In summary, the chief cells of stenodermatine bats respond differently to osmolarity than do chief cells of other phyllostomids, and mormoopids and vespertilionids as well. This difference could be of functional importance in that stenodermatine chief cells could produce more pepsinogen over longer periods of time.

Regardless of the foregoing theoretical explanations, the "zymogenic" product in *Pteronotus, Phyllostomus, Tonatia, Trachops,* and *Myotis,* on the one hand and the pale product in *Artibeus, Ametrida,* and *Chiroderma,* on the other hand, certainly are suggestive of some type of fundamental cellular difference associated with diet. This finding is given added significance by the intermediate ultrastructural characteristics (Fig. 6b) of chief cell product in the more nearly omnivorous *Carollia.* Although not everyone agrees on the exact placement of *Car-*

ollia, most systematists do not place this genus near the basal group from which the frugivores evolved (Smith, 1976).

Among phyllostomids in general the respective effects of diet and systematics cannot readily be differentiated because subdivision of tropical nutrient resources unquestionably is the evolutionary cornerstone of the family and is consistently reflected in the morphology of dentition, salivary glands, tongues, and digestive tracts (Phillips et al., 1977; Forman, 1972; Forman et al., 1979). Nevertheless, the fact that chief cells in largely animalivorous phyllostomids are most similar, ultrastructurally, to those of a representative mormoopid, *Pteronotus,* seems to imply that ultrastructure in this instance reflects diet more than relationships. Furthermore, although Ito and Winchester (1963) used a different fixative and fixation procedure, their data for *Myotis* tends to substantiate the idea that an electron dense, "zymogenic" chief cell product is correlated with a non-fruit diet.

Regardless of the respective roles of diet and genic relationships, it is clear that chief cells in *Artibeus* and other stenodermatines represent a functional divergence from the basic cell type. Demonstration of divergence in ultrastructure, which the data indicate is equivalent to divergence of a fundamental, functional nature is important because the stenodermatine chief cells now can be used as a model to explore how cellular functions can be evolutionarily modified. For example, in vitro studies could be used to assess similarities and differences in product and synthesis.

Parietal Cells

The acid-secreting parietal cell is yet another cell type that varied considerably among the species examined by us. In a previous study, Forman (1972) reported a variety of significant histological and quantitative differences among phyllostomid parietal cells. In particular, he reported that in *Artibeus* the parietal cells were extreme in being both abundant and of relatively large size (see Fig. 2), whereas in other species there appeared to be an inverse relationship between size and number (Forman, 1972). For example, in *Pteronotus* Forman (1971*a*) found that the parietal cells were small in size but abundant in number.

Our interspecific comparisons of the ultrastructure of parietal cells were complicated considerably by the highly dynamic nature of these cells (Ito and Schofield, 1978). For the most part, laboratory investigations of parietal cells stimulated experimentally with chemicals such as pentagastrin or histamine have formed the basis of our current concepts of formation, intracellular transport, membrane changes, and secretion of HCl (Ito et al., 1977; Black et al., 1980; Forte et al., 1977; Frexinos et al., 1971; Helander and Hirschowitz, 1972). Studies such as these have advanced our knowledge about parietal cells to a point wherein qualitative categorization of secretory activity is possible based on identification of the particular ultrastructural characteristics associated with the 1) resting, 2) active synthesis, and 3) secretion phases (for example, Ito and Schofield, 1978). The most prominent cytoplasmic change is in the tubulovesicular compartment of the cell, which undergoes radical re-organization as the tubulovesicular membrane fuses into the apical outer cell membrane during acid secretion (Schofield et al., 1979; Forte et al., 1977).

In making comparisons among randomly selected individuals, one might assume a priori that the parietal cells more or less would be in the same functional state in all individuals and all species. Ito and Schofield (1978) predicted that under normal circumstances (that is, not deliberately stimulated by exogenous chemicals), in a given individual the parietal cells could be expected to display a mixed ultrastructural morphology representing a combination of late synthesis and early secretory features. Such a configuration presumably would result from cells secreting at a persistent, relatively low level.

What we actually found in our specimens differed from our expectations in several ways. Firstly, although most parietal cells did indeed seem to present a combination of synthesis and secretion features, it was relatively easy to distinguish among species on the basis of appearance and abundance of intracellular secretory canaliculi, cytoplasmic vesicles, and overall size of the cells. Although our sample sizes are small, owing to difficulties of studying wild species with the TEM, parietal cell configurations nevertheless were consistent within genera. Secondly, two genera (*Pteronotus* and *Artibeus*) represented striking extremes. By way of contrast, *Phyllostomus* and *Carollia* both seemed intermediate in average parietal cell activity.

In both specimens of *Pteronotus,* the parietal cells appeared almost quiescent (Figs. 10, 11). Not only were the secretory canaliculi small relative to cell size, but the microvilli also were pressed together. Artificial stimulation of *Pteronotus* parietal cells presently is beyond the capacity of field research and, additionally, we do not have specimens that were sacrificed while feeding. Consequently, for the present we cannot determine whether or not the ultrastructural data actually mean that *Pteronotus* produces relatively little HCl. Regardless of acid secretory levels in *Pteronotus,* it was equally surprising to find that the parietal cell cytoplasm also contained relatively little indication of active synthesis. Vesicles, usually spherical rather than tubular, generally were sparse although some cells were exceptions (Figs. 10, 11). For the present, the most logical conclusion from these data is that the gastric parietal cell population in *Pteronotus* enters a quiescent or "resting" stage when these insectivorous bats are not feeding.

In contrast to *Pteronotus,* the parietal cells in stomachs of all of our specimens of *Phyllostomus* and *Carollia* clearly were more active at the time when these specimens were sacrificed. When Ito and Winchester (1963) first described the parietal cells in *Myotis lucifugus,* they noted that the typical cell contained an extensive system of intracellular canaliculi. Later, Ito (1967) commented that the secretory canaliculi were relatively more prominent in *Myotis* than in mice, cats, dogs and humans. Allowing for differences in fixation and preparation, *Myotis* seems to be very similar to *Phyllostomus.* One reasonable conclusion from these data is that average secretory activity does not in some simple way relate to diet in any of these species.

In striking contrast to *Pteronotus,* the parietal cells in *Artibeus* had extensive intracellular secretory canaliculi and open lumina (Fig. 14) that were most obviously comparable to published micrographs of parietal cells deliberately stimulated by pentagastrin or histamine from exogenous sources (Helander and Hirschowitz, 1972; Ito and Schofield, 1978). The fact that parietal cells in fasted *Artibeus* seem to maintain an exceptional level of secretory activity is of interest because our ultrastructural data thus correlate with earlier histological analysis (Forman, 1972). What would account for a high level gastric acid secretion in fasted *Artibeus*? Why would parietal cells in a fasted frugivorous bat seem to be in an unusually active state, while those in a fasted insectivorous species would be unusually quiescent? These questions obviously remain to be elucidated by future investigations.

Mucous Neck Cells

In addition to differences in parietal cell ultrastructure, *Pteronotus* and *Artibeus* also differ greatly in mucous neck cell populations (see Fig. 2). As pointed out previously by Forman (1972), mucous neck cells, which are thought to produce protective mucins (Stachura et al., 1981), are virtually absent in *Artibeus.* Our ultrastructural analysis confirms this histological observation; mucous neck cells in *Artibeus* are present but extremely sparse, small in volume, and typically contain relatively little product (Fig. 14). One possible explanation advanced by us is that large numbers of highly active parietal cells and large numbers of mucous neck cells might be mutually exclusive. We base this hypothesis on 1) experimental evidence showing that glucagon inhibits both basal and stimulated acid secretion while stimulating mucous neck cell activity (Wilson et al., 1972; Stachura et al., 1979); 2) the possibility that both parietal and mucous neck cells are derived from the same population of morphologically undifferentiated stem cells (Chen and Withers, 1975); and 3) the fact that *Pteronotus* and *Phyllostomus,* which have relatively few parietal cells, also have extremely abundant mucous neck cells (Fig. 2).

The mucus-producing cells of the stomach are an extremely complicated subject because several variables are involved. Firstly, it is clear from histochemical studies that a variety of chemically distinct "mucins" are produced by different cells (Jennings and Florey, 1956; Forman, 1972). Secondly, mucous neck and surface epithelial mucous cells quite possibly arise from different stem cell sources (Chen and Withers, 1975). Thirdly, mucous neck cells are replaced by morphologically undifferentiated cells that possibly produce a series of chemically distinctive mucins during the course of their lifespan (this could account for staining differences along a gastric gland within one individual).

Forman (1972) found that "mucus" production was greater in *Pteronotus* and in *Phyllostomus* than in *Carollia* and much greater in all of these than in *Artibeus.* In *Phyllostomus discolor,* Forman (1972) found the greatest mucus reactivity to PAS (periodic acid Schiff), toluidine blue O, and Alcian blue, and concluded that ". . . the omnivorous diet and seemingly ravenous feeding habits . . . evidently require abundant surface mucus to replenish a rapid loss of large quantities of escaping chyme." Mucous neck cells in *Pteronotus* generally reacted in a similar way, whereas *Carollia* displayed a notably weaker, less broad reactivity (Forman, 1972). Very little mucus apparently is produced in the gastric fundus of *Artibeus* and, furthermore, the mucous neck cells stain only weakly with PAS and Steedman's Alcian blue and lack metachromasia with toluidine blue (Forman, 1972).

In terms of ultrastructure of mucous neck cells, the histochemical data provide a basis for interspecific comparisons. In our present TEM analysis, specific differences in the simple abundance of mucous neck cells and cell product were obvious (Figs. 2, 16, 17, 18). Additionally, interspecific ultrastructural differences in secretory product most certainly suggest very real differences in the chemistry of the product synthesized and assembled in these particular cells. Although *Pteronotus* and *Phyllostomus* display very similar histochemical staining reactions, the mucous neck cell product in *Pteronotus* differs in ultrastructural appearance from that found in the phyllostomids, including *Phyllostomus* (Figs. 16, 18). This finding is significant because it illustrates an instance in which interfamilial histochemical similarities are not consistent with ultrastructure, which, in turn, reflects systematic relationships.

The question of gastric protection in the stomach of frugivores such as *Artibeus* is especially interesting in view of the evolution of an entire subfamily of phyllostomids that have similar, somewhat specialized stomachs (Forman, 1972, 1973). Even the glands of Brunner, which could protect the small intestine, are reduced or absent in stenodermatines (Forman, 1973; Forman et al., 1979). One explanation could be that gastric cytoprotection in *Artibeus* results more from surface-active phospholipids than from mucus secretions. Indeed, in a recent investigation acid-induced surface necrosis was shown to be significantly reduced in rats by treatment with such phospholipids (Lichtenberger et al., 1983). Another hypothesis, first advanced by Studier et al. (1983*a*), is that evolution of stenodermatine stomachs might in some way be related to salivary gland secretions. Data from intensive experimental research on rodents have demonstrated an apparent relationship between salivary gland production of EGF (epithelial growth factor) and gastric parietal cells as well as the general use of the digestive tract for absorption of both NGF (nerve growth factor) and EGF (Murphy et al., 1980; Gonzalez et al., 1981). Experimental studies such as these help establish that the stomach can be a target for salivary secretions and also a pathway for salivary gland products to reach the circulatory system.

The parotid salivary glands in *Artibeus* (and in other stenodermatines) are remarkable in that these glands typically are extremely large (Phillips et al., 1977). Beyond size, the secretory product of the parotid glands apparently differs significantly from that in other bats, at least to judge from available histochemical data (Wimsatt, 1956). The ultrastructural appearance of the secretory product in parotid acinar cells in *Artibeus* is unusual in that the granules are large and pale and have a small accumulation of electron dense material (Phillips et al., 1977). In summary, the product is neither mucoid nor rich in enzymes but apparently is watery (Wimsatt, 1956) and, therefore, the possibility exists that hydration of the product is an osmoregulatory feature associated with ionic concentration. Such a product could be high in bicarbonates, which are released in exchange for chloride ions during salivary secretion (Dawes, 1978; Izutsu, 1981). Consequently, a watery, buffered parotid saliva produced in copius amounts by the extremely large parotid salivary glands in *Artibeus* could help explain how the gastric mucosa is protected (Studier et al., 1983*a*). Co-evolution of parotid salivary glands and stomachs in stenodermatines in turn could explain the extremely large size of the parotid salivary gland and the apparently unique parotid gland product.

Studier et al. (1983*a*) also thought that copious mucus production by the "salivary glands" (presumably the submandibular and sublingual because the extremely large parotid is not mucoid) could buffer gastric secretions. To our knowledge, however, none of the salivary glands in *Artibeus* secretes copious amounts of mucus. Indeed, the submandibular glands consist of abundant serous cells with sero-mucoid demilunes (Phillips et al., 1977; Tandler et al., 1983). Consequently, the possible role of mucus remains unclear.

In conclusion, microchiropteran bats, and particularly the Phyllostomidae, clearly are an outstanding model for analysis of evolution at the cellular level. Perhaps no other group of mammals has undergone such remarkable divergence in cell and tissue features while retaining at the same time enough genic and phenotypic similarity to be regarded as closely "related." Insofar as comparative ultrastructure of homologous cells is concerned, it is apparent that such data have considerable value to potential experimental analyses of functional divergence and, ultimately, to development of a more sophisticated understanding of how cell types have evolved. The systematic value of comparative ultrastructure is not so obvious. Nevertheless, patterns found by us in parietal cells and, especially, in mucous cells certainly suggest that once more data are available, cellular comparisons may very well help unravel some complex systematic problems.

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SPECIMENS EXAMINED

The specimens used in this investigation were as follows: *Pteronotus parnelli*—Brokopondo: 3 km SW Rudi Kappelvliegveld, 320 m, 3°46'N, 56°10'W (CM 63972 ♀, CM 63974 ♀). *Phyllostomus hastatus*—Brokopondo: 1 km N Rudi Kappelvliegveld, 300 m, 3°48'N, 56°08'W (CM 64035 ♀). *Phyllostomus elongatus*—Brokopondo: 1 km N Rudi Kappelvliegveld, 300 m, 3°48'N, 56°08'W (CM 64019 ♂). *Carollia perspicillata*—Brokopondo: 1 km N Rudi Kappelvliegveld, 300 m, 3°48'N, 56°08'W (CJP 3621 ♂, CJP 3631 ♀); Saramacca: Tafelberg, Geyskes Creek, 700 m, 3°56'N, 56°10'W (CJP 3674 ♀).

Artibeus concolor—Brokopondo: Rudi Kappelvliegveld, 320 m, 3°47′N, 56°08′W (CM 63791 ♀). *Artibeus lituratus*—Brokopondo: Rudi Kappelvliegveld, 320 m, 3°47′N, 56°08′W (CM 64188 ♂).

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ANNOTATED CHECKLIST OF THE MAMMALS OF KENYA. I. CHIROPTERA

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ABSTRACT

A list of 95 species in nine families of bats known by Kenyan specimens is annotated with records of museum specimens or with references to the literature. A gazetteer of collecting localities is included.

INTRODUCTION

Although a series of books has been published recently dealing with East African mammals (Kingdon 1971, 1974*a,* 1974*b,* 1977, 1979, 1982*a,* 1982*b*), for those persons studying the taxonomy and biogeography of small mammals such as insectivores, bats, and rodents, reference must be made to the older, primary literature for identifications and distributional records. We are attempting to synthesize the pertinent literature in the form of annotated checklists. This is the first of these checklists, dealing specifically with bats. It is an attempt to update the checklist published by Harrison (1961). Knowledge of the taxonomy and geographic distribution of bats in Africa is increasing at a rapid rate. Consequently numerous taxonomic changes and many new distributional records are included in this checklist. Two species (*Myonycteris relicta* Bergmans, 1980, and *Chalinolobus kenyacolus* Pe-

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terson, 1982) have been described from Kenya since the appearance of the last checklist (Harrison, 1961).

The distributional records in the checklist are based on two sources—records from museum voucher specimens and records from the literature. We have tried as much as possible to include literature records where actual specimens were involved and not to include records based on inference from distributions of the species. Thus the lists of mammals given by Williams (1967) for the Kenyan national parks and game reserves have generally not been included unless a specific location within the park is given.

The format remains essentially as that used by Harrison (1961), including brief remarks where necessary. Because we feel it more important to know the location of a voucher specimen that constitutes a locality record, we have retained the museum reference as much as possible for those records published by Harrison (1961). Specimen records are included from the following museums. Acronyms are listed in parentheses for each of them.

Academy of Natural Sciences, Philadelphia (ANSP)
American Museum of Natural History, New York (AMNH)
British Museum (Natural History), London (BMNH)
Carnegie Museum of Natural History, Pittsburgh (CM)
Field Museum of Natural History, Chicago (FMNH)
Forschungsinstitut und Natru-Museum Senckenberg, Frankfurt a.m. (SMF)
Harrison Zoological Museum, Seven Oaks (HZM)
Michigan State University, The Museum, East Lansing (MSU)
National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM)
National Museums of Kenya, Nairobi (NMK)
Natural History Museum of Los Angeles County, Los Angeles (LACM)
Naturhistorisches Museum Wien, Vienna (NMW)
R.E. Mumford Private Collection, Purdue University, West Lafayette (REMC)
Ryksmuseum van Natuurlijke Histoire, Leiden (RMNH)
Royal Ontario Museum, Toronto (ROM)
Zoological Museum, Amsterdam (ZMA)

The distributional records included in the checklist are by no means complete. Nevertheless, it is our sincere hope that the information provided will stimulate additional interest and research on the bat fauna of Kenya.

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Additionally, Friedericke Spitzenberger, Paul Bates and David L. Harrison, and Dieter Kock graciously shared with us a list of the locality records for specimens from Kenya included in the mammal collections in Vienna, Seven Oaks, and Frankfurt a.m., respectively. C. Brian Robbins allowed us to see parts of a manuscript concerning a revision of the African representatives of the genus *Scotophilus* and to include in the checklist the additional records of museum specimens from Kenya of *S. dinganii, S. nigrita,* and *S. borbonicus viridis* that he had examined. Dieter Kock supplied an extensive list of references including many from the parasite literature. Charles O. Handley, Jr., supplied photocopies of numerous old and difficult to find articles. We thank them for their generosity and contributions.

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CHECKLIST

Order Chiroptera

Suborder Megachiroptera

Family Pteropodidae

Genus ***Eidolon*** Rafinesque, 1815

Eidolon helvum helvum (Kerr, 1792)

Vespertilio vampyrus helvus Kerr, 1792. Linnaeus' Animal Kingdom, 1:pt. 1, p. xvii, 91. No type locality given but designated as Senegal by Andersen, 1907:504.

Records.—Kaimosi (NMK); Sabatia (Kock, 1978*a*:118, NMK); Mbale (NMK); Mukumu-Kakamega (NMK); Cherangani (NMK); 20 mi S Mombasa (Coe and Isaac, 1965: 124); Mombasa (NMK); Kavirondo (Copley, 1950:16, Harrison, 1961:286); Ruiru (Theodor, 1957:532); Kakamega (Williams, 1967:171, Kingdon, 1974:150); Kaimosi (Bramwell, 1947:57; Radford, 1947:309); Ndurugu River, Ruiru Dist., 8000 ft (Hopkins and Rothschild, 1956:192); Meragoli, N. Kavirondo (Bramwell, 1947: 57); Kimingini (Bramwell, 1947:57).

Remarks.—A few specimens have been retrieved from the west slope of the Aberdares, Kabete (electrocuted), Chyulus, and northern shore of L. Natron (embedded in soda ash). No roosting colonies are known from these localities so it is likely the individuals were enroute to some other destination. Start (1972:71) doubts the record of this species reported by Coe and Isaac (1965:124).

Genus *Rousettus* Gray, 1821

Rousettus (Rousettus) aegyptiacus leachii (A. Smith, 1829)

Pteropus leachii A. Smith, 1829. Zool. J. 4:433. Cape Town, South Africa.

Records.—Mt. Elgon (BMNH, HZM, NMK, NMW, AMNH) Bahati, nr. Nakuru (AMNH, Theodor, 1955:204, Kock, 1978*b*:207); Shimoni (BMNH, CM, SMF, Falcoz, 1923:549, Kulzer, 1959:15, Kock, 1978*b*:207); Chyulu Hills (NMK, Simons, 1974:251, Kock, 1978*b*:207); Karen (NMK, Kock, 1978*b*:207); Sokoke Forest (NMK, Kock, 1978*b*: 207); Ngombeni Caves (NMK, Dulic and Mutere, 1977:232); Narok (CM); nr. Tiwi (Whitaker and Mumford, 1978:634); Kitumu Cave, Mt. Elgon National Park (SMF, Kock, 1978*b*:207); Vipingo Caves, N Mombasa (Williams, 1966:30); Vipingo, 20 mi N Mombasa (Start, 1972:71); Mida, 40 mi N Vipingo (Start, 1972:71); 30 mi N Mida on Malindi-Garsen Road (Start, 1972:72).

Remarks.—The locality recorded as Similani Cave, about 40 km S Mombasa, by Dulic and Mutere (1977:232), is the same as Ngombeni Caves. Similani Cave is a local name for the coastal cave but Ngombeni is used for the larger area.

Rousettus (Stenonycteris) lanosus kempi (Thomas, 1909)

Rousettus kempi Thomas, 1909. Ann. Mag. Nat. Hist. (8)4:543. Kirui, 6000 ft, Mt. Elgon, Kenya.

Records.—Kirui, Mt. Elgon (Thomas, 1909*b*:543); Mt. Elgon, 8000 ft (Granvik, 1924: 9); Kiega Hill, Meru Dist. (HZM); Kiambu, nr. Nairobi (BMNH); Limuru (NMK, Kock, 1978*b*:207); Kathama Kangundo Escarpment (NMK); Menengai Crater, Nakuru (NMK, USNM); nr. Nakuru (Whitaker and Mumford, 1978:634); Mount Menengai (Theodor, 1955:227, 1957:532, Keegan, 1956, Bergmans, 1982:161); Mt. Elgon (Copley, 1950:16).

Rousettus (Lissonycteris) angolensis ruwenzorii Eisentraut, 1965

Rousettus angolensis ruwenzorii Eisentraut, 1965. Bonn. Zool. Beitr., 16:3. Ruwenzori East (Mubuku Valley), Uganda.

Records.—SE slopes of Mt. Elgon (HZM); Lirandha Hill, Kakamega (HZM); Karura Forest, Nairobi (HZM, NMK, Harrison, 1960*a*:67, Kock, 1978*b*:207); Kakamega (NMK, SMF, USNM, Kock, 1978*b*:207); 20 mi SW Kitale (USNM); Ngangao Forest, Taita Hills (USNM); Saboti (USNM); Chyulu Hills (NMK); Sokoke Forest (NMK, Kock, 1978*b*: 207); Mt. Elgon Caves (NMK, Kock, 1978*b*:207); Kakamega Forest (Zimmerman, 1972: 270); Mnenenka blow holes, Chyulu Hills (NMK, Kock, 1978*b*:207); Kiminini Caves, Mt. Elgon (Simpson et al., 1968:439).

Genus *Myonycteris* Matschie, 1899

Myonycteris relicta Bergmans, 1980

Myonycteris relicta Bergmans, 1980. Zool. Med., 55(14):173. Mukanda River, Lukore area, Shimba Hills, Kenya.

Records.—Mukanda River, Lukore area, Shimba Hills (Bergmans, 1980:173).

Genus ***Hypsignathus*** H. Allen, 1861
Hypsignathus monstrosus H. Allen, 1861

Hypsignathus monstrosus H. Allen, 1861. Proc. Acad. Nat. Sci. Philadelphia, p. 157. "West Africa" = Gabon.

Records.—Shikusa, nr. Kakamega (Fleetwood, 1962:203, NMK); Kakamega Forest (Williams, 1967:172); Kaimosi (Kingdon, 1974:173).

Genus ***Epomophorus*** Bennet, 1836
Epomophorus crypturus Peters, 1852

Epomophorus crypturus Peters, 1852. Reise nach Mossambique, Saugethiere, p. 26, pl. 5; pl. 13; f. 1–6. Tette, Mozambique.

Records.—Mombasa (Peters, 1877:913).

Epomophorus wahlbergi haldemani (Halowell, 1846)

Pteropus haldemani Halowell, 1846. Proc. Acad. Nat. Sci. Philadelphia, 3:52. West Africa.

Records.—Smara, Mt. Kenya (Andersen, 1912*a*:527); Fort Hall, Mt. Kenya (Andersen, 1912*a*:527); Nyeri (HZM); Namanga (HZM, BMNH); Cherangani Hills (BMNH); Tinderet Forest, Songhor, Molo (HZM); Kakamega (HZM); Lamu (Allen and Lawrence, 1936:45); Taita Hills (Hollister, 1918:71); Vasco da Gama Pt., Malindi (HZM); Diani Beach (SMF); 10 km S Diani Beach (SMF); Malindi (AMNH, BMNH, CM, NMK, Matschie, 1899:51, Andersen, 1912*a*:525, Kock, 1969:19); Kitui (Andersen, 1912*a*:525); Kikambala, 25 km N Mombasa (Wickler and Seibt, 1976:346, SMF); Mombasa (Peters, 1880:831, Matschie, 1899:51, Andersen, 1912*a*:525, Theodor, 1968:321, 370, Kock, 1969:19, SMF); Takaungu (Matschie, 1899:51, Andersen, 1912*a*:525); Meru River (Allen, 1911:322); Chyulu Hills (NMK); Nairobi (HZM, NMK, Dulic and Mutere, 1973*b*: 389, Kingdon, 1974:158, Dulic and Mutere, 1977:232); Karen (NMK, SMF); Karura Forest, Nairobi (Loveridge, 1922:44, NMK); Kabete (NMK, SMF, Kock, 1969:19); Ruaraka, N of Nairobi (SMF); Yala River (NMK); Kericho (NMK); Donyo Sabak (NMK); Baricho (NMK); Garabani (NMK); Athi River (NMK); Kijabe (NMK); Masabubu, Garissa (NMK, AMNH); Mt. Elgon Caves (NMK); Endau Mt., Kitui Dist. (NMK); Endebess (NMK); Narok (CM); O1 Messoti, Loita Hills (CM); Hunter's Lodge, nr. Makindu (Peterson and Nagorsen, 1975:2); Upper Luazomela River, nr. Meru (Lonnberg, 1912: 47); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Kakamega Forest (Zimmerman, 1972:270).

Remarks.—The relationship in East Africa between the nominate subspecies and the more western and smaller *E. w. haldemani* requires additional study. The *Epomops franqueti* reported from Hunter's Lodge by Peterson and Nagorsen (1975:2) was a misidentified *Epomophorus wahlbergi* (Eger, personal communication). Williams (1967) recorded *E. franqueti* as occurring in the Massai-Mara Game Reserve, Marsabit National Reserve, Meru Game Reserve, Samburu-Isiolo Game Reserve, and Tsavo National Park. Presumably the inclusion of this species in the fauna of these parks and game reserves is also in error.

Epomophorus labiatus anurus Heuglin, 1864

Epomophorus anurus Heuglin, 1864. Nova Acta Acad. Caes. Leop.-Carol. 31(7):12. Bongo, Bahr el Ghazal, Sudan.

Records.—Malindi (Dobson, 1880:171, Peters, 1880:831); Turquel (Andersen, 1912*a*:534); Kirui, Mt. Elgon (Andersen, 1912*a*:534); Mumias, Mt. Elgon (BMNH); Patta Island (NMK); Barberton's farm, Kitale (USNM); Kongelai, West Pokot (USNM); Kibwezi (AMNH); Namanga (AMNH); 12 mi W Kitale (USNM); Katilo (BMNH); Nairobi (NMK, Verschuren, 1980:5); Sebaki River (Dollman, 1914*a*:88); nr. Tiwi (Whitaker and Mumford, 1978:634).

Epomophorus minor Dobson, 1880

Epomophorus minor Dobson, 1880. Proc. Zool. Soc. London, p. 715. Zanzibar.

Records.—Turquel (Thomas, 1891:182); Kanyangaren, West Pokot (NMK); Shombole (NMK); Patta Island (NMK); Ngenyi, Samburu Dist. (NMK); Wei-Wei River, Sigor (BMNH); Olebortoto River (BMNH); Southern Guaso Nyiro (Dollman, 1914*b*:308, BMNH); Nakuchett, 16 mi NNE Kacheliba (USNM); 12 mi W Kitale (USNM); Kitale (USNM); Nyeri (Harrison, 1961:287); Kaimosi (Allen and Lawrence, 1936:46); Masabubu, Garissa (AMNH); Baringo (Lonneberg, 1918:174).

Remarks.—Allen and Lawrence (1936:46) regarded *E. minor* as a subspecies of *E. labiatus* and *E. anurus* as a full species, but Kock (1969:18–24) and Largen et al. (1974:226) considered *E. minor* as a full species and *E. anurus* as a subspecies of *E. labiatus.* Koopman (1975:363–366) followed this arrangement but observed the need for further taxonomic study into the *anurus-labiatus-minor* complex.

Genus ***Micropteropus*** Matschie, 1899

Micropteropus pusillus (Peters, 1868)

Epomophorus pusillus Peters, 1868. Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 870 (for 1867). Gambia.

Records.—South Kavirondo (Copely, 1950:16, Harrison, 1961:287); Meru River (Allen, 1911:322); Barberton's farm, Kitale (USNM).

Suborder Microchiroptera

Family Rhinopomatidae

Genus ***Rhinopoma*** E. Geoffroy, 1818

Rhinopoma hardwickei macinnesi Hayman, 1937

Rhinopoma cystops macinnesi Hayman, 1937. Ann. Mag. Nat. Hist., (10)19:530. Bat Island, near Central Island, Lake Turkana, Kenya.

Records.—Bat Island, Lake Turkana (Hayman, 1937:530), Lothagam Hill, West shore Lake Turkana (NMK); Central Island, Lake Turkana (NMK, Williams, 1965:21, 1967:174); Gibralter Island, Lake Baringo (NMK, Kingdon, 1974:217); Lodwar (NMK); Kampi ya Samaki (USNM); Lesukut Island, Lake Baringo (Kock, 1969:46, HZM, SMF); Lake Baringo (Williams, 1967:174); Ferguson's Gulf (Williams, 1967:174); Lokomorinyang (Williams, 1967:174).

Family Emballonuridae
Genus **Coleura** Peters, 1867
Coleura afra afra (Peters, 1852)

Emballonura afra Peters, 1852. Reise nach Mossambique, Saugethiere, p. 51, pl. 12–13. Tette, Mozambique.

Records.—Voi (Hollister, 1918:72, NMK); Diani Mosque, South Mombasa (HZM); Ngombeni, 11 km S Mombasa (Kulzer, 1959:18, Fain, 1961; HZM, NMK, SMF); Msambweni (NMK); Kilifi (NMK); Gede (NMK); Shimoni (Kulzer, 1959:18, NMK); Tschaka (Peters, 1880:832, Dobson, 1880:193); Ferguson's Gulf (CM); Karibiti (CM); Tsavo (AMNH); 10 mi E Mwingi (AMNH); Fort Jesus, Mombasa (SMF); Lake Baringo (Kingdon, 1974:204).

Genus **Taphozous** E. Geoffroy, 1818
Taphozous (Taphozous) hildegardeae Thomas, 1909

Taphozous hildegardeae Thomas, 1909. Ann. Mag. Nat. Hist., (8)4:98. Rabai, Mombasa Dist., Kenya.

Records.—Rabai (Thomas, 1909*a*:99, NMK, NMW); Shimoni (Thomas, 1909*a*:99, Falcoz, 1923:533, Williams, 1966:30, A. Pye, 1973:84, HZM, BMNH, NMK, SMF); Msambweni (NMK); Ngombeni, 11 km S Mombasa (Kulzer, 1959:19, Kock, 1974*a*:70, NMK, SMF); Chanler's Falls (NMK); Masabubu, Tana River (NMK); Gede (NMK); Ukunda (Kock, 1974*a*:70, NMK); Tiwi (Kock, 1974*a*:70, NMK); Kilindini, in Mombasa (Kock, 1974*a*:70); Ngomeni (Kock, 1974*a*:70); Manda Island (Voeltzkow, 1923).

Remarks.—Kock (1974*a*:70) questioned whether the Ngomeni record was from Kenya or Tanzania. It is probably from the village of Ngomeni on the Ras Ngomeni peninsula. However, another village named Ngomeni exists north of the Thika-Garissa road at approximately 0°38′S, 38°25′E.

Taphozous (Taphozous) perforatus haedinus Thomas, 1915

Taphozous perforatus haedinus Thomas, 1915. Jour. Bombay Nat. Hist. Soc., 24:62. Chanler's Falls, Eusso Nyiro, Kenya.

Records.—Chanler's Falls (NMK, Thomas, 1915:63, Copely, 1950:18, Harrison, 1958: 145); Lamu Island (Allen and Lawrence, 1936:46); Masabubu, Tana River (NMK); Central Island, Lake Rudolf (NMK); Maungu (CM); Sokoke Forest (CM); Karibiti (CM).

Taphozous (Taphozous) mauritianus E. Geoffroy, 1818

Taphozous mauritianus E. Geoffroy, 1818. Description de l'Egypte, 2:127. Mauritius.

Records.—Malindi (Peters, 1880:831); Turkwel River (Dollman, 1914*b*:309); Kisumu (Hollister, 1918:73); Nairobi (HZM, NMK, Williams, 1965:21); Bulessa (De Beaux, 1923:91); Galana Ranch (NMK); Mombasa (BMNH); Takaungu (BMNH); Nuu Kitui (NMK); Aruba Lodge, Tsavo National Park, Voi (HZM, NMK, SMF); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); nr. Mt. Suswa (NMK).

Taphozous (Liponycteris) hamiltoni Thomas, 1920

Taphozous hamiltoni Thomas, 1920. Ann. Mag. Nat. Hist., (9)5:142. Mongalla, Equatoria Province, Sudan.

Records.—Central Island, Lake Turkana (Kock, 1981*a*:321, NMK, SMF); Kaitherin Hills, 40 mi W north end Lake Turkana (St. Leger, 1937:525, Koopman, 1975:372–373, BMNH).

Remarks.—The Kaitherin Hills have been included in Sudan (Kock, 1969:86, Koopman, 1975:372–373, Kock, 1981*a*:321) as often the northern boundary of Kenya in this region is given as a straight line at approximately 4°37′N, but there is a region reaching north of that line in this area to over 5°N belonging to Kenya but administered by the Sudan.

Taphozous (Liponycteris) nudiventris nudiventris Cretzschmar, 1826

Taphozous nudiventris Cretzschmar, 1826. Ruepell's Atlas Reise Nord-Ost Afrika, Saugethiere, p. 70. Giza, Egypt.

Records.—Lodwar (St. Leger, 1937:525, BMNH); Karsa, East Lake Turkana (NMK).

Taphozous (Saccolaimus) peli (Temminck, 1853)

Saccolaimus peli Temminck, 1853. Esquisses Zool. sur la côte de la Guinee, p. 82. Boutry River, Ghana.

Records.—Nandi Forest (Hayman and Hill, 1971:16, BMNH); Kaimosi (Kingdon, 1974:211).

Family Nycteridae

Genus *Nycteris* Cuvier and E. Geoffroy, 1795

Nycteris hispida aurita (Andersen, 1912)

Petalia aurita Andersen, 1912. Ann. Mag. Nat. Hist., (8)10:547. Kilifi, Kenya.

Records.—Kitui (Peters, 1878:195, Dobson, 1880:182); Sala, Tsavo National Park (Kock, 1969:89, SMF); Nairobi (Hollister, 1918:74, Koopman, 1975:378, HZM, NMK); Tana River (True, 1893:602, Hollister, 1918:74, Koopman, 1975:378); Marsabit Road (Hollister, 1918:74, Koopman, 1975:378); Ferguson's Gulf, Lake Turkana (Harrison, 1957*b*:25, Howell, 1974:14, HZM); Lodwar (St. Leger, 1937:525, BMNH); Mumias, Elgon (BMNH); Machakos (BMNH); Mt. Elgon (Granvik, 1924:10); Kaimosi (Allen and Lawrence, 1936:48, Koopman, 1975:378); Wema, Ngutana (Allen and Lawrence, 1936:48, Koopman, 1975:378); Shimba Hills (NMK); Stony Athi (NMK); Nakuru (NMK); Nginyang, nr. Lake Baringo (HZM); Makeri, Lower Tana River (AMNH); Voi (Koopman, 1975:378, AMNH); Masabubu, Garissa (Koopman, 1975:378, AMNH); Galma Galla, Garissa (Koopman, 1975:378, AMNH); Kilifi (Andersen, 1912*b*:547, Koopman, 1975:378, USNM); Athi River (USNM); Maungu (Andersen, 1912*b*:547); Njoro, north of Guaso Nyiro (Lonnberg, 1912:48); Central Island (Howell, 1974:14); Ijara (Percy et al., 1953:12); Leopard Rock, Meru National Park (SMF).

Remarks.—A study of geographic variation in *Nycteris hispida* in East Africa is needed.

Nycteris nana tristis Allen and Lawrence, 1936

Nycteris nana tristis Allen and Lawrence, 1936. Bull. Mus. Comp. Zool., 79:47. Kaimosi, Kakamega Dist., Kenya.

Records.—Yala River (Hollister, 1918:73); Kaimosi (Allen and Lawrence, 1936:47, NMK); Yala River, Kavirondo (Koopman, 1975:375, BMNH); Kakamega (HZM, SMF); Lake Naivasha (NMK).

Nycteris arge Thomas, 1903

Nycteris arge Thomas, 1903. Ann. Mag. Nat. Hist., (7)12:633. Efulen, Cameroon.

Records.—Yala River (Hollister, 1918:73); Yala River, Kavirondo (BMNH, NMK).

Nycteris thebaica labiata Heuglin, 1861

Nycteris labiata Heuglin, 1861. Nova Acta Acad. Caes. Leop.-Carol., Halle 29(8):5. Keren, Bogosland, Eritrea, Ethiopia.

Records.—Ndi (Peters, 1878:195); Taveta (Thomas, 1910:309); Archer's Post (De Beaux, 1923:91, NMK); Guaso Nyiro (Allen, 1911:323); Voi (Allen and Lawrence, 1936:49); Elgonyi (Allen and Lawrence, 1936:49); Kirui (Allen and Lawrence, 1936:49); Shimoni (CM, HZM, NMK); Nairobi (HZM, NMK); Magadi (HZM); Cherangani Hills (Ruxton, 1926:28); River Kerio Suk (Ruxton, 1926:28); Laldyka Hills, nr. Nanyuki (HZM); Machakos (BMNH); Tanganyiko, nr. Mombasa (BMNH); Kiambu, nr. Nairobi (HZM); Lake Naivasha (HZM); Rongai (HZM); Molo (HZM); Karen (HZM); Eldoret (HZM); Marsabit Mountains (HZM); Athi River (HZM); Gilgil (HZM); Yatta Escarpment (HZM); Mrima Hill (HZM); Lake Elmenteita (HZM, NMK); Elgon Caves (NMK); Ol Kalou (NMK); Langata Forest, Nairobi (NMK); Ngong Hills (NMK); Molo River (NMK); Konza (NMK); Soysambu (NMK); Malindi (NMK); Lokori, southern Turkana (NMK); Watamu (NMK); Mt. Suswa (Nader and Kock, 1983:10, NMK, SMF); Nakuru (NMK); Kibwezi (NMK); Kijabe (NMK); Msambweni Cave (NMW); Karibiti (CM); Juja Farm (Lonnberg, 1916:5); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Gedi National Park (Nader and Kock, 1983:10, SMF); 10 km S Diani Beach (Nader and Kock, 1983:10, SMF); Olorgesailie, 45 mi SW Nairobi (Hermsen and Jabbar, 1968:158); Bushwhacker's Safari Camp (Nader and Kock, 1983:10, SMF).

Nycteris macrotis luteola Thomas, 1901

Nycteris aethiopica luteola Thomas, 1901. Ann. Mag. Nat. Hist., (7)8:30. Kitui, Kenya.

Records.—Kitui (Thomas, 1901*c*:31); Frere Town (Loveridge, 1922:45); Mt. Kenya (BMNH); Mombasa (NMK, BMNH); Fort Hall (BMNH); 4.5 mi SW Ijara (AMNH); Kiamba, nr. Nairobi (FMNH); Kilifi (HZM); Lake Naivasha (NMK); Kaimosi (NMK); Diani (NMK); Voi (MCZ); Masabubu, Garissa (AMNH, CM); 1.5 mi E Masabubu (CM); Mazeras (Hollister, 1918:74, USNM); Ngombeni (USNM); Ribe (NMW); 10 km S Diani Beach (SMF).

Nycteris grandis Peters, 1865

Nycteris grandis Peters, 1865. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 358; for 1870 p. 906, 1871. "Guinea."

Records.—10 km S Diani Beach (Kock, 1981*a*:323, SMF).

Family Megadermatidae

Genus *Cardioderma* Peters, 1873

Cardioderma cor (Peters, 1872)

Megaderma cor Peters, 1872. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 194. Abyssinia.

Records.—Malindi (Dobson, 1880:182, Peters, 1880:831); Taveta (True, 1892:469); Chesegon, Cheptulel (NMK); Archer's Post (Hollister, 1918:81, De Beaux, 1923:97, NMK); Magadi (HZM, NMK); Tharaka, Meru Dist. (HZM); Tsavo Park (HZM); Lodwar (St. Leger, 1937:525, CM); Mombasa (Peters, 1877:913, Dobson, 1880:182, Theodor, 1956:385, 1957:495, BMNH, HZM); Pata Island (Voeltzkow, 1923); Voi (BMNH, NMK, SMF); Ndara Hills, Voi (BMNH); Eusso Nyiro (NMK, BMNH); Chanler's Falls (NMK, BMNH); Tiwi, 24 km S Mombasa (Kulzer, 1957:20, SMF); Diani (HZM); Ukunda, south of Mombasa (NMK); Ukazzi (HZM, SMF); Lamu Island (Allen and Lawrence, 1936:50, NMK); Garba Tula (NMK); Yatta Escarpment, Voi (NMK); Lorugumo, Turkana (NMK); Olorgesailie (Toschi, 1949:28, NMK); Habaswein (NMK); Shimoni (CM, NMK, Williams, 1966:30); Fisherman's Cave, Kenya Coast (NMK); Sokoke Forest (NMK); Ngombeni (USNM, Theodor, 1968:341, 344); Masabubu, Garissa (AMNH); Karibiti (CM); Maungu (CM); Sebaki River (Dollman, 1914*a*:88); Bushwhacker's Safari Camp, 10½ km N, 17 km E Kibwezi (Vaughan, 1976:228); Tsavo West National Park (Vaughan, 1976:230); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Ferguson's Gulf (Howell, 1974:14); Tseikuru (Theodor, 1968:341); Kilifi Creek (Theodor, 1968:341); Buffalo Springs (SMF); Tiwi beach (A. Pye, 1973:84).

Genus ***Lavia*** Gray, 1838
Lavia frons rex Miller, 1905

Lavia rex Miller, 1905. Proc. Biol. Soc. Washington, 18:227. Taveta, Kenya.

Records.—Taveta (True, 1892:469, Neumann, 1900:538, Miller, 1905:227, Thomas, 1910:309, Hollister, 1918:77); Nguruman Escarpment, West Lake Magadi (NMK); Stony Athi (NMK); Narok (NMK); Athi Station (Hollister, 1918:77); Kisumu (Hollister, 1918:77, NMK); Machakos Road (Hollister, 1918:77); Southern Guaso Nyiro (Hollister, 1918:77); Telek River, Sotik (Hollister, 1918:77); Ulukenia Hills (Hollister, 1918:77); Nanyuki (HZM); Narrosurra River (Kollman, 1914:319, 1919); River Kerio Suk (Lonnberg, 1918:175, Ruston, 1926:28); Lopi River (St. Leger, 1937:525); Lamu Coast (BMNH); Fort Hall (BMNH, NMK); Amala River (Dollman, 1914*b*:308, BMNH); Lorian Swamp (BMNH); Archer's Post (De Beaux, 1923:96); Bulessa (De Beaux, 1923:96); Kaimosi (Allen and Lawrence, 1936:50); Kitau, Manda Island (Allen and Lawrence, 1936:50); Mkonumbi (Allen and Lawrence, 1936:50); Golbanti (Allen and Lawrence, 1936:50); Garabani (NMK); Kanjira (NMK); Olorgesailie (Toschi, 1949:28, NMK); Isiolo (NMK, USNM); Cherangani, Kitale (NMK); Rusinga (NMK); Lamu Island (NMK); Uasso Nyiro (NMK); Potha, nr. Machakos (NMK); Nairobi (HZM, NMK); Katilia, South Turkana (NMK); nr. Garba Tula (CM); nr. Malca Muda (CM); Kacheliba (CM); Lodwar (CM); Maungu (CM); Lokitanyala Escarpment, 70 mi W (by road) Lodwar (CM); Masabubu, Garissa (AMNH); Marungu, Tsavo River (ANSP); Kindu Bay, Kisumu (NMK, Granvik, 1924:11); Mumias, Mt. Elgon (BMNH); Embu Boma (Kock, 1969:103); 2.5 mi SE Embu Boma (SMF); Meru (Allen, 1911:325); Northern Guaso Nyiro (Allen, 1911:325); Uasin Gishu Plateau (Allen, 1914:343); 30 mi NW Baringo (Dollman, 1914*b*:308); Kozibiri River (Dollman, 1914*b*:308); Ssio-Bay (Neumann, 1900:538); Kitui (Peters, 1878:195); Kau, Osi River (Dobson, 1880:182, Peters, 1880:831); Lake Hannington (Berger, 1910:336); North of Guaso Nyiro, below Chanler's Falls (Lonnberg, 1912:47); Lekiundu River (Lonnberg, 1912:47); Shella, Lamu Island (Allen and Loveridge, 1936:50); Yala River (NMK); Manda Island (Voeltzkow, 1923); Kipini, Tana River mouth (SMF); Baringo (Lonnberg, 1918:175); Ferguson's Gulf (Howell, 1974:14).

Family Rhinolophidae
Genus ***Rhinolophus*** Lacepede, 1799
Rhinolophus hildebrandtii Peters, 1878

Rhinolphus hildebrantii Peters, 1878. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 195, pl. 1, f. 1, 1a. Ndi, Kenya.

Records.—Ndi (Peters, 1878:196); Taita (Matschie, 1895:20, Andersen, 1905*b*:651); Machokos (Andersen, 1905*b*:651); Ulukenia Hills (Hollister, 1918:84, HZM); Fort Hall (BMNH); Voi (Allen and Lawrence, 1936:51, AMNH, MCZ); Athi River (NMK); Ol Donyo Sabuk (NMK); Diani (NMK); Northern Uaso Nyiro (NMK, USNM); Mt. Mbololo (NMK); Mt. Suswa (NMK); Mt. Elgon (NMK); Nakuru (NMK); Barberton Cave, Kitale (NMK, USNM); Koru, Legetet Hill Cave (USNM, NMK); Ribe (NMW); nr. Kibwezi (Vaughan and Bateman, 1980:70); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); nr. Mtito Andei (AMNH); Kimakia Cave, North Chyulu Hills (Simons, 1974:250); Koru (HZM, Theodor, 1968:316, 347).

Rhinolophus fumigatus exsul K. Andersen, 1905

Rhinolophus fumigatus exsul K. Andersen, 1905. Ann. Mag. Nat. Hist., (7)15:74. Kitui, Kenya.

Records.—Kitui (Andersen, 1905*a*:74); Loldyka Hills, nr. Nanyuki (HZM); Taveta (Thomas, 1910:309, BMNH); Shimoni (Kulzer, 1959:23); Marsabit Mountain (HZM); Kirui (Allen and Lawrence, 1936:52); Sokoke Forest (CM); Menengai, Nakuru (USNM); Lake Naivasha (USNM); Sultan Hamud (REMC); 10 mi W Chuka (Allen and Lawrence, 1936:52); Murka, Tsavo West National Park (SMF); Langata (SMF).

Rhinolophus clivosus keniensis Hollister, 1916

Rhinolophus keniensis Hollister, 1916. Smithsonian Misc. Coll., 66(1):2. West side Mt. Kenya, 7000 ft, Kenya.

Records.—Mt. Kenya (Hollister, 1916:2, Koopman, 1975:386); Mt. Elgon (HZM, NMK, AMNH, Granvik, 1924:11, Harrison, 1959:230, Koopman, 1966:157, 1975:386); Londiani (Harrison, 1959:230, HZM); Limuru, Nairobi (Harrison, 1959:230, HZM); Endebess, Kitale (HZM); Kaptagat (Harrison, 1959:230, HZM); Cherangani Hills (Ruxton, 1926:28, Koopman, 1975:386); Molo (HZM); Elmenteita (HZM); Bukwa, Mt. Elgon (BMNH); nr. Kimilili Forest Station, Mt. Elgon (Dulic and Mutere, 1974:32); Tanganyiko, nr. Mombasa (BMNH); Shimo na Kitu Cave, Rongai Valley (Rode, 1935:168); North Larogie (NMK); Elburgon (NMK); Gura River (NMK); Kericho (NMK); Mau Narok (Koopman, 1975:386, AMNH); Kitale (USNM); Nakuru (USNM); Mt. Elgon (Theodor, 1957:513, 1968:316, 347).

Remarks.—The pattern of distribution of subspecies of *R. clivosus* in East Africa is still confusing. Koopman (1975:285–286) discussed the geographic distribution of *R. c. acrotis* and *R. c. keniensis.* He (1975:286) noted the occurrence in south-central Kenya of specimens of intermediate size, between the large *R. c. keniensis* and small *R. c. acrotis,* and pointed out that each distinct population differed to a greater or lesser extent from every other. We have tentatively referred all records in Kenya to *R. c. keniensis* pending a detailed review of geographic variation in the species in East Africa.

Rhinolophus landeri lobatus Peters, 1852

Rhinolophus lobatus Peters, 1852. Reise nach Mossambique, Saugethiere, p. 41. Sena, south bank of Zambesi River, Sena Dist., Mozambique, restricted by Moreau et al., 1946:399.

Records.—Gelitja (Peters, 1880:831); Lake Naivasha (Hollister, 1918:84, HZM); Kijabe Station (Hollister, 1918:84); Nairobi (HZM, NMK, Williams, 1965:21); Malindi (Matschie, 1895:20); Taveta (Thomas, 1910:309, BMNH, NMK); Voi (AMNH, BMNH, NMK); Shimoni (NMK); Langata Forest, Nairobi (HZM, SMF, Kock, 1969:115); Ithundu (SMF); Murka, Tsavo West National Park (SMF); Marsabit (HZM); Mt. Elgon (NMK); Kapsakwany, Mt. Elgon (SMF); Kapretwa, 6500 ft, Mt. Elgon (Jobling, 1939:155, 1940: 404); Kapenguria (NMK); Mt. Suswa Caves (NMK, USNM); Athi River (USNM); Sulten Hamud (USNM); Ribe (NMK); Ukunda (HZM); Mombasa (Andersen, 1906*c*:189); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Kiminini Caves, Mt. Elgon (Simpson et al., 1968:439).

Rhinolophus deckenii Peters, 1868

Rhinolophus deckenii Peters, 1868. Monatsb. K. Preuss. Akad. Wiss. Berlin, p. 705 (for 1867). Coast of East Africa, probably opposite Zanzibar Island.

Records.—Tanganyiko, nr. Mombasa (Thomas, 1913:315, BMNH); Gebbi (BMNH); 6 mi S Kilifi (REMC); Shimoni (Kulzer, 1959:23); Well south of Mombasa (USNM).

Remarks.—Harrison (1961:289) re-examined the specimen recorded by Kulzer (1959:23) from Shimoni and identified it as *R. deckenii.* Although Hayman and Hill (1971:23) considered *R. deckenii* as a synonym of *R. clivosus,* we follow Koopman (1975:386) in considering it as a distinct species.

Rhinolophus simulator simulator K. Andersen, 1904

Rhinolophus simulator Andersen, 1904. Ann. Mag. Nat. Hist., (7)14:384. Mazoe, northern Mashonaland, Zimbabwe.

Records.—Mt. Elgon (Koopman, 1975:386); Kipsiryori Cave, 11 km WSW Kiminini (NMW); 25 mi NW Kitale (HZM); 20 mi W Kilifi (REMC).

Rhinolophus eloquens K. Andersen, 1905

Rhinolophus hildebrandti eloquens K. Andersen, 1905. Ann. Mag. Nat. Hist., (7)15:74. Entebbe, Uganda.

Records.—Lake Naivasha (Hollister, 1918:84); Nyuki River, northern Guaso Nyiro (Hollister, 1918:84, NMK); southern Guaso Nyiro River (Hollister, 1918:84); Mt. Elgon (Rode, 1935:168, Ferris and Usinger, 1939:16, NMW, HZM); Londiani (HZM); Thomson's Falls (HZM); 25 mi NW Kitale (HZM, SMF); Elmenteita (HZM); Kirui, Elgon (Allen and Lawrence, 1936:51, BMNH); Cherangani Hills (BMNH); Machakos (BMNH); Kitale (HZM); Elgonyi (Allen and Lawrence, 1936:51, CM); Kinangop (NMK); Koru (REMC); Mt. Mbololo, Voi (NMK); Narok (NMK); Diani (NMK); Diani Beach (SMF); Ribe (NMW); 10 km S Diani Beach (SMF); Kiminini Caves, Mt. Elgon (Simpson et al., 1968:439); Lion Hill, Lake Nakuru (SMF); Kapsakwany, Mt. Elgon (SMF); Ithundu, Chyulu Hills (SMF).

Family Hipposideridae

Genus ***Hipposideros*** Gray, 1831

Hipposideros caffer caffer (Sundevall, 1846)

Hipposideros caffer Sundevall, 1846. Ofversigt af Kongl. Svenska Ver.-Akad. Forhandl., Stockholm, 3(4):118. Near Port Natal [=Durban], South Africa.

Records.—Kiambu (Kulzer, 1959:23, HZM, SMF); Voi, Tsavo Park (NMK, HZM, AMNH); Londiani (HZM); Molo (HZM); Cherangani Hills (Ruxton, 1926:28); Archer's Post (Hollister, 1918:85); Juja Farm (Hollister, 1918:85); Kijabe (Hollister, 1918:85);

Nairobi (Hollister, 1918:85); Nairobi River (Hollister, 1918:85); Northern Guaso Nyiro (Hollister, 1918:85); Southern Guaso Nyiro (Hollister, 1918:85); Machakos (Andersen, 1906*b*:276, Granvik, 1924:12, BMNH); Kirui, Mt. Elgon (BMNH); Eldoret (HZM); Taveta (BMNH); Kitui (BMNH); Garbat Ullah, N.F.D. (BMNH); Elgonyi, Mt. Elgon (BMNH); Lion Hill, Lake Nakuru (SMF); Kakamega (HZM, NMK); Kilifi (HZM); Takaungu (Andersen, 1906*b*:277, BMNH); Fort Hall (Andersen, 1906*b*:276, BMNH); Ngombeni, 11 km S Mombasa (Kulzer, 1959:24, SMF); Langata Forest, Nairobi (HZM); Shimoni (Falcoz, 1923:536,548, Kulzer, 1959:23, J. Pye, 1972:324, NMK, SMF); Sobukia (HZM); Mt. Elgon Caves (NMK); Ngong (HZM, NMK); Nakuru (NMK); Mau Summit (NMK); Kabete (NMK); Karen, Nairobi (NMK, Vercammen-Grandjean, 1964: 318, Vercammen-Grandjean and Minter, 1964:488); North Cherangani Hills (CM); Karibiti (CM); Yatta Escarpment (HZM); Makindu (NMK); Koru, West Kenya (HZM, NMK); Nandi Hills (NMK); Nakuru (NMK); Ngulia Lodge, Tsavo National Park (HZM); Mt. Elgon (Granvik, 1924:12, NMK); Frere Town (Loveridge, 1923:693); Tsavo (Allen and Lawrence, 1936:52); El Dongo eb Urru, 415 mi up Mombasa-Uganda Railway (Andersen, 1906*b*:276); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981: 489); Langata (Vercammen-Grandjean, 1964:318, Vercammen-Grandjean and Minter, 1964:488, Theodor, 1968:344); Kakamega Forest (Zimmerman, 1972:270); Kericho (Theodor, 1957:513); Koru (Theodor, 1968:344).

Remarks.—Harrison (1961:290) mentioned the taxonomic confusion existing between *H. caffer* and *H. ruber* in Kenya. This situation requires detailed review from throughout the geographic range of the two species (Hayman and Hill, 1971:28–29, Koopman, 1975:391–393). We have attempted to separate the two species based on museum specimens and literature records but this is only a provisional arrangement. Geographic variation within *H. caffer* needs additional study in East Africa.

Hipposideros ruber centralis K. Andersen, 1906

Hipposideros caffer centralis K. Andersen, 1906. Ann. Mag. Nat. Hist., (7)17:275. Entebbe, Uganda.

Records.—Karibiti (CM); Lirandha Hill, Kakamega (HZM); Kilifi (HZM); Nairobi (Hollister, 1918:85); Kirui (Allen and Lawrence, 1936:53); Elgonyi (Allen and Lawrence, 1936:53); Mt. Elgon (Lawrence, 1964:3); 10 km S Diani Beach (SMF).

Hipposideros megalotis (Heuglin, 1861)

Phyllorhina megalotis Heuglin, 1861. Nova Acta Acad. Caes. Leop.-Carol., Halle, 29(8): 4. Bogos Land, Eritrea, Ethiopia.

Records.—Nakuru (Hayman, 1954:285, Williams, 1967:176, Kock et al., 1975:30, BMNH, HZM, NMK, SMF); Kinangop (Hayman, 1954:285, Williams, 1967:176, NMK); Lake Elementeita (HZM); Mt. Suswa (NMK, Kock et al., 1975:30); Njoro (Kock et al., 1975:30); Lake Baringo (Kock et al., 1975:30); 10 km W Nakuru (Kock et al., 1975:30); Exodus Cave, Mt. Suswa (SMF); Naivasha (Williams, 1967:176); Elmentaita (Williams, 1967:176).

Hipposideros cyclops (Temminck, 1853)

Phyllorhina cyclops Temminck, 1853. Esquisses Zool. sur la côte de Guine, p. 75. Boutry River, Ghana.

Records.—Yala River (Hayman, 1935:48, NMK); Kaimosi (NMK).

Hipposideros commersoni marungensis (Noack, 1887)

Phyllorhina commersonii marungensis Noack, 1887. Zool. Jb., 2:272. Qua Mpala in Marungu, West Shore of Lake Tanganyika, Zaire.

Hipposideros commersoni mostellum Thomas, 1904. Ann. Mag. Nat. Hist., (7)13:385. Tana River, Kenya.

Records.—Malindi (Dobson, 1880:179, Peters, 1880:831, Matschie, 1895:20, NMK); Tana River (Thomas, 1904*b*:386, Andersen, 1906*a*:41); Makueni, southeast of Machakos (NMK); Ngombeni, 11 km S Mombasa (NMK); Shimoni (Williams, 1966:30, Theodor, 1968:321, 344, 370, J. Pye, 1972:324, A. Pye, 1973:84, CM, HZM, NMK); Rabai (NMK); Ribe (NMK); Ngomeni, northeast of Mwingi (NMK); nr. Tiwi (Whitaker and Mumford, 1978:634); Bushwhacker's Safari Camp, 10½ km N, 17 km E Kibwezi (Vaughan, 1977: 238); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Galana River, Tsavo National Park (Williams, 1967:78).

Remarks.—Based upon ecological and behavioral differences (Aggundey, unpublished data) and a study of constant frequency echolocation signals (J. Pye, 1972), there seem to be two subspecies of *H. commersoni* occurring together in southeastern Kenya. We have tentatively referred the larger of these to *H. c. gigas.* Final resolution of the situation requires additional study.

Hipposideros commersoni gigas (Wagner, 1845)

Rhinolophus gigas Wagner, 1845. Arch. f. Naturgesch., 11 (1):148. Benguela, Angola.

Records.—Shimoni (J. Pye, 1972:324, A. Pye, 1973:84, NMK, NMW, SMF); Rabai (NMK, NMW).

Genus ***Cleotis*** Thomas, 1901

Cleotis percivali percivali Thomas, 1901

Cleotis percivali Thomas, 1901. Ann. Mag. Nat. Hist., (7)8:28. Takaungu, North of Mombasa, Kenya.

Records.—Takaungu (Thomas, 1901*c*:30); Kenya Coast (Kingdon, 1974:259).

Genus ***Triaenops*** Dobson, 1871

Triaenops persicus afer Peters, 1877

Triaenops afer Peters, 1877. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 913 (for 1876). Mombasa, Kenya.

Records.—Mombasa (Peters, 1877:913); Ngombeni Caves, 11 km S Mombasa (Kulzer, 1959:25, Dulic and Mutere, 1977:232, Kock and Felton, 1980:3, NMK, SMF); Shimoni (BMNH, NMK, J. Pye, 1972:324, A. Pye, 1973:84); Gede (NMK); Sokoke Forest (CM); nr. Tiwi (Whitaker and Mumford, 1978:634); Kilaguni Lodge, Tsavo National Park (Williams, 1967:78, J. Pye, 1972:324, Kingdon, 1974:261); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Kimakia Cave, North Chyulu Hills (Simons, 1974:250); Lake Baringo (Kingdon, 1974:261); Ferguson's Gulf (Kock and Felton, 1980: 3, NMK); Waa Beach, nr. Likoni (Kock and Felton, 1980:3); Ithundu Caves, Chyulu Hills (Kock and Felton, 1980:3); Maddo Erelle (Thomas, 1896:105).

Remarks.—The locality recorded as Similani Cave, about 40 km S Mombasa, by Dulic and Mutere (1977:232) is the same as Ngombeni Caves. Similani Cave is a local name for the coastal cave but Ngombeni is used for the larger area.

Family Vespertilionidae

Subfamily Vespertilioninae

Genus *Myotis* Kaup, 1829

Myotis bocagei hildegardeae Thomas, 1904

Myotis hildegardeae Thomas, 1904. Ann. Mag. Nat. Hist., (7)13:209. Fort Hall, Kenya.

Records.—Fort Hall (Thomas, 1904:209); Yala River (Hollister, 1918:89, NMK); Nyama Nyango, Eusso Nyiro (BMNH); Archer's Post (De Beaux, 1923:97); Ol Donyo Sabuk (NMK); Hoey's Bridge (CM); North Cherangani Hills (CM); nr. Tiwi (Whitaker and Mumford, 1978:634); Karen (SMF); Ruiru dam (NMK); Ruaraka (SMF).

Myotis tricolor (Temminck, 1832)

Vespertilio tricolor Temminck, 1832. In Smuts Enum. Mamm. Capensium, p. 106. Cape Town, Cape of Good Hope, South Africa.

Records.—Nakuru (HZM); 25 mi NW Kitale (HZM); Mt. Elgon (Rode, 1935:169, Williams, 1967:177); Tarasha River, Gilgil (NMK); Ol Donyo Sabuk (NMK); Kampi ya Samaki (ROM); Mt. Elgon Caves (NMK, NMW); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Mt. Suswa (SMF); Mt. Menengai (Theodor, 1957:471, 513, FMNH, SMF, USNM).

Remarks.—Rode (1935:169) reported a specimen from Mt. Elgon as *Myotis emarginatus* but Harrison (1961:292) re-identified it as *M. tricolor.*

Myotis welwitschii (Gray, 1866)

Scotophilus welwitschii Gray, 1866. Proc. Zool. Soc. London, 1866:211. Angola.

Records.—Endebess (Harrison and Fleetwood, 1958:111); Hoey's Bridge (ROM); Kakamega Forest (ROM); Trans Nzoia Dist. (NMK).

Genus ***Pipistrellus*** Kaup, 1829

Pipistrellus deserti Thomas, 1902

Pipistrellus deserti Thomas, 1902. Proc. Zool. Soc. London, 1902, 2:4. Murzuk, Libya.

Records.—Bulessa (De Beaux, 1923:97).

Remarks.—Koopman (1975:401) identified the Meru River record of Allen (1911:325) as *Pipistrellus nanus helios* and indicated that the records reported by Dollman (1914*b*:308) from Kenya and Uganda are *Eptesicus somalicus.* The Bulessa record requires a re-examination.

Pipistrellus nanus helios Heller, 1912

Pipistrellus helios Heller, 1912. Smithsonian Misc. Coll., 60(12):3. Merelle Water, 30 mi S Mt. Marsabit, Kenya.

Records.—Ndi (Peters, 1878:198, Dobson, 1880:187); Kitui (Peters, 1878:198, Dobson, 1880:187); Merelle Water, 30 mi S Mt. Marsabit (Heller, 1912:3, Hollister, 1918:90); Yala River (Hollister, 1918:89, NMK, USNM); Archer's Post (Hollister, 1918:90, De Beaux, 1923:97, HZM); Lakiundu River (Hollister, 1918:90, USNM); Northern Guaso Nyiro (Hollister, 1918:90, NMK); Fort Hall (BMNH, HZM); Kitale (HZM, NMK); Cherangani Hills (Ruxton, 1926:28); Mumias, Elgon (BMNH); Kamuuani (HZM); Kakamega (BMNH, CM, HZM); Nidji Hills, Voi (BMNH); Voi (HZM); Mazeras (BMNH); Muumandu Area, Machakos Dist. (HZM); Eusso Nyiro (BMNH, NMK); Kaimosi (Allen and Lawrence, 1936:53, CM); Mt. Mbololo (Allen and Lawrence, 1936:53, CM); Golbanti (Allen and Lawrence, 1936:53); Marsabit Lake (NMK); Mbooni, Machakos Dist. (NMK); Londiani (NMK); Maranda School, Nyanza (NMK); Ol Donyo Sabuk (NMK); Muhoroni (NMK); Ol Kalou (NMK); Bulessa (De Beaux, 1923:97); Ndoto (BMNH); Chanler's Falls (BMNH); Lodermoru Water (BMNH); Laisamis, Marsabit Road (BMNH); Nyama Nyango, Eusso Nyiro (BMNH); Lorian (BMNH); Meru River (Allen, 1911:325); Bushwhacker's Safari Camp, 10½ km N, 17 km E Kibwezi (Vaughan, 1976:240, 241, O'Shea, 1980:172); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Moshi-Voi (Demeter and Topal, 1982:46); Lake Jipe (Demeter and Topal, 1982:46); Muhoroni (Keegan, 1956); Ferguson's Gulf (Howell, 1974:14); Kalakol, Lake Turkana (Howell, 1974:14).

Pipistrellus nanulus Thomas, 1904

Pipistrellus nanulus Thomas, 1904. Ann. Mag. Nat. Hist., (7)14:198. Efulen, Cameroon.

Records.—8 mi SE Kakamega (USNM).

Pipistrellus kuhlii fuscatus Thomas, 1901

Pipistrellus kuhlii fuscatus Thomas, 1901. Ann. Mag. Nat. Hist., (7)8:34. Naivasha, Kenya.

Records.—Naivasha (Thomas, 1901*c*:34, Copley, 1950:19); Eldoret (HZM); Songhor, nr. Kisumu (HZM); Molo (HZM, USNM); Kabalolot Hill (Hollister, 1918:90); Sotik (Hollister, 1918:90); Nairobi (Hollister, 1918:90, Copley, 1950:19, USNM); Ngong (HZM, USNM); South Kiniangop (HZM); Engare Narok River (Hollister, 1918:90, USNM); Lake Naivasha (Hollister, 1918:90, USNM); Kitale (USNM); Kapsowat, Marakwet (HZM); Kilifi (USNM); Athi River, nr. Nairobi (FMNH); Lake Amboseli, nr. Namanga (AMNH); Makalia Falls, Lake Nakuru National Park (Schwann and Hikes, 1979:21); Eastern part Mt. Elgon National Park (SMF); Baharini Farm, Lake Nakuru (SMF); Nakuru (Copley, 1950:19).

Pipistrellus aero Heller, 1912

Pipistrellus aero Heller, 1912. Smithsonian Misc. Coll., 60(12):3. Mt. Garguez, Mathews Range, Kenya.

Records.—Mt. Garguez, Mathews Range (Heller, 1912:3); Marsabit Lake (BMNH); Ngong (NMK).

Pipistrellus rusticus marrensis Thomas and Hinton, 1923

Pipistrellus marrensis Thomas and Hinton, 1923. Proc. Zool. Soc. London, p. 249. Foothills of southern Jebel Marra, Dafur, Sudan, 4000 ft.

Records.—Kongelai, Suam River, West Pokot (Hill, 1976:629).

Pipistrellus rueppelli fuscipes Thomas, 1913

Pipistrellus fuscipes Thomas, 1913. Ann. Mag. Nat. Hist., (8)11:315. 60 mi W Entebbe, Uganda.

Records.—Naivasha (NMK).

Genus *Eptesicus* Rafinesque, 1820

Eptesicus tenuipinnis tenuipinnis (Peters, 1872)

Vesperus tenuipinnis Peters, 1872. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 263. Guinea.

Records.—Kisumu (HZM); Maji Moto, Baringo (USNM); Maragat, Baringo (USNM); West Lake Naivasha (USNM); Lake Baringo (Kock, 1981*b*:332, NMK).

Eptesicus rendalli phasma Allen, 1911

Eptesicus phasma Allen, 1911. Bull. Mus. Comp. Zool., 54:327. Meru River, Northern Guaso Nyiro, Kenya.

Records.–Nyama Nyango, Eusso Nyiro (BMNH); Archer's Post (Hollister, 1918:92, USNM); Meru River (Allen, 1911:327, Koopman, 1965:14, AMNH); Lakiundu River, Northern Guaso Nyiro (Hollister, 1918:92, USNM); Tana River (True, 1893:602, Hollister, 1918:92, USNM); Aruba Dam, Tsavo East (Kock, 1981*b*:333, SMF); Ribe (NMW); nr. Tiwi (Whitaker and Mumford, 1978:634); Chanler's Falls (BMNH); Kilaguni Lodge, Tsavo West National Park (A. Pye, 1973:84).

Eptesicus somalicus (Thomas, 1901)

Vespertilio minutus somalicus Thomas, 1901. Ann. Mag. Nat. Hist., (7)8:32. Hargeisa, Somalia.

Records.—Archer's Post (Hollister, 1918:92, USNM); Marsabit Road (Hollister, 1918: 92, USNM); Guaso Nyiro (Allen, 1911:327, NMK); Parklands, Nairboi (NMK); Ushingo (NMK); Kongelai (USNM); Kitale (HZM, USNM); Maji Moto, Baringo (USNM); Kozibiri River (Dollman, 1914*b*:308); Wei-Wei River (Dollman, 1914*b*:308); 50 mi S Moctow (Koopman, 1975:405); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Remarks.—This species and *E. capensis* are in need of taxonomic review. Voucher specimens for literature records, especially the older ones, should be re-examined.

Eptesicus loveni Granvik, 1924

Epetiscus (sic) *loveni* Granvik, 1924. Acta Univ. Lund, (2)21(3):12. Eastern Slopes of Mt. Elgon, 8000 ft, Kenya.

Records.—Eastern slopes, Mt. Elgon (Granvik, 1924:12).

Remarks.—The distinguishing characters of pointed ear and tragus for this species seem strange for an *Eptesicus*. The holotype of this species should be re-examined.

Eptesicus capensis (A. Smith, 1829)

Vespertilio capensis A. Smith, 1829. Zool. J., 4:435. "Cape," restricted to Grahamstown, Cape Province, South Africa, by Roberts, 1951:89.

Records.—Southern Guaso Nyiro (Hollister, 1918:92, 93); Mara River, nr. Tanzanian border (USNM); Karen, Nairobi (USNM); Barbeton's farm, Kitale (USNM); Maji Moto, Baringo (USNM); Jacaranda Station, nr. Ruiru, north of Nairobi (Kock, 1981*b*:332, SMF); Buffalo Springs (Kock, 1981*b*:332, SMF); Lukenya Mt. (FMNH); Cherangani Hills (HZM); Saboti, south of Mt. Elgon (ROM); Kabolet River, Cherangani Hills (ROM); Kakamega Forest (Zimmerman, 1972:270).

Genus ***Laephotis*** Thomas, 1901

Laephotis wintoni Thomas, 1901

Laephotis wintoni Thomas, 1901. Ann. Mag. Nat. Hist., (7)7:460. Kitui, Kenya.

Records.—Kitui (Thomas, 1901*b*:462); Namanga (Peterson, 1971*a*:885); Nyeri (HZM); Nanyuki, 23 mi W Mount Kenya (Peterson, 1973:601).

Genus ***Mimetillus*** Thomas, 1904

Mimetillus moloneyi (Thomas, 1891)

Vesperugo (Vesperus) moloneyi Thomas, 1891. Ann. Mag. Nat. Hist., (6)7:528. Lagos, Nigeria.

Records.—Cherangani (LACM); Selengai (NMK); Kakamega Forest (HZM); Ngomeni, Kitui (NMK); Kapsarok, Kericho (NMK); Kipsain River, Northeast Cherangani Hills (HZM); Wei-Wei River, Sigor, West Pokot (Start, 1969:223).

Genus ***Chalinolobus*** Peters, 1867

Remarks.—Ryan (1966) considered the taxonomic relationships of the African *Glauconycteris* Dobson, 1875, and Australasian *Chalinolobus* Peters, 1867. Koopman (1971) placed *Glauconycteris* as a subgenus of *Chalinolobus.* We follow that generic arrangment here. Peterson (1982) tentatively retained *Glauconycteris* as a distinct genus.

Chalinolobus (Glauconycteris) variegatus papilio (Thomas, 1905)

Glauconycteris papilio Thomas, 1905. Ann. Mag. Nat. Hist., (7)15:77. Entebbe, Uganda.

Records.—Garissa (HZM); Kakamega Forest (HZM).

Chalinolobus (Glauconycteris) argentatus Dobson, 1875

Chalinolobus argentatus Dobson, 1875. Proc. Zool. Soc. London, 1875:385. Cameroon Mountain, Cameroon.

Records.—Kiambu (HZM); Nandi Forest (BMNH); Nairobi (NMK); Karen (HZM, SMF); Kikuyu (Allen and Lawrence, 1936:53, CM, NMK, USNM); 20 mi SW Kitale (USNM).

Chalinolobus (Glauconycteris) kenyacolus (Peterson, 1982)

Glauconycteris kenyacola Peterson, 1982. Canadian J. Zool., 60(10):2521. Galole Road, 8.5 km N Garsen, Kenya (2°12′S, 40°05′E).

Records.—8.5 km N Garsen (Peterson, 1982:2521).

Chalinolobus (Glauconycteris) humeralis (J. A. Allen, 1917)

Glauconycteris humeralis J. A. Allen, Bull. Amer. Mus. Nat. Hist., 37:448. Medje, Zaire.

Records.—No specific locality (Peterson and Smith, 1973:7).

Genus *Nycticeius* Rafinesque, 1819
Nycticeius schlieffenii Peters, 1859

Nycticeius schlieffenii Peters, 1859. Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 223. Cairo, Egypt.

Nycticeius africanus G.M. Allen, 1911. Bull. Mus. Comp. Zool., 54:328. Meru River, Kenya.

Records.—Meru River (Allen, 1911:328); Archer's Post (De Beaux, 1923:100, Hollister, 1918:93); Kara River, Marsabit Road (Hollister, 1918:93); Lakiundu River (USNM, Hollister, 1918:93); Mount Lololokwi (Hollister, 1918:93); Quoy, Marsabit Road (Hollister, 1918:93); Lorian (BMNH); Lodwar (St. Leger, 1937:525); 30 mi NW Baringo (Dollman, 1914:309, BMNH); Mara River (BMNH); Nyama Nyango, Eusso Nyiro (BMNH); Chanler's Falls (BMNH, NMK); Maji Moto, Baringo (USNM); Kozibiri River (Dollman, 1914*b*:309); Wei-Wei River (Dollman, 1914*b*:309); Turkwel River (Dollman, 1914*b*:309); Mombasa (Anderson and de Winton, 1902:88); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Ferguson's Gulf (Howell, 1974:14); Mt. Kenya (Copley, 1950:21).

Genus *Scotoecus* Thomas, 1901
Scotoecus albofuscus woodi Thomas, 1917

Scotoecus woodi Thomas, 1917. Ann. Mag. Nat. Hist., (8)19:280. Chiromo, 200 ft, Malawi.

Records.—nr. Tiwi (Whitaker and Mumford, 1978:634).

Scotoecus hindei hindei Thomas, 1901

Scotoecus hindei Thomas, 1901. Ann. Mag. Nat. Hist., (7)7:264. Kitui, Kenya, 3500 ft.

Scotoecus artinii De Beaux, 1923. Atti Soc. Ital. Sci. Nat. Milano, 62:98. Archer's Post, Northern Guaso Nyiro, Kenya.

Records.—Kitui (Thomas, 1901*a*:265); Archer's Post (Hollister, 1918:94, De Beaux, 1923:98); Lakiundu River (Hollister, 1918:94); Northern Guaso Nyiro (Hollister, 1918:94); Guaso Nyiro (Allen, 1911:330); Lorian (Hill, 1974:182, BMNH, NMK); Kapsania, Sigor (SMF); Kisiaunet, West Pokot (NMK); Othaya, Nyeri Dist. (SMF); Mara River (NMK); Kimana, nr. Loitokitok (NMK); Governor's Camp, Mara River (SMF); Buffalo Springs, Isiolo Game Reserve (SMF); nr. Mtito Andei (AMNH); Wei-Wei River, Sigor, 3000 ft (Dollman, 1914*b*:309, Hill, 1974:181); Nyangala Hill (Nagorsen et al., 1976:9); nr. Kibwezi (Vaughan and Bateman, 1980:70); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Remarks.—We follow the taxonomic arrangement of Hill (1974) for the species in East Africa.

Scotoecus hindei albigula Thomas, 1909

Scotoecus albigula Thomas, 1909. Ann. Mag. Nat. Hist., (8)4:544. Kirui, 6000 ft, Mt. Elgon, Kenya.

Records.—Kirui, Mt. Elgon (Thomas, 1909*b*:544); Cherangani Hills, 6000 ft (Hill, 1974:182).

Genus *Scotophilus* Leach, 1821
Scotophilus dinganii colias Thomas, 1904

Scotophilus nigrita colias Thomas, 1904. Ann. Mag. Nat. Hist., (7)13:207. Fort Hall, Kenya.

Records.—Archer's Post (Hollister, 1918:94); Amboseli Reserve (MSU); 30 mi NW Baringo (Dollman, 1914*b*:308, BMNH); Bura (LACM); below Chanler's Falls (BMNH); Cherangani Mts. (LACM); Eusso Nyiro (LACM, BMNH); 30 mi E Falls, Eusso Nyiro (NMK); Fort Hall (Thomas, 1904*a*:208, BMNH, ROM, Zimmerman, 1972:270); 8.5 km N Garsen (ROM); Gilgil River (BMNH); Isiolo (LACM, USNM); Kabete, 7 km N Nairobi (Kulzer, 1959:25, Kock, 1969:193, FMNH, SMF); Kakamega Forest (ROM, Zimmerman, 1972:270); Kakamega, Rondo Forest (ROM); Karen (BMNH, USNM); Karibiti (CM); Kiambu (LACM, USNM, NMK); 4 mi NW Kiambu (ROM); Kiboko (USNM); Kibwezi (USNM); Kilifi (BMNH, HZM, Harrison and Brownlow, 1978:127); Kikuyu (Spinage, 1959:139); Kitale (USNM); Kongelai (ROM); Konza (RMNH); Kwale (RMNH, ZMA); Langata Forest (LACM); Lakiundu River (Hollister, 1918:94); Lake Baringo (ROM); Lake Jippe (MSU); Loli Hills (CM); Lamu (HZM, Harrison and Brownlow, 1978:127); Maji Moto (USNM); Machakos (LACM); Makindu (ROM); Mara River (ROM); Malindi (BMNH); Markwijit (ROM); Maungu (ROM); Merelle River, Marsabit Road (Hollister, 1918:94); Mbero Rock (LACM); Milimani (LACM); Molo (LACM); 4 mi E Molo (USNM); Mombasa (HZM); Mtito Andei (ROM); Muthara (LACM); Muumandu (LACM); Nairobi (Hollister, 1918:94, Kock, 1969:193, FMNH, LACM, NMK, ROM, SMF, USNM); 10 mi N Naivasha (USNM); Nanyuki (CM); Ngong (LACM, NMK, ROM, USNM); Nyangala Hills (ROM); Ortum (ROM); Rift Valley (BMNH); Ruiru, Nairobi (HZM, Harrison and Brownlow, 1978:127); Saiwa River (ROM); Sarmai (ROM); Shimba Hills (ROM); Sigor (ROM); Sokoke Forest (LACM, NMK, ZMA); Swam River (ROM); nr. Tiwi (Whitaker and Mumford, 1978:634); Tiwi Beach (ZMA); Turkwel River (ROM); 30 km E Voi (ROM); Wei-Wei River (BMNH); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Scotophilus nux Thomas, 1904

Scotophilus nigrita nux Thomas, 1904. Ann. Mag. Nat. Hist., (7)13:208. Efulen, Cameroon.

Records.—8 mi SE Kakamega (USNM).

Remarks.—Robbins (personal communication) refers the dark, forest-dwelling *S. nux* to the status of full species. In Kenya both *S. nux* and *S. dinganii colias* occur together in the vicinity of Kakamega.

Scotophilus leucogaster Cretzschmar, 1826

Nycticejus leucogaster Cretzschmar, 1830. *In* Senck. Naturf. Ges.: Atlas Reise nordl. Afrika E. Rueppell, Saugethiere, p. 71, pl. 28a. Bir Nedger, Kordofan, Sudan.

Records.—Turkwel River, Lodwar (CM); 30 mi E (in Kenya) Tororo (ROM); Governor's Camp, Mara River (SMF).

Scotophilus nigrita (Schreber, 1774)

Vespertilio nigrita Schreber, 1774. Saugethiere, 1:171, pl. 58. Senegal.

Records.—Shimba Hills (RMNH).

Scotophilus borbonicus viridis (Peters, 1852)

Nycticejus viridis Peters, 1852. Reise nach Mossambique, Saugethiere, p. 67, pl. 17, f. 2, a–e. Mozambique Island, Mozambique.

Records.—Mombasa (Peters, 1877:914); nr. Tiwi, 25 km SSE Mombasa (Whitaker and Mumford, 1978:632); Sokoke Forest (Whitaker and Mumford, 1978:632, LACM, RMNH, ZMA); Bura, Tana River (LACM); Malindi (NMK); Ribe (NMW); Diani Forest (RMNH, ZMA); Kwale (RMNH, ZMA); Watamu (RMNH); Milimani, Boni Forest (LACM); Nakuru (USNM); Shimba Hills, Mukanda River (ROM); 5 mi E Kompini (ROM).

Remarks.—Hill (1980) has shown that *S. viridis* (Peters, 1852) of southern Africa is a synonym of the earlier named *S. borbonicus* (E. Geoffroy, 1803) of Reunion Island. We have tentatively assigned these records of small *Scotophilus* from eastern and southeastern Kenya to this species.

Subfamily Kerivoulinae

Genus ***Kerivoula*** Gray, 1842

Kerivoula lanosa harrisoni Thomas, 1900

Kerivoula harrisoni Thomas, 1900. Proc. Zool. Soc. London, 1900:802. Walamo, between lakes Zwai and Margheritta, Ethiopia.

Records.—Kinangop, east of Naivasha (HZM); Marsabit (HZM); Nyeri (BMNH); Nginyang, nr. Lake Baringo (HZM); Taveta (BMNH, Aellen, 1960:223); Ngong (NMK); Koru (NMK); Kaibibich Forest, Cherangani (Taylor, 1971:74).

Kerivoula argentata Tomes, 1861

Kerivoula argentata Thomes, 1861. Proc. Zool. Soc. London, p. 32. Otjoro, Namibia.

Records.—Kibwezi (AMNH).

Kerivoula smithii Thomas, 1880

Kerivoula smithii Thomas, 1880. Ann. Mag. Nat. Hist., (5)6:166, text-f. Old Calabar, Nigeria.

Records.—Bura, Garissa (Harrison, 1963:307, NMK).

Kerivoula cuprosa Thomas, 1912

Kerivoula cuprosa Thomas, 1912. Ann. Mag. Nat. Hist., (8)10:41. Bitye, Ja River, Cameroon.

Records.—Fort Warwick (Harrison, 1957*a*:47, HZM).

Subfamily Miniopterinae

Genus ***Miniopterus*** Bonaparte, 1837

Miniopterus fraterculus Thomas and Schwann, 1906

Miniopterus fraterculus Thomas and Schwann, 1906. Proc. Zool. Soc. London, 1:162. Knysna, South Africa.

Records.—Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Miniopterus natalensis (A. Smith, 1834)

Vespertilio natalensis A. Smith, 1834. South African Quart. J., 2:59. Natal.

Records.—Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Remarks.—The taxonomic arrangements of *Miniopterus* in Kenya follows O'Shea and Vaughan, 1981.

Miniopterus minor Peters, 1867

Miniopterus minor Peters, 1867. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 885 (for 1866). Coast of Zanzibar, Tanzania.

Records.—Shimoni (Falcoz, 1923:548, NMK, NMW, SMF); Moto Cave, Diani Coast (NMK); Ngombeni, 8 km S Mombasa (NMK); Well south of Mombasa (USNM); Ribe (NMW); nr. Tiwi (Whitaker and Mumford, 1978:634).

Miniopterus inflatus africanus Sanborn, 1936

Miniopterus africanus Sanborn, 1936. Zool. Ser., Field Mus. Nat. Hist., 20:111. Sanford's Ranch, Mulo Shoa Dist., northwest of Addis Ababa, Ethiopia.

Records.—Ulukenia Hills (Sanborn, 1936:112); Baharini Farm, Lake Nakuru (Kock, 1974*b*:162); Lirandha Hill, Kakamega (HZM); Kariandus (NMK); Elmenteita (HZM); Busia (AMNH); Koru (USNM, Theodor, 1968:344, 347); Barberton's farm, Kitale (USNM); Mathioni Cave, Chyulu Hills (SMF); Mt. Suswa (HZM, USNM); 8 mi SE Kakamega (USNM); Baharini Farm, Lake Nakuru (SMF); Nakuru (HZM, USNM); Kapsakwany, Mt. Elgon (SMF); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Miniopterus schreibersi arenarius Heller, 1912

Miniopterus natalensis arenarius Heller, 1912. Smithsonian Misc. Coll., 60(12):2. Guaso Nyuki, Northern Guaso Nyiro, Kenya.

Records.—Guaso Nyuki (Heller, 1912:2); Lake Naivasha (Hollister, 1918:95); Cave of God, nr. Lake Naivasha (NMK); Ngare Nyuki (Hollister, 1918:95); Ulukenia Hills (Hollister, 1918:95); Kapretwa, 6500 ft, Mt. Elgon (Jobling, 1939:163, Hopkins and Rothschild, 1956:319, 352, Theodor, 1957:466, Maa, 1965:323, Theodor, 1968:362); Endebess (HZM, NMK); 25 mi NW Kitale (HZM, SMF); Elmenteita (HZM); Daraja ya Mungu, Nyamindi River, 10 mi W Embu (HZM); Devil's Cave, Kitale (HZM); Kirui, Mt. Elgon (BMNH); Mt. Menengai (Theodor, 1957:471, 513, Maa, 1965:323, FMNH, SMF); Ngong (NMK, Arthur, 1956:189); Nairobi (NMK); Kericho (NMK); Elgon Caves (NMK); Mt. Suswa (NMK); Chyulu Hills (NMK); Saboti (NMK); Kakamega (USNM); nr. Kiboko (Whitaker and Mumford, 1978:634); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Mt. Elgon (Jackson, 1939:180, Theodor, 1957:465, 513); Mountain Lodge, southwest slopes Mt. Kenya (SMF); Kiminini Caves, Mt. Elgon (Simpson et al., 1968:439); Skull Cave, Chyulu Hills (SMF); Kimakia Cave, Chyulu Hills (SMF); Kapsakwany, Mt. Elgon (SMF); Kilaguni Lodge, Tsavo West National Park (A. Pye, 1973:84).

Family Molossidae

Genus ***Platymops*** Thomas, 1906

Platymops setiger (Peters, 1878)

Mormopterus setiger Peters, 1878. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 196. Ndi, Kenya.

Platymops barbatogularis parkeri Harrison and Fleetwood, 1960. Durban Mus. Novit., 5(20):270. Lualeni Borehole, Maktau, Kenya.

Records.—Ndi (Peters, 1878:198, Dobson, 1880:195); Taita (Matschie, 1895:27); Lualeni Borehole, Maktau (Harrison and Fleetwood, 1960:269, NMK); Nadapal, Turkana (NMK); Lokichoggio (NMK); Wanjalu Hill, nr. Voi (NMK); Karibiti (CM); Sultan Hamud (CM, SMF); Granite Hills, Simba Road (HZM); Kampi ya Samaki (AMNH); 2 mi NW Kibodo [=Kiboko] (Peterson, 1965:15, 19); Lake Baringo (Williams, 1967:178, Koopman, 1975:430); 10 mi N Kiboko (Freeman, 1981:10); 100 mi SE (on Mombasa Road) Nairobi (Peterson, 1965:15, 19); Wei-Wei River, 1 mi SE Sigor (Warner et al., 1974:175); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Kiboko (SMF); Garibete Water Hole (SMF); Isiolo (HZM, Williams, 1967:178); Maktau (Williams, 1967:178); Simba River (Williams, 1967:178).

Genus *Tadarida* Rafinesque, 1814

Tadarida (Tadarida) aegyptiaca aegyptiaca (E. Geoffroy, 1818)

Nyctinomus aegyptiacus E. Geoffroy, 1818. Description de l'Egypte, 2:128. Egypt.

Records.—Mudanda Rock, Voi (Harrison, 1959:225, HZM, NMK); Juja Farm (Hollister, 1918:100); Sultan Hamud (Freeman, 1981:5, CM); Mathaitani Farm, South Mua Hills, Machakos Dist. (Nader and Kock, 1980:132); Nyangala Hill (Nagorsen et al., 1976: 9); Endoposei River, nr. Kalema (Nagorsen et al., 1976:9); Maungu (CM); Sokoke Forest (CM); Granite Hills, Simba Road (HZM); Mbevo Hill, Machakos Dist. (HZM); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Tadarida (Tadarida) lobata (Thomas, 1891)

Nyctinomus lobatus Thomas, 1891. Ann. Mag. Nat. Hist., (6)7:303. Turquel, Suk, Kenya.

Records.—Turquel, Suk (Thomas, 1891*a*:303, 1891*b*:182); Kaibibich, Cherangani Hills (Peterson and Harrison, 1970:5, Harrison, 1971:4, Taylor, 1971:74, Freeman, 1981:6); Kapenguria (Peterson, 1974:1); Maungu Hill, ca. 30 km S Voi (Peterson, 1974:1, Freeman, 1981:6).

Tadarida (Tadarida) fulminans (Thomas, 1903)

Nyctinomus fulminans Thomas, 1903. Ann. Mag. Nat. Hist., (7)12:501. Fianarantsoa, eastern Betsileo, Madagascar.

Records.—Nairobi (Harrison, 1960*b*:74, 1971:4, HZM).

Tadarida (Tadarida) ventralis (Heuglin, 1861)

Nyctinomus (Dysopes) ventralis Heuglin, 1861. Nov. Acad. Caes. Leop.-Carol., 29(8):4, 11. Keren, Eritrea, Ethiopia.

Nyctinomus africanus Dobson, 1876. Ann. Mag. Nat. Hist., (4)17:348. Transvaal, South Africa.

Records.—Menengai, 20 mi W Nakuru (Start, 1966:509); Wei-Wei River, 2 mi S Sigor, West Pokot Dist. (Freeman, 1981:5).

Remarks.—Kock (1975) has shown that *T. africana* is a synonym of *T. ventralis.*

Tadarida (Chaerephon) pumila hindei (Thomas, 1904)

Nyctinomus hindei Thomas, 1904. Ann. Mag. Nat. Hist., (7)13:210. Fort Hall, Kenya.

Chaerephon pumilus naivashae Hollister, 1916. Smithsonian Misc. Coll., 66(1):4. Naivasha Station, Kenya.

Records.—Kitui (Peters, 1878:196, Dobson, 1880:195); Fort Hall (Thomas, 1904*b*: 210, Braestrup, 1933:271); Naivasha Station (Hollister, 1916:4); Frere Town (Loveridge, 1922:48); Ruiru (NMK, HZM); Voi (NMK, HZM, AMNH, Kock, 1969:140); Thika (HZM); Ijara (Percy et al., 1953:12); Malindi (HZM); Mombasa (Allen, 1911:331, Loveridge, 1922:48, Braestrup, 1933:272, Demeter and Topal, 1982:47, HZM); Lamu (HZM); Limuru (HZM, SMF); Kiboko (Kulzer, 1959:28, 31, Kock, 1969:140); Machakos (HZM); Kilindini, nr. Mombasa (BMNH); Msambweni (HZM); Rongai (HZM); Witu (Allen and Lawrence, 1936:55); Tsavo (NMK); Ngong (NMK); Simba (NMK); Kiambu (NMK); Mara River (AMNH); Namanga (AMNH); Nyeri (HZM); Konza area, Machakos Dist. (HZM); Ndauni area, Machakos Dist. (HZM); Taru (NMK); Athi River (NMK, USNM); Nairobi (NMK, SMF); Langata (NMK); Kibwezi (AMNH); Galma Galla, Garissa (AMNH); Ukunda, Kwale Dist. (SMF); Shimoni (CM); Karibiti (CM); West slopes Mt. Kenya (Kock, 1969:140); Lake Naivasha (NMK, HZM); Gilgil (HZM); Buffalo Springs (SMF); Othaya, Nyeri Dist. (SMF); Taveta (Thomas, 1910:309, Braestrup, 1933:272); Elementeita (HZM, NMK); Baharini Farm, Lake Nakuru (SMF); Nakuru (Kock, 1969: 140, HZM); Eusso Nyiro (BMNH); Lake Baringo (NMK); Nyeri Station (NMK); Bura Irrigation Scheme (NMK); Njoro (Keegan, 1956, NMK); Musanda (Dulic and Mutere, 1973*a*:62); Naivasha (Freeman, 1981:7); 2 mi N Kilifi (Freeman, 1981:7); Kilima Nbogo, Ol Donyo Sabuk (SMF); Donyo Sabuk Mountains, 32 mi E Nairobi (Freeman, 1981:7); nr. Tiwi (Whitaker and Mumford, 1978:634); nr. Njoro, 18 km SW Nakuru (Whitaker and Mumford, 1978:632); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981: 489); Pata Island (Voeltzkow, 1923); Kilindini Harbor, Mombasa (Allen and Loveridge, 1933:71).

Remarks.—Harrison (1961:291) listed this species from Mtoto Andei as recorded by Allen (1911). However, Allen (1911) only reported the species from Mombasa. The *Tadarida limbata-pumila* complex in East Africa requires additional study.

Tadarida (Chaerephon) ansorgei (Thomas, 1913)

Nyctinomus ansorgei Thomas, 1913. Ann. Mag. Nat. Hist., (8)11:318. Malange, Angola.

Records.—Endoposei River, base of Nguruman Escarpment (Eger and Peterson, 1979: 1889); Uasu Nyiro River bridge, Nguruman Escarpment (Eger and Peterson, 1979:1889); Kapenguria (Eger and Peterson, 1979:1889); Lake Hannington (Eger and Peterson, 1979: 1889); Kanyangareng, Suam River (Eger and Peterson, 1979:1889); Mount Nasolet, 9.6 km S Turkwell Gorge (Eger and Peterson, 1979:1889); Maji ya Moto (Eger and Peterson, 1979:1889); Kampi ya Samaki (Eger and Peterson, 1979:1889); Mara River (Eger and Petersen, 1979:1889); Kisumu (Eger and Peterson, 1979:1889).

Tadarida (Chaerephon) bivittata (Heuglin, 1861)

Nyctinomus bivittatus Heuglin, 1861. Nova Acta Acad. Caes. Leop.-Carol., Halle, 29(8): 4. Keren, Eritrea, Ethiopia.

Records.—Makueni (Hayman and Harrison, 1966:220, NMK); Mt. Elgon (Hayman and Harrison, 1966:220, NMK); Nairobi (Hayman and Harrison, 1966:220, NMK); Maji ya Moto (Eger and Peterson, 1979:1889, USNM); Kabete (NMK); Mombasa (FMNH, Eger and Peterson, 1979:1889); nr. Machakos (FMNH); Lake Amboseli, nr. Namanga (AMNH, Eger and Peterson, 1979:1889); 8 mi NW Makindu (Peterson and Nagorsen, 1975:2); Wei-Wei River, 2 mi S Sigor (Freeman, 1981:6, SMF); Ngong Hills (Hayman and Harrison, 1966:222, NMK); Yala River (Hayman and Harrison, 1966:222, NMK); South Kavirondo (Hayman and Harrison, 1966:224); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489); Lake Baringo (Kingdon, 1974:325); Lake Hannington

(Kingdon, 1974:325, Eger and Peterson, 1979:1889); Akiriamet (Eger and Peterson, 1979: 1889); Kampi ya Samaki (Eger and Peterson, 1979:1889); Kanyangareng, Suam River (Eger and Peterson, 1979:1889); Kapenguria (Eger and Peterson, 1979:1889); 10.4 km N, 12.6 km E Kibwezi (Eger and Peterson, 1979:1889); Kisumu (Eger and Peterson, 1979:1889); Kongelai, Kaiboni River (Eger and Peterson, 1979:1889); Perakera River, Marigat (Eger and Peterson, 1979:1889); Sigor, Wei-Wei River (SMF, Eger and Peterson, 1979:1889); Turkwell Gorge (Eger and Peterson, 1979:1889); 30 km SE Voi (Eger and Peterson, 1979:1889).

Tadarida (Chaerephon) bemmelini cistura (Thomas, 1903)

Nyctinomus cisturus Thomas, 1903. Ann. Mag. Nat. Hist., (7)12:502. Mongalla, Equatoria Prov., Sudan.

Records.—Nyangala Hill (Nagorsen et al., 1976:9); Ngong (NMK); Yala River (NMK); Kabete (NMK); Kampi ya Moto, 20 mi W Nakuru (Start, 1969:219, Peterson, 1971: 1347, BMNH); Menengai (BMNH, HZM); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981:489).

Tadarida (Mops) nanula (J. A. Allen, 1917)

Mops (Allomops) nanulus J. A. Allen, 1917. Bull. Am. Mus. Nat. Hist., 37:477. Niangara, Zaire.

Records.—Wei-Wei River, Sigor, West Pokot (Start, 1969:220, SMF); 2 mi S Sigor, Wei-Wei River (Freeman, 1981:7).

Tadarida (Mops) condylura (A. Smith, 1833)

Nyctinomus condylurus A. Smith, 1833. South African Quart. J., 1:54. Port Natal, South Africa.

Records.—Malindi (HZM); Ruanda (HZM); Diani (HZM); Lake Naivasha (HZM); Lamu (HZM); Ukunda (SMF); Limuru (SMF); Athi River (HZM, NMK, USNM); Taveta (Thomas, 1910:309, BMNH); Kiboko (Kulzer, 1959:27, USNM); Bellazoni (Allen and Lawrence, 1936:54); Ngatana (Allen and Lawrence, 1936:54, CM); Sukori, Thika (Harrison, 1961:291); Mtito Andei (USNM); Ijara, Garissa (AMNH); Mara River (AMNH); Kilifi Veterinary Station (Freeman, 1981:7); Kisumu (Loveridge, 1923:695); Mombasa (Kock, 1969:152, SMF); Masalani, 20.1 km NE Kibwezi (O'Shea and Vaughan, 1981: 489).

Tadarida (Mops) midas midas (Sundevall, 1843)

Dysopes midas Sundevall, 1843. Kgl. Svenska Vetensk. Akad. Handl., p. 207. Bahr el Abiad [=White Nile], Sudan (restricted by Koopman, 1975:429, to west bank, White Nile, ca. 11°45'N, 33°30'E, Blue Nile Province, Sudan).

Records.—2 mi S Sigor, Wei-Wei River, West Pokot Dist. (Freeman, 1981:7).

Tadarida (Mops) brachyptera (Peters, 1852)

Dysopes brachypterus Peters, 1852. Reise nach Mossambique, Saugethiere, p. 59, pl. 15, f. 1. Island of Mozambique, Mozambique.

Records.—Malindi (Peters, 1879:832, Dobson, 1880:194).

Remarks.—This is a poorly known taxon originally described from Mozambique and its taxonomic status is unclear. Allen (1939:107) listed it as a distinct species whereas Hayman and Hill (1971:59) proposed that it could be an earlier name for either *T. thersites* or *T. leonis.* Koopman (1975:420) discussed its relationship to the above two taxa as well as *T. spurrelli* and *T. nanulus* and considered that it could be the eastern representative of any of these four taxa. El-Rayah (1981:2, 6) synonymized *T. leonis* with *T. brachyptera.*

Genus ***Otomops*** Thomas, 1913
Otomops martiensseni martiensseni (Matschie, 1897)

Nyctinomus martiensseni Matschie, 1897. Arch. Naturgesch., 63(1):84. Magrotto plantation, Usambara Mountains, west of Tanga, Tanzania.

Records.—Kwale (NMK); nr. Kibwezi (HZM); Nairobi (Harrison, 1961:290, Williams, 1967:178); Mt. Suswa (NMK, SMF, Glover et al., 1964:58, Harrison, 1965:2, Williams, 1967:178, Mutere, 1968:20, Dulic and Mutere, 1973*a*:61, Kinoti, 1973:129, Valdivieso et al., 1979:5, Freeman, 1981:10); Ithundu Caves, Kiboko (NMK, SMF, Dulic and Mutere, 1973*a*:61, Valdivieso et al., 1979:5); Lake Naivasha (Valdivieso et al., 1979:5); 19 km W Makindu (Valdivieso et al., 1979:5); Kampi ya Moto, Lake Baringo (Valdivieso et al., 1979:5); nr. Kiboko (Whitaker and Mumford, 1978:634); Wei-Wei River, 1 mi SE Sigor (Warner et al., 1974:175); Shimba Hills (Williams, 1967:178); Hunter's Lodge (A. Pye, 1973:84); Chyulu Hills (Kinoti, 1973:129); Kimakia Cave, Northern Chyulu Hills (Simons, 1974:250).

GAZETTEER

Locality names are listed in alphabetical order with variant names cross-referenced to the standard names. Standard names are taken from the second edition of the official standard names gazetter for Kenya published in 1978 and approved by the United States Board on Geographic Names. Most of the entities can be identified and located on the 1978 version of the Kenya and Northern Tanzania Route Map published in English, French, and German by the Survey of Kenya.

Coordinates for locality names were taken mostly from the Kenyan gazetteer listed above. In addition, Loveridge (1937), Moreau et al. (1945), Chapin (1954), and Davis and Misonne (1964) were consulted together with place modifiers in the original references for published records. In the case of rivers, when no place modifiers were available for the published records or on the specimen labels, coordinates are given for the river mouth or confluence.

In a number of instances, more than one entity exists in Kenya for a place name. This generally does not cause a real problem but does in the case of the locality cited as Euaso Ngiro and its variants, especially the older specimens labeled Guaso Nyiro. In this latter instance, we have given coordinates for both the southern and northern Euaso Ngiro rivers in the gazetteer.

Akiriamet	1°20′N, 35°42′E
Amala River	1°02′S, 35°14′E
Amboseli Reserve	2°30′S, 37°00′E

Archer's Post	0°39′N, 37°41′E
Aruba Dam, Tsavo East	3°21′S, 38°49′E
Aruba Lodge, Tsavo National Park	3°21′S, 38°49′E
Athi River	1°27′S, 36°59′E
Athi Station [=Athi River]	1°27′S, 36°59′E
Baharini Farm	0°18′S, 36°06′E
Bahati, nr. Nakuru	0°09′S, 36°06′E
Balesa	3°36′N, 37°22′E
Barberton Cave, Kitale	
Barberton's farm, Kitale	
Baricho	3°06′S, 39°47′E
Baringo [=Mukutan]	0°38′N, 36°16′E
Bat Island	3°27′N, 36°04′E
Belazoni	ca. 2°31′S, 40°22′E
Bellazoni [=Belazoni]	ca. 2°31′S, 40°22′E
Berkeley Bay	0°14′N, 33°58′E
Buffalo Springs	0°37′N, 37°39′E
Bukura	0°14′N, 34°47′E
Bukwa [=Bukura]	0°14′N, 34°47′E
Bulessa [=Balesa]	3°36′N, 37°22′E
Bura	1°06′S, 39°57′E
Bura Irrigation Scheme	3°30′S, 38°18′E
Bushwhacker's Safari Camp	2°19′S, 38°07′E
Busia	0°28′N, 34°06′E
Cave of God	0°46′S, 36°21′E
Central Island	3°30′N, 36°03′E
Chanler's Falls	0°47′N, 38°05′E
Cherangani Hills	1°15′E, 35°27′E
Chesegon	1°18′N, 35°37′E
Chuka	0°20′S, 37°39′E
Chyulu Hills	2°35′S, 37°50′E
Daraja ya Mungu, Nyamindi River	0°34′S, 37°24′E
Devil's Cave, Kitale	
Diani	4°18′S, 39°34′E
Diani Beach	4°18′S, 39°35′E
Diani Forest	4°15′S, 39°34′E
Diani Mosque	4°18′S, 39°34′E
Donyo Sabak [=Ol Doinyo Sapuk]	1°08′S, 37°15′E
Donyo Sabuk Mountains [=Ol Doinyo Sapuk]	1°08′S, 37°15′E
Eastern Part, Mt. Elgon National Park	ca. 1°03′N, 34°46′E
Elburgon	0°18′S, 35°49′E
Eldoinyo Lengamlo	2°10′S, 37°33′E
El Dongo eb Urru [=Ol Doinyo Opuru]	0°38′S, 36°14′E
Eldoret	0°31′N, 35°17′E
Elementeita [=Elmenteita]	0°29′S, 36°09′E
Elgon Caves [=Mt. Elgon Caves]	
Elgonyi, Mt. Elgon	0°58′N, 34°40′E
Elmenteita	0°29′S, 36°09′E
Embu	0°32′S, 37°27′E
Embu Boma [=Embu]	0°32′S, 37°27′E
Endau Mt.	1°16′S, 38°35′E
Endebess	1°04′N, 34°51′E
Endoposei River, nr. Kalema [=Endosapia River]	1°46′S, 36°05′E
Endosapia River	1°46′S, 36°05′E

Engare Nanyuki	0°21′N, 36°55′E
Engare Narok	1°09′N, 36°35′E
Eusso Nyiro [=Ewaso Ngiro]	
Ewaso Ngiro (Northern)	0°37′N, 36°55′E–0°28′N, 39°55′E
Ewaso Ngiro (Southern)	0°35′N, 35°47′E–2°04′S, 36°07′E
Exodus Cave, Mt. Suswa	1°08′S, 36°22′E
Ferguson's Gulf	3°31′N, 35°55′E
Fisherman's Cave, Kenya Coast	
Fort Hall [=Muranga]	0°43′S, 37°09′E
Fort Jesus	4°04′S, 39°41′E
Fort Warwick	
Frere Town	4°01′S, 39°42′E
Galana Ranch	3°20′S, 39°20′E
Galma Galla	1°11′S, 40°47′E
Garabani	
Garba Tula	0°32′N, 38°31′E
Garbat Ullah [=Garba Tula]	0°32′N, 38°31′E
Garibete Water Hole	3°23′S, 39°16′E
Garissa	0°28′S, 39°38′E
Garsen	2°16′S, 40°07′E
Gebbi [=Lake Jipe]	3°35′S, 37°45′E
Gede	3°18′S, 40°01′E
Gede National Park	3°18′S, 40°01′E
Gedi National Park [=Gede National Park]	3°18′S, 40°01′E
Gelitja	2°32′S, 40°31′E
Gibralter Island	0°36′N, 36°04′E
Gilgil	0°30′S, 36°19′E
Gilgil River	0°43′S, 36°21′E
Golbanti	2°27′S, 40°12′E
Governor's Camp, Mara River	
Granite Hills, Simba Road [=Eldoinyo Lengamlo]	2°10′S, 37°33′E
Guaso Nyiro [=Ewaso Ngiro]	1°00′N, 39°27′E
Guaso Nyuki [=Engare Nanyuki]	0°21′N, 36°55′E
Gura River	0°31′S, 37°05′E
Habaswein	1°01′N, 39°29′E
Hoey's Bridge [=Moi's Bridge]	0°53′N, 35°07′E
Hunter's Lodge, nr. Makindu	2°14′S, 37°42′E
Ijara	1°36′S, 40°31′E
Isiolo	0°21′N, 37°35′E
Ithundu Caves, Kiboko	2°20′S, 37°44′E
Juja Farm	1°11′S, 37°07′E
Kabalolot Hill	ca. 1°00′S, 35°23′E
Kabete	1°16′S, 36°43′E
Kabolet River	
Kacheliba [=Kuchelebai]	1°29′N, 35°01′E
Kaibibich	1°12′N, 35°17′E
Kaibibich Forest	ca. 1°12′N, 35°17′E
Kaimosi	0°08′N, 34°51′E
Kaitherin Hills [=Kathiren]	4°48′N, 35°16′E
Kakamega	0°17′N, 34°45′E
Kakamega Forest	0°09′N–0°22′N, 34°50′E–34°58′E

Kalakol	3°33′N, 34°54′E
Kampi ya Moto	0°08′S, 35°56′E
Kampi ya Samaki	0°36′N, 36°01′E
Kamuuani	
Kanjira	0°21′S, 34°33′E
Kanyangaren [=Kanyangareng]	1°47′N, 35°08′E
Kanyangareng	1°47′N, 35°08′E
Kapenguria	1°14′N, 35°07′E
Kapretwa, Mt. Elgon	
Kapsakwany [=Kapsakwony]	0°51′N, 34°43′E
Kapsakwony	0°51′N, 34°43′E
Kapsania, Sigor	
Kapsarok	0°18′S, 35°03′E
Kaptagat	0°26′N, 35°29′E
Kara River	
Karen	1°20′S, 36°42′E
Kariandus	0°25′S, 36°18′E
Karibiti	
Karsa	3°38′N, 36°20′E
Karura Forest	1°14′S, 36°50′E
Kathama Kangundo Escarpment	1°19′S, 37°21′E
Kathiren	4°48′N, 35°16′E
Katilia	2°07′N, 36°07′E
Katilo	
Kau, Osi River	2°29′S, 40°26′E
Kavirondo	1°08′N–1°23′S, 33°56′E–35°07′E
Kericho	0°22′S, 35°17′E
Kiambu	1°10′S, 36°50′E
Kiboko	2°11′S, 37°43′E
Kibwezi	2°25′S, 37°58′E
Kiega Hill [=Kieiga]	0°07′N, 37°48′E
Kieiga	0°07′N, 37°48′E
Kijabe	0°56′S, 36°34′E
Kijabe Station	0°55′S, 36°35′E
Kikambala	3°54′S, 39°47′E
Kikuyu	1°15′S, 34°40′E
Kilaguni Lodge	2°54′S, 38°04′E
Kilifi	3°38′S, 39°51′E
Kilifi Creek	3°38′S, 39°51′E
Kilima Mbogo	1°04′S, 37°14′E
Kilindini	4°04′S, 39°39′E
Kimakia Cave, Chyulu Hills	2°20′S, 37°44′E
Kimana	2°48′S, 37°32′E
Kimilili Forest Station	
Kimingini	0°11′N, 34°46′E
Kiminini	0°54′N, 34°55′E
Kiminini Caves	0°57′N, 34°50′E
Kinangop	0°44′S, 36°40′E
Kindu Bay [=Kendu Bay]	0°21′S, 34°38′E
Kipini	2°32′S, 40°31′E
Kipsain River	1°07′N, 35°06′E
Kipsiryori Cave	0°50′N, 34°50′E
Kirui, Mt. Elgon [=Kirui’s]	0°50′N, 34°40′E

Kirui's	0°50′N, 34°40′E
Kisiaunet	1°17′N, 35°05′E
Kisumu	0°06′S, 34°45′E
Kitale	1°01′N, 35°00′E
Kitau, Manda Island	2°18′S, 40°56′E
Kitui	1°22′S, 38°01′E
Kitumu Cave, Mt. Elgon National Park	
Kompini	
Kongelai	1°28′N, 35°01′E
Konza	1°45′S, 37°07′E
Koru Legetet Hill	
Kozibiri River	2°55′N, 35°25′E
Koru	0°11′S, 35°16′E
Kuchelebai	1°29′N, 35°01′E
Kwale	4°11′S, 39°27′E
Laisamis	1°36′N, 37°48′E
Lake Amboseli	2°37′S, 37°08′E
Lake Baringo	0°38′N, 36°05′E
Lake Bogoria	0°15′N, 36°06′E
Lake Elementeita [=Lake Elmenteita]	0°27′S, 36°15′E
Lake Elmenteita	0°27′S, 36°15′E
Lake Hannington [=Lake Bogoria]	0°15′N, 36°06′E
Lake Jipe	3°35′S, 37°45′E
Lake Jippe [=Lake Jipe]	3°35′S, 37°45′E
Lake Naivasha	0°46′S, 36°21′E
Lakiundu River [=Ngaramara River]	0°36′N, 37°37′E
Laldyka Hills, nr. Nanyuki [=Loldaiga Mountains]	0°12′N, 37°07′E
Lali Hills	3°00′S, 39°15′E
Lamu	2°16′S, 40°54′E
Lamu Coast	2°18′S, 40°53′E
Lamu Island	2°17′S, 40°52′E
Langata	1°24′S, 36°46′E
Langata Forest	1°24′S, 36°46′E
Lekiundu River [=Ngaramara River]	0°36′N, 37°37′E
Leopard Rock	0°13′N, 38°13′E
Lesukut Island	0°35′N, 36°04′E
Limuru	1°06′S, 36°39′E
Lion Hill, Lake Nakuru	
Liranda Hill	0°14′N, 34°48′E
Lirandha Hill, Kakamega [=Liranda Hill]	0°14′N, 34°48′E
Lodermoru water	
Lodwar	3°07′N, 35°36′E
Lokichoggio [=Lokichokio]	4°12′N, 34°21′E
Lokichokio	4°12′N, 34°21′E
Lokitanyala Escarpment	2°22′N, 34°57′E
Lokomorinyang	
Lokori	1°57′N, 36°01′E
Loldaiga Mountains	0°12′N, 37°07′E
Loldyka Hills, nr. Nanyuki [=Loldaiga Mountains]	0°12′N, 37°07′E
Loli Hills [=Lali Hills]	3°00′S, 39°15′E
Londiani	0°10′S, 35°36′E
Lopi River	
Lorian [=Lorian Swamp]	0°40′N, 39°35′E

Lorian Swamp	0°40′N, 39°35′E
Lorogi	1°00′N, 36°51′E
Lorugumo, Turkana	2°53′N, 35°15′E
Lothagam Hill	2°55′N, 36°04′E
Lualeni Borehole	3°35′S, 38°13′E
Luanda	0°16′N, 34°47′E
Lukenya Hills	1°28′S, 37°03′E
Lukenya Mountain [=Lukenya Hills]	1°28′S, 37°03′E
Machakos	1°31′S, 37°16′E
Machakos Road	1°32′S, 37°09′E
Maddo Erelle	3°54′N, 41°05′E
Magadi	1°54′S, 36°17′E
Maji ya Moto	0°16′N, 36°04′E
Maji Moto [=Maji ya Moto]	0°16′N, 36°04′E
Makalia Falls	0°29′S, 36°04′E
Makere	1°52′S, 40°07′E
Makeri [=Makere]	1°52′S, 40°07′E
Makindu	2°17′S, 37°49′E
Maktau	3°24′S, 38°08′E
Makueni	1°49′S, 37°47′E
Malca Muda [=Melka Mude]	2°31′N, 38°08′E
Malindi	3°13′S, 40°07′E
Manda Island	2°17′S, 40°57′E
Maragat, Baringo	0°28′N, 35°59′E
Maragoli	0°06′N, 34°43′E
Maranda School	0°05′S, 34°13′E
Mara River	1°03′S, 35°14′E
Markwijit	
Marsabit	2°20′N, 37°59′E
Marsabit Lake	ca. 2°17′N, 37°32′E
Marsabit Mountain	2°17′N, 37°57′E
Marsabit Road	0°39′N, 37°41′E
Masabubu	1°13′S, 40°00′E
Massabuku [=Masabubu]	1°13′S, 40°00′E
Masalani	2°19′S, 38°07′E
Mathaitani Farm, South Mua Hills [=Mathatani Estate]	1°29′S, 37°06′E
Mathatani Estate	1°29′S, 37°06′E
Mathioni Cave, Chyulu Hills	2°19′S, 37°43′E
Mau Narok	0°36′S, 36°00′E
Maungu	3°33′S, 38°45′E
Maungu Hills	3°33′S, 38°45′E
Mau Summit	0°10′S, 35°41′E
Mazeras	3°58′S, 39°33′E
Mbale	3°24′S, 38°23′E
Mbero Rock	
Mbevo Hill	1°38′S, 37°17′E
Mbooni	1°40′S, 37°27′E
Melka Mude	2°31′N, 38°08′E
Meneneka blow holes, Chyulu Hills	
Menengai	0°12′S, 35°58′E
Menengai Crater	0°12′S, 36°04′E
Merelle River, Marsabit Road [=Merille River]	1°23′N, 37°44′E

Merelle Water [=Merille River]	1°23′N, 37°44′E
Merille River	1°23′N, 37°44′E
Merogoli [=Maragoli]	0°06′N, 34°43′E
Meru	0°03′N, 37°39′E
Meru River	
Mida	3°19′S, 39°58′E
Milimani	1°46′S, 40°50′E
Mkonumbi [=Mkunumbi]	2°18′S, 40°42′E
Mkunumbi	2°18′S, 40°42′E
Moctow [=Maktau]	3°24′S, 38°08′E
Molo	0°15′S, 35°44′E
Molo River	0°32′N, 36°05′E
Mombasa	4°03′S, 39°40′E
Moto Cave, Diani Coast	
Mountain Lodge	0°20′S, 37°09′E
Mt. Elgon	1°08′N, 34°33′E
Mt. Elgon Caves	
Mt. Garguez [=Warges]	0°57′N, 37°24′E
Mount Lololokwi [=Ol Doinyo Sabachi]	0°50′N, 37°32′E
Mt. Mbololo	3°17′S, 38°28′E
Mt. Menengai	0°14′S, 36°06′E
Mt. Nasolet	1°49′N, 35°18′E
Mt. Suswa [=Ol Doinyo Nyukie]	1°09′S, 36°21′E
Mrima Hill	4°29′S, 39°16′E
Msambweni	4°28′S, 39°29′E
Msambweni Cave	ca. 4°28′S, 39°29′E
Mtito Andei	2°41′S, 38°10′E
Mudanda Rock	3°10′S, 38°31′E
Muhoroni	0°09′S, 35°12′E
Mukanda River, Lukore area, Shimba Hills	
Mukumu-Kakamega Escarpment	
Mukutan	0°38′N, 36°16′E
Mumias	0°20′N, 34°29′E
Murka	3°22′S, 37°56′E
Musanda	0°13′N, 34°26′E
Muthara	0°13′N, 37°48′E
Muumandu	1°40′S, 37°17′E
Mwingi	0°56′S, 38°04′E
Nadapal, Turkana	4°26′N, 34°16′E
Nairobi	1°17′S, 36°49′E
Nairobi River	1°13′S, 37°07′E
Naivasha	0°43′S, 36°26′E
Naivasha Station	0°43′S, 36°26′E
Nakuchett [=Nakuijit]	1°38′N, 35°10′E
Nakuijit	1°38′N, 35°10′E
Nakuru	0°17′S, 36°04′E
Namanga	2°33′S, 36°47′E
Nandi Forest	0°09′N–0°30′N, 34°58′E–35°09′E
Nanyuki	0°01′N, 37°04′E
Narok	1°05′S, 35°52′E
Narosura River	1°33′S, 35°53′E
Narrosurra River [=Narosura River]	1°33′S, 35°53′E

Ndara Hills	3°31′S, 38°36′E
Ndarugu River	1°07′S, 37°10′E
Ndauni	1°43′S, 37°44′E
Ndi	3°14′S, 38°30′E
Ndoto	1°45′N, 37°10′E
Ndurugu River [=Ndarugu River]	1°07′S, 37°10′E
Ngangao Forest, Taita Hills	3°22′S, 38°20′E
Ngaramara River	0°36′N, 37°37′E
Ngare Nyuki [=Engare Nanyuki]	0°21′N, 36°55′E
Ngatana	2°13′S, 40°11′E
Ngenyi, Sambura Dist.	
Nginyang	0°58′N, 36°01′E
Ngombeni Caves	4°08′S, 39°39′E
Ngomeni	3°00′S, 40°11′E
Ngomeni, Kitui	0°39′S, 38°24′E
Ngomeni, NE Mwingi	0°39′S, 38°24′E
Ngong	1°22′S, 36°39′E
Ngong Hills	1°24′S, 36°38′E
Ngulia Lodge	2°59′S, 38°12′E
Nguruman Escarpment	1°45′S, 36°02′E
Nidji Hills, Voi	
Njoro	0°20′S, 35°56′E
North Cherangani Hills	1°15′N, 35°27′E
North Larogie [=Lorogi]	1°00′N, 36°51′E
Northern Guaso Nyiro [=Ewaso Ngiro]	0°37′N, 36°55′E–0°28′N, 39°55′E
Nuu, Kitui	1°04′S, 38°21′E
Nyahururu	0°02′N, 36°22′E
Nyama Nyango, Eusso Nyiro [=Samburu Game Lodge, Uaso Nyiro]	0°34′N, 37°35′E
Nyangala Hill	3°37′S, 38°44′E
Nyeri	0°25′S, 36°57′E
Nyeri Station	0°23′S, 37°00′E
Nyuki River [=Engare Nanyuki]	0°21′N, 36°55′E
Ol Doinyo Nyukie	1°09′S, 36°21′E
Ol Doinyo Opuru	0°38′S, 36°14′E
Ol Doinyo Sabachi	0°50′N, 37°32′E
Ol Doinyo Sapuk	1°08′S, 37°15′E
Ol Donyo Sabuk [=Ol Doinyo Sapuk]	1°08′S, 37°15′E
Olebortoto River [=Oloibortoto River]	1°48′S, 36°05′E
Olengarua	2°05′S, 36°07′E
Ol Kalou	0°16′S, 36°23′E
Ol Messoti [=Olmesutye]	1°54′S, 35°46′E
Olmesutye	1°54′S, 35°46′E
Oloibortoto River	1°48′S, 36°05′E
Olorgasailie	1°34′S, 36°27′E
Olorgesailie [=Olorgasailie]	1°34′S, 36°27′E
Ortum	1°26′N, 35°21′E
Othaya	0°34′S, 36°57′E
Pata Island [=Pate Island]	2°07′S, 41°03′E
Pate Island	2°07′S, 41°03′E
Patta Island [=Pate Island]	2°07′S, 41°03′E
Perakera River, Marigat	0°29′N, 35°59′E

Potha, nr. Machakos	1°34′S, 37°10′E
Quoy, Marsabit Road	ca. 0°55′N, 37°38′E
Rabai	3°56′S, 39°34′E
Ras Shaka	2°33′S, 40°37′E
Ribe	3°53′S, 39°38′E
Rift Valley	0°30′N, 36°00′E
River Kerio Suk	2°59′N, 36°07′E
Rondo Forest	0°14′N, 34°53′E
Rongai	0°10′S, 35°51′E
Ruanda [=Luanda]	0°16′N, 34°47′E
Ruaraka	1°14′S, 36°53′E
Ruiru	1°09′S, 36°58′E
Ruiru Dam	1°02′S, 36°45′E
Rusinga	0°01′N, 36°11′E
Sabaki River	3°09′S, 40°08′E
Sabatia	0°02′S, 35°45′E
Saboti	0°56′N, 34°50′E
Sabukia	0°03′N, 36°14′E
Saiwa River	1°06′N, 35°07′E
Sala	3°04′S, 39°11′E
Samburu Game Lodge	0°34′N, 37°35′E
Sarmai	1°46′N, 35°28′E
Sebaki River [=Sabaki River]	3°09′S, 40°08′E
Selengai	2°11′S, 37°10′E
Shela	2°18′S, 40°55′E
Shella [=Shela]	2°18′S, 40°55′E
Shikusa	0°19′N, 34°49′E
Shimba Hills	4°13′S, 39°25′E
Shimo ma Kitu Cave, Rongai Valley	
Shimoni	4°39′S, 39°23′E
Shombole [=Olengarua]	2°05′S, 36°07′E
Sigor, West Pokot	1°29′N, 35°28′E
Simba	2°10′S, 37°36′E
Simba River	
Skull Cave, Chyulu Hills	2°18′S, 37°43′E
Smara, Mt. Kenya	
Sobukia [=Sabukia]	0°03′N, 36°14′E
Sokoke Forest	3°29′S, 39°50′E
Songhor	0°03′S, 35°14′E
Sotik	0°41′S, 35°07′E
South Kavirondo	0°45′S, 34°25′E
South Kinangop	ca. 0°42′S, 36°42′E
South Kiniangop [=South Kinangop]	ca. 0°42′S, 36°42′E
Southern Guaso Nyiro [=Ewaso Ngiro]	0°35′N, 35°47′E–2°04′S, 36°07′E
Soysambu	2°08′S, 37°22′E
Ssio-Bay [=Berkeley Bay]	0°14′N, 33°58′E
Stony Athi	1°35′S, 37°00′E
Suam River	2°01′N, 35°27′E
Sukari	1°15′S, 37°06′E
Sukori [=Sukari]	1°15′S, 37°06′E
Sultan Hamud	2°01′S, 37°22′E
Sulten Hamud [=Sultan Hamud]	2°01′S, 37°22′E

Taita	3°25′S, 38°20′E
Taita Hills	3°25′S, 38°20′E
Takaungu	3°41′S, 39°51′E
Talek River	1°26′S, 35°04′E
Tana River	2°32′S, 40°31′E
Tanganyika	4°19′S, 39°24′E
Tanganyiko, nr. Mombasa [=Tanganyika]	4°19′S, 39°24′E
Tarasha River, Gilgil	
Taru	3°44′S, 39°09′E
Taveta	3°24′S, 37°41′E
Telek River [=Talek River]	1°26′S, 35°04′E
Tharaka	0°18′S, 38°01′E
Thika	1°03′S, 37°05′E
Thomson's Falls [=Nyahururu]	0°02′N, 36°22′E
Tinderet Forest, Songhor	0°07′S–0°11′N, 35°19′E–35°34′E
Tiwi	4°14′S, 39°35′E
Tiwi Beaches	4°14′S, 39°36′E
Tororo (Uganda)	0°42′N, 34°12′E
Trans Nzoia Dist.	0°50′N, 35°00′E
Tsavo	2°59′S, 38°28′E
Tsavo West National Park	2°59′S, 38°28′E
Tschaka [=Ras Shaka]	2°33′S, 40°37′E
Tseikuru	0°18′S, 38°13′E
Turkwel River	3°06′N, 36°06′E
Turkwell Gorge	1°50′N, 35°25′E
Turkwell River [=Turkwel River]	3°06′N, 36°06′E
Turquel [=Turkwel River]	3°06′N, 36°06′E
Uasin Gishu Plateau	0°10′N–0°56′N, 34°50′E–35°32′E
Uasu Nyiru River bridge	1°50′S, 36°07′E
Ukazi	0°53′S, 38°24′E
Ukazzi [=Ukazi]	0°53′S, 38°24′E
Ukunda	4°17′S, 39°34′E
Ulukenia Hills [=Lukenya Hills]	1°28′S, 37°03′E
Upper Luazomela River, nr. Meru	
Ushingo	2°46′S, 39°40′E
Vipingo	3°49′S, 39°48′E
Vipingo Caves	ca. 3°49′S, 39°48′E
Voi	3°23′S, 38°34′E
Waa Beach	4°11′S, 39°38′E
Wanjala	3°15′S, 38°09′E
Wanjalu Hill [=Wanjala]	3°15′S, 38°09′E
Warges	0°57′N, 37°24′E
Watamu	3°21′S, 40°01′E
Wei-Wei River	2°00′N, 35°27′E
Wema	2°13′S, 40°11′E
Witu	2°23′S, 40°26′E
Yala River	0°04′N, 34°09′E
Yatta Escarpment	3°00′S, 38°45′E

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MORPHOMETRIC VARIATION IN THE VOLCANO MOUSE, *PEROMYSCUS* (*NEOTOMODON*) *ALSTONI* (MAMMALIA: CRICETIDAE)

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Abstract

The volcano mouse, *Peromyscus* (*Neotomodon*) *alstoni*, occurs at high elevations in the transvolcanic belt of México. Recent fieldwork in the state of Tlaxcala resulted in large series of *P. alstoni* from populations located between the two recognized subspecies (*P. a. alstoni* and *P. a. perotensis*). Morphometrical analyses were conducted to test the value of described subspecific characters as well as redefine the boundary of the subspecies. Univariate and multivariate analyses were used to determine age, secondary sexual, individual, and geographic variation. Significant differences were found among four age classes. There were no significant differences in secondary sexual variation. Analysis of geographical variation failed to differentiate samples of *P. alstoni*, thus indicating that the species is monotypic.

Introduction

The volcano mouse, *Peromyscus* (*Neotomodon*) *alstoni*, was originally described as one of three species (*alstoni*, *orizabae*, and *perotensis*) in the genus *Neotomodon* (Merriam, 1898) which is endemic to the higher elevations of the transvolcanic belt of México. Although there was considerable speculation about the systematic relationship of the volcano mouse to other rodents (Miller and Rehn, 1901; Goldman, 1910; Miller, 1924; Ellerman, 1941), Davis and Follansbee (1945)

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concluded that *Neotomodon* was most closely related to *Peromyscus* based on shape of skull, dental characters, and habits. Davis (1944) and Davis and Follansbee (1945) synonymized *orizabae* and *perotensis* with *alstoni,* and recognized two geographic races, *N. a. alstoni* and *N. a. perotensis* (included *orizabae*). Subsequent investigators (Burt, 1960; Hooper, 1959; Klinginer, 1968; Rodriguez-Romero et al., 1975; Uribe et al., 1974) have supported the close relationship of *Neotomodon* and *Peromyscus.* Yates et al. (1979) synonymized the two genera under *Peromyscus*—thus at the time of this study the nomenclature of the volcano mouse consisted of *Peromyscus alstoni alstoni* and *Peromyscus alstoni perotensis.*

Davis and Follansbee (1945) reported that "specimens from west of the Río Balsas are noticeably larger than those from localities to the east." With collecting localities from Cofre de Perote and Mt. Orizaba representing the eastern subspecies (*P. a. perotensis*) and localities west of the Río Atoyac representing the western subspecies (*P. a. alstoni*), it appeared that the two taxa were geographically distinct and isolated from each other by approximately 140 kilometers. Thus, Hall and Kelson (1959) and Hall (1981) designated the geographic boundary between the two subspecies to be in the central regions of Tlaxcala and Puebla, near Río Atoyac.

As a result of recent cooperative fieldwork between Carnegie Museum of Natural History and Universidad Autónoma Metropolitana Iztapalapa, large samples of *P. alstoni* have been collected from several localities throughout Tlaxcala, thus indicating that the subspecies of *P. alstoni* may not be as isolated as previously believed. With this new material available it was possible to test the value of the characters that differentiate the subspecies and then, if possible, redefine the geographic boundary of the two taxa.

To examine the status of *P. a. alstoni* and *P. a. perotensis,* specimens throughout the range of the species were subjected to univariate and multivariate morphometrical analyses. Nongeographic and geographic variation were examined. These analyses and data from over 1100 specimens were used to reassess the taxonomy and zoogeography of the geographical races of *P. alstoni.*

METHODS

Four external and 10 cranial measurements were taken from each specimen for purposes of morphometrical analysis. External measurements (total length, tail length, length of hind foot, and ear length) were taken from specimen labels. Cranial measurements (Fig. 1) were taken by means of dial calipers (accurate to one-tenth millimeter) and include the following:

1) *Greatest length of skull*—Least distance between two vertical lines, one touching the posteriormost part of the skull above the foramen magnum and the other touching the anteriormost part of the nasal bones.

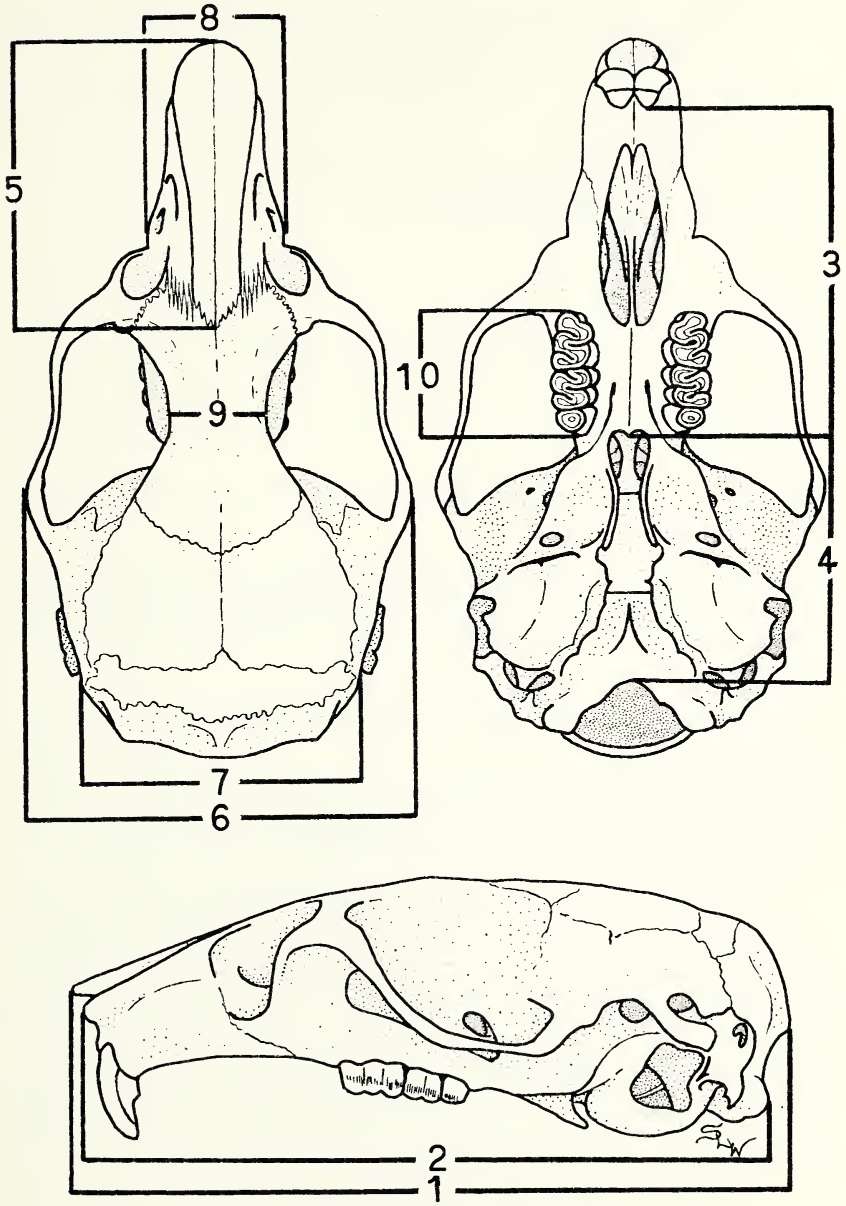

Fig. 1.—Skull of *Peromyscus alstoni* illustrating points between which cranial measurements (described in text) were taken.

2) *Condylobasal length*—Least distance on skull from a line connecting the posteriormost projections of the exoccipital condyles to a line connecting the anteriormost projections of the premaxillary bones.
3) *Palatilar length*—Distance on skull from the anteriormost point on the posterior border of the palate to a line connecting the posteriormost margins of the alveoli of the first upper incisors.
4) *Postpalatal length*—Distance on skull from the anteriormost margin of the foramen magnum to the posterior border of the palate.
5) *Nasal length*—Greatest length of nasal bones.
6) *Zygomatic breadth*—Greatest distance across zygomatic arches perpendicular to long axis of skull.
7) *Mastoid breadth*—Greatest distance across mastoid bones perpendicular to long axis of skull.
8) *Rostral breadth*—Greatest distance across rostrum at the anteriormost projection of the zygomatic plate, perpendicular to long axis of skull.
9) *Interorbital constriction*—The least distance across the top of the skull between the orbits.
10) *Length of maxillary toothrow*—Greatest distance of the alveoli of one toothrow between the M^1 and M^3.

Male and female specimens were separated and then assigned to one of five age groups which generally follow aging procedures used by Hoffmeister (1951). The five age groups were distinguished as follows:

Age class 1—Includes those individuals in which M^3 is just breaking through the bony covering of the jaw and shows no wear whatsoever.

Age class 2—Includes those individuals in which M^3 is worn smooth except for the labial cusps, and M^1 and M^2 show little or no wear; complete re-entrant angle on M^3 is evident.

Age class 3—Includes those individuals in which M^3 is worn smooth, but M^1 and M^2 with labial cusps showing little wear and lingual cusps not quite worn smooth; three complete re-entrant angles on M^1 and M^2 are evident; the re-entrant angle on M^3 is incomplete.

Age class 4—Includes those individuals in which the lingual cusps are worn smooth, and the labial cusps show considerable wear; only two re-entrant angles on M^2 are evident; the third re-entrant angle is incomplete or totally worn away; two to three complete re-entrant angles are evident on M^1.

Age class 5—Includes those individuals in which the cusps are worn smooth and two to three of the re-entrant angles on M^1 and M^2 are either incomplete or missing.

Computer analyses were performed on a DEC-10 at the University of Pittsburgh. Analysis of non-geographic variation was performed on the population from the vicinity of Río Frío in the states of México and Puebla. For analysis of geographic variation, adult specimens were grouped into 15 samples (Fig. 2) as follows: *sample 1*—Patamban, Michoacán; *sample 2*—Mount Tancítaro, Michoacán; *sample 3*—Nahuatzin, Michoacán; *sample 4*—vicinity of Opopeo, Michoacán; *sample 5*—vicinity of Ciudad Hidalgo, Michoacán; *sample 6*—vicinity of Zitácuaro, Michoacán; *sample 7*—volcano Nevada de Toluca, México; *sample 8*—vicinity of México City in the states of Distrito Federal, México, and Morelos; *sample 9*—vicinity of Río Frío in the states of México and Puebla; *sample 10*— vicinity of Mount Popocatépetl, in the states of México and Puebla; *sample 11*—vicinity of Calpulalpan, Tlaxcala; *sample 12*—vicinity of Tlaxco in the states of Tlaxcala and Puebla; *sample 13*—vicinity of La Malinche, Tlaxcala; *sample 14*—vicinity of Cofre de Perote, Veracruz; *sample 15*—vicinity of Mount Orizaba, in the states of Puebla and Veracruz. Acronyms used for listing specimens examined are given in the section for acknowledgements. The acronyms CM and UAMI used in the text refer to

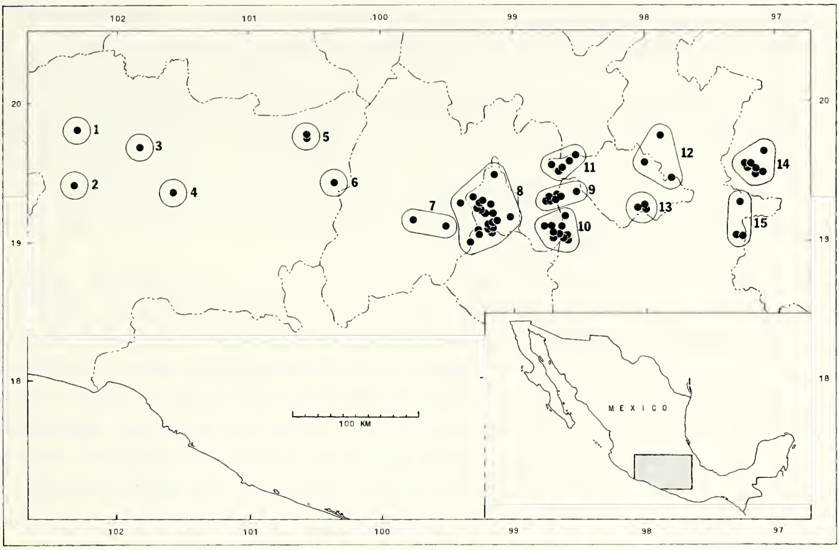

Fig. 2.—Geographic areas in the transvolcanic belt of México, included in the 15 samples of *Peromyscus alstoni.* Dots represent collecting localities of specimens examined in this study. See text for localities included in each sample.

Carnegie Museum of Natural History and Universidad Autónoma Metropolitana Iztapalapa, respectively.

Univariate analyses were performed using the program UNIVAR. This program yields standard statistics (mean, range, standard deviation, standard error of mean, variance, and coefficient of variation), and employs a single-classification analysis of variance (F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sum of Squares Simultaneous Test Procedure (SS-STP) developed by Gabriel (1964) was used to determine maximally nonsignificant subsets.

Multivariate analyses were performed using the BMDP statistical package (Dixon and Brown, 1977). Discriminant and canonical analyses are used to define and separate groups. The program performs a multiple discriminant analysis in a stepwise manner, selecting the variable entered by finding the variable with the greatest F-value. The F-value for inclusion was set at 0.01, and the F value for deletion was set at 0.05. Canonical coefficients were derived by multiplying the coefficients of each discriminant function by the mean of each corresponding variable. The program also classifies individuals by placing them with the group to which they are nearest on the discriminant function.

Results

Nongeographic Variation

The sample of *Peromyscus alstoni* from the vicinity of Río Frío (sample 9) was subjected to univariate analyses to determine the extent of nongeographic variation in the species. Three types of nongeographic variation were examined—age, secondary sexual, and individual.

Variation with age.—Table 1 gives the results of the analyses for variation with age. Males and females were analyzed separately.

Nine out of 14 measurements from each sex revealed significant variation with age. Those measurements that did not reveal significant variation were length of hind foot, rostral breadth, interorbital constriction, length of maxillary toothrow, length of ear in males only, and length of tail in females only.

For males overlapping subsets occurred with total length, length of tail, zygomatic breadth, and mastoid breadth. For greatest length of skull, condylobasal length, palatilar length, postpalatal length, and length of nasals, age classes 2 and 3 formed a nonoverlapping subset that was significantly different from a subset formed by age classes 4 and 5. For those measurements revealing significant variation with age, age class 5 had the largest mean values and age class 2 had the smallest mean values; age class 4 had the second largest mean for the same measurements, except for length of tail in which age class 3 was the second largest.

For measurements revealing significant variation with age among females, five (total length, length of ear, condylobasal length, zygomatic breadth, mastoid breadth) formed two nonsignificant subsets and four (greatest length of skull, palatilar length, postpalatal length, nasal length) formed three nonsignificant subsets. Nonoverlapping subsets were formed with total length, condylobasal length, palatilar length, zygomatic breadth, and mastoid breadth. For those measurements revealing significant variation with age, age class 5 had the largest mean values for seven measurements and age class 4 had the largest mean for two measurements. Age class 2 had the smallest mean values for all of the same measurements. Adults represented by age class 4 were used in subsequent analyses.

The sample of *P. alstoni* from the vicinity of Río Frío did not have a sufficient number of specimens of age class 1 to include in the computer analysis. For purposes of comparison, age class 1 measurements for two males from 15 km SW Río Frío (UAMI 987, UAMI 989), and one male from Portilla de Santa Rosa, Distrito Federal (UMMZ 89015) are as follows: total length, 124, 144, 132; length of tail, 55, 61, 53; length of hind foot, 21, 21, 24; length of ear, 19, 17, 16.5; greatest length of skull, 24.0, 24.3, 24.2; condylobasal length, 21.7, 21.7, 22.0; palatilar length, 9.1, 9.2, 11.3; postpalatal length, —, —, 8.6; length of nasals, 10.0, 9.5, 9.8; zygomatic breadth, 12.3, 12.2, 12.3; mastoid breadth, 10.3, 10.2, 11.3; rostral breadth, 4.2, 4.1, 4.6; interorbital constriction, 3.8, 3.4, 4.2; length of maxillary toothrow, 3.7, 4.0, 4.6. Compared to males of other age classes, these age class 1 individuals had the smallest values for all measurements except length of hind

Table 1.—*Variation with age in external and cranial measurements of* Peromyscus alstoni *from the vicinity of Río Frío in the State of México. Age classes were tested for significant differences at the 0.05 level. Group means that were found to be significantly different were tested with SS-STP to determine the maximally nonsignificant subsets. The adult samples listed as age class 4 in this table were used to test for secondary sexual variation. There were no measurements that indicated significant (0.05) secondary sexual variation.*

Sex and age class	N	Mean (range) ± 2 SE	CV	Results of SS-STP	
		Total length			
Males					
5	14	213.0 (187–250) ± 8.40	7.4	│	
4	32	204.4 (179–227) ± 3.89	5.4	│	│
3	20	201.9 (174–217) ± 5.64	6.2	│	│
2	8	193.5 (169–203) ± 7.78	5.7		│
Females					
5	11	212.4 (196–220) ± 4.77	3.7	│	
4	16	211.1 (192–240) ± 6.31	6.0	│	
3	14	197.9 (177–222) ± 6.41	6.1		│
2	3	183.0 (169–198) ± 16.77	7.9		│
		Length of tail			
Males					
5	14	94.9 (77–107) ± 4.19	8.3	│	
3	20	91.0 (79–104) ± 3.11	7.6	│	│
4	32	90.7 (80–103) ± 1.86	5.8	│	│
2	8	86.5 (77–93) ± 3.66	6.0		│
Females					
5	11	95.8 (89–100) ± 2.22	3.8	n.s.	
4	16	94.1 (86–111) ± 3.64	7.7		
2	3	92.3 (90–96) ± 3.71	3.5		
3	14	89.6 (80–104) ± 3.77	7.9		
		Length of hindfoot			
Males					
5	14	25.9 (24–28) ± 0.51	3.7	n.s.	
3	20	25.9 (22–28) ± 0.62	5.3		
4	32	25.8 (24–27) ± 0.31	3.6		
2	8	25.8 (25–27) ± 0.53	2.9		
Females					
2	3	25.7 (25–26) ± 0.67	2.2	n.s.	
4	16	25.6 (24–28) ± 0.54	4.2		
3	14	25.6 (20–27) ± 0.98	7.1		
5	12	25.1 (23–26) ± 0.52	3.6		
		Length of ear			
Males					
3	20	21.2 (19–24) ± 0.57	6.0	n.s.	
5	14	20.9 (18–23) ± 0.68	6.1		
4	32	20.8 (18–25) ± 0.49	6.7		
2	8	19.7 (18.5–21) ± 0.65	4.7		

Table 1.—*Continued.*

Sex and age class	N	Mean (range) ± 2 SE	CV	Results of SS-STP		
Females						
5	12	22.0 (21–23) ± 0.35	2.7	|		
4	16	21.1 (19–23) ± 0.59	5.6	|	|	
3	14	20.7 (16–24) ± 0.93	8.4	|	|	
2	3	19.5 (19–20) ± 0.58	2.6		|	
		Greatest length of skull				
Males						
5	14	29.9 (28.9–30.8) ± 0.27	1.7	|		
4	31	29.7 (28.3–31.3) ± 0.25	2.3	|		
3	19	29.1 (27.9–30.5) ± 0.31	2.3		|	
2	8	28.6 (27.0–29.7) ± 0.57	2.8		|	
Females						
5	11	30.0 (28.4–31.0) ± 0.45	2.5	|		
4	16	29.9 (27.9–31.6) ± 0.40	2.7	|	|	
3	14	29.1 (27.2–30.5) ± 0.45	2.9		|	|
2	3	27.8 (27.5–28.1) ± 0.35	1.1			|
		Condylobasal length				
Males						
5	14	28.8 (27.6–29.6) ± 0.29	1.9	|		
4	32	28.5 (27.3–30.3) ± 0.24	2.4	|		
3	20	27.7 (26.6–29.1) ± 0.33	2.6		|	
2	7	27.2 (25.7–28.4) ± 0.66	3.2		|	
Females						
4	16	28.8 (26.8–30.7) ± 0.41	2.8	|		
5	11	28.7 (26.6–30.0) ± 0.54	3.1	|		
3	14	27.6 (26.0–28.9) ± 0.45	3.0		|	
2	3	26.3 (26.1–26.5) ± 0.24	0.8		|	
		Palatilar length				
Males						
5	14	13.8 (13.2–14.5) ± 0.19	2.6	|		
4	32	13.5 (12.8–14.5) ± 0.14	2.9	|		
3	20	13.2 (12.7–14.0) ± 0.16	2.7		|	
2	8	12.9 (12.3–13.3) ± 0.26	2.9		|	
Females						
5	12	13.7 (12.7–14.4) ± 0.27	3.5	|		
4	17	13.6 (12.8–14.3) ± 0.22	3.3	|		
3	14	13.1 (12.2–13.8) ± 0.21	3.0		|	
2	3	12.3 (12.2–12.5) ± 0.18	1.2			|
		Postpalatal length				
Males						
5	14	11.1 (10.4–11.5) ± 0.17	2.8	|		
4	32	11.0 (10.2–11.7) ± 0.12	3.1	|		
3	20	10.5 (9.8–11.3) ± 0.20	4.4		|	
2	7	10.3 (9.7–10.9) ± 0.34	4.4		|	

Table 1.—*Continued.*

Sex and age class	N	Mean (range) ± 2 SE	CV	Results of SS-STP		
Females						
4	16	11.0 (10.2–12.1) ± 0.22	4.1	│		
5	11	10.9 (9.6–11.7) ± 0.33	4.9	│	│	
3	13	10.5 (9.8–11.3) ± 0.27	4.6		│	│
2	3	10.0 (9.9–10.3) ± 0.27	2.3			│
		Nasal length				
Males						
5	14	12.6 (11.9–13.2) ± 0.19	2.8	│		
4	31	12.5 (11.7–13.8) ± 0.17	3.8	│		
3	20	12.1 (11.2–13.3) ± 0.26	4.8		│	
2	8	11.6 (10.7–12.2) ± 0.33	4.1		│	
Females						
5	12	12.9 (11.7–13.9) ± 0.33	4.5	│		
4	16	12.5 (11.7–13.5) ± 0.27	4.3	│	│	
3	14	12.0 (11.0–12.9) ± 0.32	5.0		│	│
2	3	11.6 (10.7–12.6) ± 1.11	8.3			│
		Zygomatic breadth				
Males						
5	13	15.7 (14.6–16.6) ± 0.28	3.2	│		
4	28	15.7 (15.0–16.7) ± 0.14	2.3	│		
3	17	15.4 (14.5–16.4) ± 0.24	3.2	│	│	
2	6	14.9 (14.5–15.3) ± 0.22	1.8		│	
Females						
5	10	16.0 (15.0–16.5) ± 0.28	2.8	│		
4	15	15.7 (14.9–16.3) ± 0.22	2.7	│		
3	12	15.5 (14.8–16.0) ± 0.24	2.7	│		
2	3	14.2 (13.8–14.6) ± 0.47	2.8		│	
		Mastoid breadth				
Males						
5	14	12.9 (12.5–13.4) ± 0.14	2.0	│		
4	32	12.8 (12.1–13.4) ± 0.12	2.6	│	│	
3	20	12.7 (12.2–13.3) ± 0.11	1.9	│	│	
2	7	12.5 (12.2–12.8) ± 0.16	1.7		│	
Females						
5	11	13.1 (12.8–13.6) ± 0.13	1.6	│		
4	17	13.0 (12.1–13.6) ± 0.20	3.2	│		
3	14	12.9 (12.4–13.6) ± 0.17	2.5	│		
2	3	12.2 (12.0–12.4) ± 0.24	1.7		│	
		Rostral breadth				
Males						
5	14	5.3 (5.0–5.3) ± 0.12	2.3	n.s.		
4	32	5.3 (4.9–5.4) ± 0.07	3.1			
3	20	5.2 (4.9–5.7) ± 0.07	3.7			
2	8	5.2 (4.8–5.7) ± 0.08	4.3			

Table 1.—*Continued.*

Sex and age class	N	Mean (range) ± 2 SE	CV	Results of SS-STP
Females				
5	12	5.3 (5.1–5.6) ± 0.10	3.2	n.s.
4	17	5.3 (4.8–5.8) ± 0.12	4.8	
3	14	5.2 (4.8–5.6) ± 0.12	4.4	
2	3	5.2 (5.1–5.2) ± 0.07	1.1	
		Interorbital breadth		
Males				
5	14	4.2 (3.9–4.6) ± 0.11	4.7	n.s.
2	8	4.2 (3.9–4.4) ± 0.11	3.7	
4	32	4.2 (3.9–4.5) ± 0.05	3.7	
3	20	4.1 (3.8–4.5) ± 0.09	4.8	
Females				
3	14	4.3 (4.1–4.5) ± 0.07	2.9	n.s.
2	3	4.2 (4.1–4.4) ± 0.18	3.6	
5	12	4.2 (3.8–4.4) ± 0.10	4.1	
4	17	4.2 (3.9–4.5) ± 0.08	4.1	
		Length of maxillary toothrow		
Males				
3	20	5.1 (4.8–5.3) ± 0.06	2.8	n.s.
4	32	5.0 (4.8–5.3) ± 0.05	2.7	
5	14	5.0 (4.8–5.3) ± 0.08	3.0	
2	8	5.0 (4.6–5.2) ± 0.13	3.5	
Females				
4	17	5.1 (4.8–5.5) ± 0.10	4.0	n.s.
3	14	5.0 (4.8–5.3) ± 0.09	3.2	
5	12	5.0 (4.7–5.4) ± 0.12	4.1	
2	3	5.0 (4.8–5.2) ± 0.23	4.0	

foot, length of ear, interorbital constriction, and length of maxillary toothrow.

Secondary sexual variation.—Analyses of secondary sexual variation (see Table 1) for all external and cranial measurements revealed no significant difference attributable to secondary sexual variation. In 12 of the 14 measurements taken, females had slightly larger mean values than the males. Thus, males and females were combined for subsequent analyses of geographical variation.

Individual variation.—For the external and cranial measurements, the coefficients of variation for age class 4 males ranged from 6.7 (length of ear) to 2.3 (greatest length of skull and zygomatic breadth); age class 4 females ranged from 7.7 (length of tail) to 0.4 (condylobasal length)

(Table 1). The means of the coefficients of variation of the external measurements and cranial measurements for males were 5.4 and 2.9 respectively; for females the means were 5.9 and 3.3, respectively. In 12 of the 14 measurements analyzed, the coefficients of variation of females were greater than those of males.

Geographic Variation

Univariate analyses.—Samples having three or more specimens were subjected to univariate analyses. Results of the analysis of variance and SS-STP analysis for these samples are shown in Table 2. Samples 4 and 7 were not included in these analyses because of small sample size.

No trends, common to all characters, were evident when comparing ranked means among samples. Although samples 2, 3, 8, and 9 generally had larger means, only sample 8 had large means for all characters. Samples 13 and 15 were mostly characterized with small means. No other sample or geographical assemblage of samples revealed any relationship based on sizes of individual characters.

All external (except length of ear) and cranial measurements exhibited significant geographic variation and were characterized with broadly overlapping nonsignificant subsets consisting of six to 12 samples each. The length of tail had the largest number with five subsets; condylobasal length, palatilar length, and nasal length had four subsets; total length, length of hind foot, greatest length of skull, postpalatal length, and zygomatic breadth had three subsets; mastoid breadth, rostral breadth, interorbital breadth, and length of maxillary toothrow had two subsets.

Multivariate analysis.—Ten cranial characters of 15 samples of *Peromyscus alstoni* were used in multivariate analyses of geographical variation of the species.

Canonical analysis provides a mechanism for geographically representing phenetic relationships among samples with the characters weighted by variance-covariance analysis. In Table 3, characters used in these analyses are listed from the most useful to the least useful in discriminating groups. A two-dimensional plot of 15 samples of *Peromyscus alstoni* is given in Fig. 3. Variate I accounts for 32.1% of the total dispersion, and Variate II accounts for 22.1%. The plot consists of a single aggregation including all of the samples. Samples 8, 9, 10, 11, and 14 were characterized with broad clusters which encompassed a majority of the plot.

The classification matrix for *Peromyscus alstoni* is given in Table 4. Only 30.3% of the total sample was classified correctly. Samples 4 and 7 (represented by single specimens) were listed with all cases correctly

Table 2.—*ContinuedGeographic variation of external and cranial measurements of* Peromyscus alstoni. *Samples are defined in text and were tested for significant differences at the 0.05 level. Sample means that were found to be significantly different were tested with SS-STP to determine the maximally nonsignificant subsets. Males and females were combined in these analyses because there was no significant differences in secondary sexual variation. Samples 4 and 7 (and 1 and 3 for length of ear) were omitted from this table because sample sizes were less than three individuals.*

Sample number	N	Mean (range) ± 2 SE	CV	Results of SS-STP				
		Total length						
3	4	219.7 (214.0–225.0) ± 4.79	2.2	|				
5	6	217.3 (196.0–234.0) ± 11.43	6.4	|	|			
2	6	214.0 (205.0–225.0) ± 6.07	3.5	|	|			
8	47	211.1 (190.0–235.0) ± 3.28	5.3	|	|	|		
10	24	210.5 (189.0–230.0) ± 4.33	5.0	|	|	|		
11	28	209.4 (194.0–233.0) ± 4.05	5.1	|	|	|		
12	13	208.9 (193.0–233.0) ± 6.83	5.9	|	|	|		
6	7	207.6 (176.0–230.0) ± 12.47	7.9	|	|	|		
9	57	206.9 (179.0–240.0) ± 3.12	5.7	|	|	|		
14	29	205.9 (194.0–222.0) ± 3.10	4.1	|	|	|		
1	4	202.5 (193.0–210.0) ± 7.59	3.7	|	|	|		
13	17	199.3 (183.0–220.0) ± 4.30	4.4		|	|		
15	4	192.0 (187.0–195.0) ± 3.56	1.9			|		
		Length of tail						
3	4	101.3 (96.0–104.0) ± 3.59	3.5	|				
11	28	96.4 (86.0–113.0) ± 2.29	6.3	|	|			
2	6	95.3 (87.0–105.0) ± 5.90	7.6	|	|	|		
12	13	95.1 (84.0–113.0) ± 4.45	8.4	|	|	|	|	
10	24	93.7 (81.0–112.0) ± 3.08	8.1	|	|	|	|	|
8	47	93.1 (76.0–112.0) ± 2.28	8.4	|	|	|	|	|
5	6	92.8 (85.0–104.0) ± 7.07	9.3	|	|	|	|	|
9	57	92.4 (80.0–111.0) ± 1.76	7.2	|	|	|	|	|
14	29	89.2 (78.0–104.0) ± 2.12	6.4		|	|	|	|
1	4	88.0 (84.0–92.0) ± 4.62	5.3		|	|	|	|
13	17	87.7 (80.0–104.0) ± 2.86	6.7			|	|	|
6	7	86.4 (71.0–96.0) ± 5.97	9.1				|	|
15	4	84.0 (81.0–88.0) ± 2.94	3.5					|
		Length of hind foot						
3	4	26.5 (25.5–28.0) ± 1.08	4.1	|				
5	6	26.0 (24.0–27.5) ± 1.06	5.0	|				
2	6	25.8 (24.0–28.0) ± 1.20	5.7	|				
9	57	25.8 (24.0–28.0) ± 0.25	3.7	|	|			
8	48	25.7 (20.0–29.0) ± 0.45	6.1	|	|	|		
10	24	25.6 (23.0–27.0) ± 0.43	4.1	|	|	|		
1	4	25.5 (25.0–26.0) ± 0.58	2.3	|	|	|		
15	4	25.3 (24.0–26.0) ± 0.96	3.8	|	|	|		
11	28	25.1 (24.0–27.0) ± 0.39	4.1	|	|	|		
12	15	24.9 (24.0–26.0) ± 0.38	3.0	|	|	|		
14	30	24.7 (21.0–27.0) ± 0.42	4.6		|	|		
6	7	24.7 (24.0–26.0) ± 0.57	3.1		|	|		
13	17	24.6 (23.0–25.0) ± 0.30	2.5			|		

Table 2.—*Continued.*

Sample number	N	Mean (range) ± 2 SE	CV	Results of SS-STP			
		Length of ear					
5	6	22.2 (21.0–23.5) ± 0.67	3.7	n.s.			
13	17	21.9 (20.0–23.0) ± 0.54	5.1				
11	27	21.8 (19.0–24.0) ± 0.43	5.1				
8	37	21.4 (15.0–25.0) ± 0.57	8.2				
10	21	21.4 (17.0–24.0) ± 0.70	7.5				
6	7	21.3 (20.0–22.0) ± 0.57	3.5				
14	26	21.2 (20.0–24.0) ± 0.37	4.4				
12	15	21.1 (19.0–23.0) ± 0.60	5.5				
15	1	21.0 (21.0–21.0) ± 0.00	0.0				
2	4	20.7 (20.0–22.0) ± 0.96	4.6				
9	57	20.5 (16.0–25.0) ± 0.41	7.6				
		Greatest length of skull					
3	3	30.1 (29.7–30.6) ± 0.52	1.5	│			
8	49	30.1 (28.6–31.6) ± 0.21	2.5	│			
2	5	29.8 (29.0–30.8) ± 0.71	2.7	│	│		
9	54	29.8 (29.7–31.6) ± 0.19	2.3	│	│		
6	7	29.7 (28.3–31.1) ± 0.63	2.8	│	│	│	
14	27	29.5 (28.1–30.9) ± 0.23	2.1	│	│	│	
10	24	29.5 (29.7–30.9) ± 0.34	2.8	│	│	│	
11	27	29.4 (27.4–30.5) ± 0.32	2.8		│	│	
1	4	29.3 (28.7–30.0) ± 0.65	2.2		│	│	
5	5	29.3 (28.4–30.1) ± 0.70	2.7		│	│	
12	14	29.0 (27.0–30.3) ± 0.50	3.2		│	│	
15	5	28.8 (28.0–29.9) ± 0.68	2.6		│	│	
13	16	28.7 (27.8–29.7) ± 0.21	1.5			│	
		Condylobasal length					
3	4	29.2 (28.5–30.5) ± 0.90	3.1	│			
8	49	28.9 (27.4–30.8) ± 0.22	2.7	│	│		
2	5	28.8 (28.1–29.8) ± 0.72	2.8	│	│	│	
6	6	28.7 (27.1–29.9) ± 0.75	3.2	│	│	│	
9	56	28.6 (26.8–30.7) ± 0.19	2.5	│	│	│	
1	4	28.3 (27.4–29.0) ± 0.80	2.8	│	│	│	│
5	5	28.2 (27.4–29.1) ± 0.72	2.9	│	│	│	│
11	26	28.2 (26.8–29.7) ± 0.35	3.1		│	│	│
10	24	28.2 (26.8–29.3) ± 0.30	2.6			│	│
14	29	28.1 (27.1–29.3) ± 0.20	1.9			│	│
12	15	28.0 (26.5–29.1) ± 0.46	3.2			│	│
13	16	27.6 (26.8–29.0) ± 0.27	1.9				│
15	5	27.4 (27.1–27.9) ± 0.28	1.1				│

Table 2.—*Continued.*

Sample number	N	Mean (range) ± 2 SE	CV	Results of SS-STP			
		Palatilar length					
3	4	14.1 (13.7–14.9) ± 0.55	3.9	│			
2	6	13.9 (13.3–14.3) ± 0.32	2.8	│			
5	6	13.8 (13.1–14.6) ± 0.42	3.7	│	│		
8	51	13.8 (12.9–14.7) ± 0.12	3.0	│	│		
9	57	13.6 (12.8–14.5) ± 0.10	2.9	│	│	│	
14	30	13.5 (12.8–14.1) ± 0.11	2.3	│	│	│	
6	7	13.5 (13.1–13.8) ± 0.17	1.7	│	│	│	│
11	28	13.4 (12.4–14.1) ± 0.16	3.1		│	│	│
12	15	13.3 (12.5–14.1) ± 0.25	3.6			│	│
10	25	13.3 (12.3–13.9) ± 0.17	3.3			│	│
1	4	13.1 (12.9–13.2) ± 0.14	1.1			│	│
15	5	13.0 (12.6–13.6) ± 0.37	3.2			│	│
13	17	12.9 (12.3–13.7) ± 0.20	3.2				│
		Postpalatal length					
2	5	11.0 (10.6–11.6) ± 0.40	4.1	│			
9	57	10.9 (10.2–11.7) ± 0.09	3.1	│			
1	4	10.9 (10.5–11.5) ± 0.44	4.1	│	│		
8	49	10.9 (10.3–11.8) ± 0.10	3.2	│	│		
6	7	10.9 (10.1–11.4) ± 0.34	4.1	│	│	│	
3	4	10.9 (10.4–11.4) ± 0.46	4.2	│	│	│	
15	5	10.8 (10.3–11.5) ± 0.40	4.1	│	│	│	
11	28	10.7 (9.9–11.5) ± 0.16	4.0	│	│	│	
10	25	10.7 (10.2–11.4) ± 0.12	2.8	│	│	│	
14	29	10.7 (10.0–11.3) ± 0.12	3.0	│	│	│	
13	16	10.7 (10.2–11.5) ± 0.19	3.6		│	│	
12	15	10.6 (9.9–11.4) ± 0.23	4.2		│	│	
5	5	10.3 (10.0–11.0) ± 0.35	3.8			│	
		Nasal length					
6	7	12.8 (11.9–13.3) ± 0.35	3.6	│			
8	51	12.8 (11.3–13.8) ± 0.16	4.6	│	│		
10	24	12.6 (11.6–13.5) ± 0.22	4.2	│	│	│	
11	27	12.5 (11.3–13.5) ± 0.25	5.2	│	│	│	│
9	55	12.5 (11.7–13.8) ± 0.13	3.9	│	│	│	│
2	6	12.3 (11.5–13.1) ± 0.45	4.4	│	│	│	│
5	6	12.3 (12.0–12.7) ± 0.25	2.5	│	│	│	│
14	29	12.2 (11.4–12.9) ± 0.16	3.4		│	│	│
12	13	12.2 (11.2–13.4) ± 0.42	6.2			│	│
3	3	12.2 (11.7–12.8) ± 0.64	4.5			│	│
13	17	11.9 (11.1–12.8) ± 0.23	4.0			│	│
15	5	11.9 (11.1–12.5) ± 0.51	4.8				│
1	4	11.9 (11.2–12.7) ± 0.62	5.2				│

Table 2.—*Continued.*

Sample number	N	Mean (range) ± 2 SE	CV	Results of SS-STP
		Zygomatic breadth		
2	4	16.1 (15.5–16.8) ± 0.61	3.8	
3	4	15.9 (15.1–16.2) ± 0.52	3.3	
8	48	15.8 (14.7–16.9) ± 0.17	3.7	
9	52	15.7 (14.9–16.7) ± 0.11	2.5	
11	28	15.7 (14.8–16.8) ± 0.22	3.7	
14	28	15.6 (14.8–16.4) ± 0.14	2.5	
5	6	15.5 (15.1–15.9) ± 0.24	1.9	
12	14	15.5 (14.5–16.2) ± 0.25	3.1	
1	4	15.4 (14.9–16.0) ± 0.49	3.2	
10	25	15.2 (14.6–16.2) ± 0.15	2.5	
6	7	15.2 (14.8–15.6) ± 0.22	1.9	
13	17	15.2 (14.2–15.8) ± 0.19	2.6	
15	5	15.1 (14.8–15.4) ± 0.21	1.6	
		Mastoid breadth		
5	6	13.0 (12.5–13.5) ± 0.29	2.7	
8	50	12.9 (12.2–13.5) ± 0.09	2.5	
9	58	12.9 (12.1–13.8) ± 0.10	2.9	
11	28	12.9 (12.1–13.5) ± 0.15	3.0	
2	5	12.9 (12.4–13.5) ± 0.42	3.6	
3	4	12.9 (12.6–13.1) ± 0.21	1.6	
12	15	12.8 (12.3–13.3) ± 0.15	2.3	
14	30	12.8 (12.3–13.6) ± 0.11	2.3	
10	24	12.7 (12.2–13.5) ± 0.14	2.6	
1	4	12.7 (12.5–13.2) ± 0.33	2.6	
6	7	12.7 (12.1–12.9) ± 0.22	2.3	
15	4	12.7 (12.5–12.7) ± 0.10	0.8	
13	17	12.5 (11.9–12.8) ± 0.11	1.8	
		Rostral breadth		
5	6	5.3 (5.1–5.5) ± 0.14	3.2	
8	52	5.3 (4.8–5.9) ± 0.07	4.6	
9	57	5.3 (4.8–5.8) ± 0.06	4.1	
6	7	5.3 (5.1–5.4) ± 0.07	1.9	
11	28	5.2 (4.6–5.7) ± 0.10	5.1	
12	14	5.2 (4.9–5.5) ± 0.10	3.6	
1	4	5.2 (5.1–5.4) ± 0.14	2.7	
3	4	5.2 (4.8–5.4) ± 0.26	5.1	
14	30	5.2 (4.8–5.5) ± 0.07	3.7	
10	25	5.1 (4.9–5.6) ± 0.06	3.0	
13	15	5.1 (4.8–5.6) ± 0.11	4.0	
2	6	5.1 (4.7–5.3) ± 0.18	4.4	
15	5	4.9 (4.7–5.2) ± 0.16	3.7	

Table 2.—*Continued.*

Sample number	N	Mean (range) ± 2 SE	CV	Results of SS-STP	
		Interorbital breadth			
3	4	4.5 (4.2–4.6) ± 0.17	3.9	│	
1	4	4.4 (4.3–4.4) ± 0.05	1.1	│	
2	6	4.3 (4.2–4.5) ± 0.09	2.5	│	│
6	7	4.3 (4.2–4.4) ± 0.04	1.3	│	│
8	52	4.3 (3.8–4.7) ± 0.05	4.1	│	│
5	6	4.3 (4.0–4.4) ± 0.11	3.2	│	│
10	25	4.2 (4.0–4.6) ± 0.06	3.7	│	│
11	27	4.2 (3.9–4.5) ± 0.06	3.5	│	│
15	5	4.2 (4.2–4.3) ± 0.04	1.1	│	│
9	58	4.2 (3.9–4.6) ± 0.04	4.0	│	│
14	30	4.2 (3.9–4.6) ± 0.06	3.9	│	│
12	15	4.2 (3.8–4.4) ± 0.10	4.7	│	│
13	17	4.1 (3.9–4.3) ± 0.06	2.9		│
		Length of maxillary toothrow			
3	4	5.3 (4.9–5.5) ± 0.30	5.7	│	
8	52	5.2 (4.6–5.6) ± 0.07	4.6	│	
2	6	5.1 (4.8–5.4) ± 0.20	4.9	│	│
10	25	5.1 (4.7–5.5) ± 0.08	3.9	│	│
5	6	5.1 (4.9–5.2) ± 0.10	2.4	│	│
12	15	5.0 (4.8–5.3) ± 0.10	3.8	│	│
9	58	5.0 (4.6–5.5) ± 0.05	3.7		│
11	28	5.0 (4.4–5.6) ± 0.10	5.3		│
1	4	5.0 (4.9–5.2) ± 0.15	3.0		│
13	17	4.9 (4.7–5.3) ± 0.09	3.7		│
6	7	4.9 (4.6–5.2) ± 0.17	4.5		│
14	30	4.9 (4.5–5.4) ± 0.06	3.5		│
15	5	4.9 (4.5–5.2) ± 0.23	5.2		│

classified. Samples 5 and 6 had the next highest percentage of correct classifications with 60.0% and 66.7%, respectively. At the other extreme, samples 9 and 11 had 14.9% and 12.0%, respectively, classified correctly.

Taxonomic Conclusions

Based on the univariate and multivariate analyses performed in this study, it was not possible to differentiate geographical groups of *Peromyscus alstoni.* The amount of within sample variation observed was often as great as that observed among samples throughout the entire species. This is in agreement with findings of Davis and Follansbee (1945). Davis and Follansbee (1945) regarded *P. a. alstoni* and *P. a. perotensis* to be distinct subspecies because of an apparent discontinuous distribution and a tendency for specimens occurring west of the Río Balsas to be larger than specimens occurring east of the river. Additional specimens have indicated the distribution to be more continuous than was previously believed, and that the geographical size-relationship suggested by Davis and Follansbee (1945) to be inconsis-

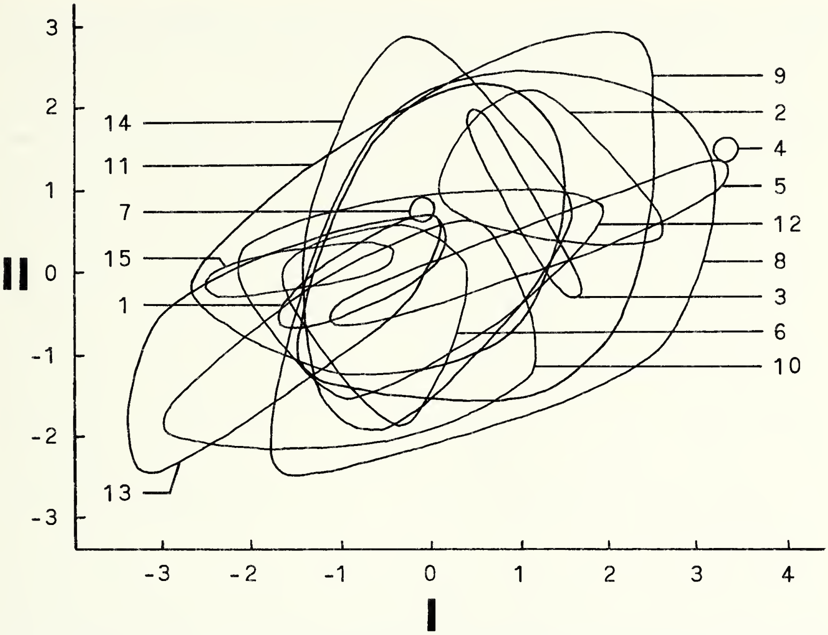

Fig. 3.—Plot of first two canonical variates, showing phenetic relationships among samples of *Peromyscus alstoni.* See Fig. 2 and text for explanation of samples.

Table 3.—*Variables used in discriminant function analysis of* Peromyscus alstoni. *Characters are listed in order of their usefulness in distinguishing groups with the character with the greatest between-group variance and the least within-groups variance being selected first. Other traits are ranked using the same criteria. The statistics are recalculated at each step. Because of no significant secondary sexual variation in* P. alstoni *males and females were combined.*

Step	Character	F-value	U-statistic
1	Palatilar length	6.77	0.6849
2	Nasal length	3.17	0.5631
3	Postpalatal length	2.59	0.4783
4	Length of maxillary toothrow	2.67	0.4040
5	Zygomatic breadth	2.43	0.3457
6	Condylobasal length	1.71	0.3088
7	Greatest length of skull	1.89	0.2727
8	Interorbital breadth	1.39	0.2483
9	Mastoid breadth	1.29	0.2276
10	Rostral breadth	1.16	0.2102

Table 4.—*Classification matrix for 15 samples of* Peromyscus alstoni, *based upon the discriminant functions of 10 cranial measurements. Values indicate the number of individuals classified into each group.*

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1
2	0	2	0	0	0	0	0	1	0	0	0	0	0	1	0
3	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	3	0	0	0	1	0	0	1	0	0	0
6	1	0	0	0	0	4	0	0	0	1	0	0	0	0	0
7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
8	1	2	2	1	3	3	6	16	1	6	2	0	0	1	1
9	3	3	3	1	2	5	2	5	7	2	4	2	1	5	2
10	0	0	0	0	0	4	1	1	1	10	0	0	4	1	1
11	0	3	1	0	1	3	3	1	1	3	3	1	3	1	1
12	1	0	1	0	1	0	0	1	2	0	0	4	2	0	0
13	2	0	0	0	0	1	0	0	1	1	2	1	5	0	2
14	2	3	1	0	0	2	0	2	2	2	1	3	1	7	0
15	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2

tant. Furthermore, genetic data (Rodriguez-Romero et al., 1975; Uribe et al., 1974) does not support differentiating the nominal taxa. Therefore, we have chosen to recognize *Peromyscus alstoni* as a monotypic species.

ACCOUNT OF SPECIES

Peromyscus (*Neotomodon*) *alstoni* (Merriam, 1898)

1898. *Neotomodon alstoni,* Merriam, Proc. Biol. Soc. Washington, 12:127–129.
1979. *Peromyscus alstoni,* Yates, Baker, and Barnett, Sys. Zool., 28:40–48.
1898. *Neotomodon perotensis,* Merriam, Proc. Biol. Soc. Washington, 12:127–129.
1944. *Neotomodon alstoni perotensis,* Davis, J. Mamm., 25:370–403.
1898. *Neotomodon orizabae* Merriam, Proc. Biol. Soc. Washington, 12:127–129.

Holotype.—Adult male, skin and skull, USNM 50534; Nahuatzin, Michoacán, México; collected 13 October 1892 by E. W. Nelson. Original number, 3580.

Measurement of holotype.—Total length, 225; length of tail, 103; length of hindfoot, 28; length of ear, —; greatest length of skull, —; condylobasal length, 30.5; palatilar length, 14.9; postpalatal length, 11.4; nasal length, —; zygomatic breadth, 16.2; mastoid breadth, 12.9; rostral breadth, 5.2; interorbital constriction, 4.5; length of maxillary toothrow, 5.5.

Distribution.—Restricted to the transvolcanic belt of central México, specifically the states of (northern) Michoacán, México, Distrito Federal, (northern) Morelos, Tlaxacala, (central) Puebla, and (west-central) Veracruz.

Specimens examined (1146).—DISTRITO FEDERAL: 7 km NW Ajusco, 3260 m, 10 (CB); 5 km NW Ajusco, 3050 m, 14 (CB); Jusco (=Ajusco), 11 (USNM); Canjada Contreras, 6 (UMMZ); Cañón Çontreras, 1 (UMMZ); Canyon Contreras, 13 (UMMZ); 2.5 km SW Contreras, 2850 m, 3 (2 UNAM, 1 KU); La Cima, 43 km S México City, 7 (UMMZ); 2 mi S La Cima, 9650 ft, 15 (MSU); 20 mi S México, 2900 m, 6 (3 UNAM, 3 KU); 33 km S, 2 km NW México, 2080 m, 9 (UNAM); 33 km S México, 2970 m, 16 (UNAM); 40 km S México City, 3500 m, 3 (AMNH); 42 km S México City, 1 (AMNH); 1 mi W Cerro Ocopixco, 2950 m, 4 (2 UNAM, 2 KU); Parres, 34 km S Cuidad de México, 8 (UNAM); 2 km S, 2 km W Parres, 2900 m, 15 (CB); 2 km SW Parres, 2900 m, 2 (UNAM); 2 km SSW Parres, 3 (UNAM); 2.5 km S, 2.0 km W Parres, 2900 m, 20 (19 CB, 1 UAMI); 2.6 km SW Parres, 1 (UNAM); 2.6 km SSW Parres, 3 (UNAM); 4 km S Parres, 3000 m, 3 (UNAM); 5 km SW Parres, 5 (CB); San Bartolomé, 4 (UMMZ); San Mathens, Boca de la Loma, 5 (UMMZ); Santa Rosa, 3000 m, 9 (6 FMNH, 3 UMMZ); Portilla de Santa Rosa, 6 (UMMZ); 3 km Santiago, Milpa Alta, 1 (UNAM); La Venta, 2850 m, 1 (UNAM); El Zarco, 3 (CB); Estación Piscicola, "El Zarco," 1 (UNAM); límites entre el Distrito Federal y Estado de Morelos, 1 (UNAM). MEXICO: Amecameca, 1 (USNM); 5 mi E Amecameca, 9600 ft, 10 (MVZ); Paso de Cortés, 23 km E Amecameca, 3450 m, 1 (KU); Paso de Cortés, 30 km E Amecameca, 3450 m, 3 (KU); Paso de Cortés, 34 km E Amecameca, 4 (UNAM); 12 km ESE Amecameca, 11,500 ft, 1 (KU); 1 km S, 2 km W Chimalpa, 2900 m, 1 (CB); Hacienda Córdoba, 1 (UMMZ); 2 km N, 4.5 km E Cabeza Iztaccíhuatl, 3600 m, 1 (CB); ½ mi NW Llano Grande, 10,600 ft, 11 (MSU); 40 km E México, 2870 m, 4 (UNAM); 45 km ESE México City, 22 (4 FMNH, 4 KU, 14 TCWC); 55 km ESE México City, 10,500 ft, 14 (2 KU, 12 TCWC); between México City and Puebla, 10,300 ft, 14 (AMNH); N slope Mt. Popocatépetl, 15 (6 MVZ, 9 TCWC); La Providencia, NW slope Popocatépetl, 17 (MVZ); Mt. Popocatépetl, 8 (USNM); Volcán Popocatépetl, 1 (UNAM); Puerto Lengua de Vaca, 8 (UMMZ); 1 km N, 8.5 km W Río Frío, 3450 m, 2 (CB); 9 km W Río Frío, 3050 m, 7 (CB); 5 mi W Río Frío, 10,000 ft, 2 (KU); 3 mi W Río Frío, 7 (TTU); 3 km W Río Frío, 3000 m, 3 (2 CB, 1 UAMI); Río Frío, 3000 m, 23 (7 FMNH, 1 UNAM, 15 UMMZ); 1 km S, 2½ km W Río Frío, 45 (CM); 1 mi S, 2 mi W Río Frío, 10,500 ft, 6 (KU); 2 mi ESE Río Frío, 8 (KU); 2 km S, 5 km W Río Frío, 9 (CB); 3 mi SW Río Frío, 5 (KU); 3 km S, 4 km W Río Frío, 3250 m, 11 (CB); Zoquiapan, 5 km SW Río Frío, 3220 m, 2 (UNAM); Zoquiapan, 15 km SW Río Frío, 20 (UAMI); 1 mi W Salazar, 9850 ft, 1 (KU); Salazar, 9 (1 AMNH, 8 USNM); 2 mi E Salazar, 10,200 ft, 4 (MSU); 2 mi WSW Salazar, 4 (KU); 1 mi WSW Salazar, 9500 ft, 12 (9 KU, 3 MSU); 5.2 km E San Pedro Nexapa, 3250 m, 5 (CB); 5.5 km E San Pedro Nexapa, 3250 m, 3 (CB); 20 km ENE Texcoco, Tlaxcala border, 4 (ANMH); 3.4 km N Tlamacas, 3600 m, 6 (CB); N slope Volcáno Toluca, 4 (USNM); Toluca Valley, 1 (USNM); 10 mi E Zitácuarto, 10 (UMMZ). MICHOACAN: 10 mi N Hidalgo, Cerro San Andrés, 9400 ft, 6 (UMMZ); 16 mi (N) Cuidad Hidalgo, 9150 ft, 1 (KU); 12 mi (N) Cuidad Hidalgo, 9150 ft, 13 (KU); Nahuatzin, 7 (1 MCZ, 6 USNM); 5 mi SE Opopeo, 4 (KU); Patamban, 15 (USNM); Mt. Tancítaro, 24 (22 FMNH, 2 USNM). MORELOS: 2 mi W Huitzilac, 10,000 ft, 5 (TCWC); Huitzilac, 1 (USNM); Cerro Cruz del Marquez, 2440 m, 10 (7 UNAM, 3 KU); 45 km S México City, 9400 ft, 7 (TCWC); km 46, México City—Acapulco Hwy, 30 (UMMZ); 5 km N Tres Cumbres, 10,200 ft, 20 (TCWC); 4 km N Tres Cumbres, 10,200 ft, 8 (MVZ); 3 km NNE Tres Cumbres, 3126 m, 8 (UNAM); 1.5 mi SSW Tres Cumbres, 8400 ft, 1 (MSU); Atexcapa, Zempoala, 1 (UNAM); Joya de Atexcapa, Zempoala, 3 (UNAM); Lagunas de Zempoala, 10 (UNAM); Parque Nacional Lagunas Zempoala, 1 (UMMZ). PUEBLA: 3 mi SSW Alchichica, 1 (TTU); 6 km E La Loma, 2750 m, 2 (UAMI); W slope Mt. Orizaba, 9 (TCWC); Mt. Orizaba, 5 (USNM); 7 mi (E) Río Frío, 1 (MCZ); Río Otlati, 15 km NW San Martín, 8700 ft, 8 (TCWC); Tlamacas, 3850 m, 7 (CB); Cerro Tlamacas, 3900 m, 8 (CB); 300 m SW Tlamacas, 3900 m, 1 (CB). TLAXCALA: 6½ km N Atlzayaca, 2600 m, 1 (CM); 21 km N, 10 km E Apizaco, 2900 m, 1 (CM); 21 km N, 11 km E Apizaco, 2900 m, 23 (CM); 10 km NE Calpulalpan, 3100 m, 10 (CB); 2 km W Calpulalpan, 2 (TTU);

Calpulalpan, 13 (UNAM); 5½ km S, 4 km W Calpulalpan, 28 (CM); 8 km S, 7 km W Calpulalpan, 2900 m, 78 (73 CM, 5 UAMI); 3 km S, 3 km E Graciano Sánchez, 2920 m, 3 (UAMI); 2 km S, 16 km W Huamantla, 2900 m, 3 (TTU); 3 km S, 11 km W Huamantla, 2950 m, 1 (TTU); 8 km S, 7 km W Huamantla, La Malinche Mt., 3800 m, 37 (CM); 9 km N, 1 km E Tlaxco, 3000 m, 10 (UAMI); 7 km N Tlaxco, 14 (10 TTU, 4 UAMI); 3 km N, 1 km E Tlaxco, 3000 m, 7 (UAMI). VERACRUZ: N slope Cofre de Perote, 34 (17 TCWC, 17 UMMZ); Cofre de Perote, 6 (USNM); Perote, 1 (USNM); 7 km E Perote, 2750 m, 9 (UNAM); 8 km E Perote, 2900 m, 1 (UNAM); 9 km Perote, 2 (CB); 10 km E Perote, 10 (1 CB, 9 UNAM); 1½ mi S Perote, 8500 ft, 1 (UMMZ); 10 km SE Perote, 12 (1 CB, 2 UNAM, 7 KU, 2 MCZ); Las Vigas, 1 (USNM); 1 km NW Pescados, 10,500 ft, 61 (KU).

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A RE-ANALYSIS OF GEOGRAPHIC VARIATION AND SYSTEMATICS IN THE YELLOW MUD TURTLE, *KINOSTERNON FLAVESCENS* (AGASSIZ)

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ABSTRACT

Geographic variation in *Kinosternon flavescens* is analyzed using univariate and multivariate phenetic analyses of 28 mensural and four meristic characters. A measure of shell reflectance is described. Characters useful in diagnosing the subspecies of *K. flavescens* are discussed. The results of the analyses suggest that *K. f. flavescens, K. f. arizonense,* and *K. f. durangoense* are phenetically distinctive valid subspecies, but that *K. f. spooneri* is synonymous with *K. f. flavescens.*

INTRODUCTION

Systematic relationships among mud turtles of the genus *Kinosternon* in North America and Mexico were in a general state of disarray prior to the 1970's. Misidentifications of museum specimens and literature records were so common that Iverson (1978*b,* 1979*a,* 1979*b,* 1982), Iverson and Berry (1979), Conant and Berry (1978), and Berry and Legler (1980) devoted considerable attention to these problems. Confusion over taxonomic relationships among *Kinosternon* resulted from inconsistencies and errors in earlier literature, which was based generally on insufficient comparative material and inadequate understand-

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ing of distributions and variation in morphology. The only general treatise on the Kinosternidae was that of Siebenrock (1907).

During the 1970's and 1980's, a series of modern, quantitative analyses of variation and systematic relationships of *Kinosternon* species has been published (Berry, 1978; Berry and Iverson, 1980; Berry and Legler, 1980; Iverson, 1978*a,* 1982), including two studies of *K. flavescens* (Iverson, 1979*b*; Houseal et al., 1982). This recent interest in taxonomic relationships among subspecies of *Kinosternon flavescens* has been prompted in part by proposed listing of the Illinois Mud Turtle, *K. f. spooneri,* on the Federal Endangered Species list (Federal Register, 6 July 1978). Dodd (1982, 1983) has reviewed the controversy surrounding this proposal as of early 1983.

The two thorough, analytical studies of variation and systematics of *Kinosternon flavescens* mentioned above (Iverson, 1979*b*; Houseal et al., 1982) came to opposite conclusions regarding the taxonomic validity of *K. flavescens spooneri.* The protected status of populations of *Kinosternon flavescens* assigned to *K. f. spooneri* is not legally contingent on the taxonomic validity of the subspecies, but many authorities felt that these populations might ultimately be affected by such a change in taxonomic status (C. K. Dodd and F. W. King, personal communication). A panel, the membership of which was selected by the National Academy of Sciences, attempted to determine which of these studies reflected more accurately the taxonomic status of *K. f. spooneri* (Berry et al., 1980). The panel recommended that a third objective study of variation and systematic relationships in *Kinosternon flavescens* be performed. This study was commissioned in response to the panel's recommendation. Its general purpose is to re-examine taxonomic relationships among populations of *Kinosternon flavescens,* with the ultimate objective of determining the status of *K. f. spooneri.*

Kinosternon flavescens occupies permanent and temporary pools, ponds, and backwaters from areas of sandy soil in Illinois, Iowa, and Nebraska in the north, southwestward across the central United States, and into northern Mexico (Sonora, Chihuahua, and Durango to Tamaulipas and Veracruz) (Conant, 1975; Conant and Berry, 1978; Seidel, 1978; Iverson, 1979*b*; Houseal et al., 1982). Four subspecies of *Kinosternon flavescens* have been recognized (Smith and Smith, 1979; Iverson, 1979*b*; Houseal et al., 1982). These are *K. f. flavescens* (Agassiz, 1857) which occurs from central Nebraska across the central United States and northeastern Mexico; *K. f. arizonense* Gilmore, 1922, from southern Arizona and Sonora, Mexico; *K. f. durangoense* Iverson, 1979, from the Río Nazas in Durango, and the Bolsón de Mapimí in Coahuila and Chihuahua, Mexico; and *K. f. spooneri* P. W. Smith, 1951, from the Mississippi River basin in Illinois, Iowa, and Missouri. Distribution maps are given in Iverson (1979*b*) and Houseal et al. (1982).

MATERIALS AND METHODS

A total of 929 specimens of *Kinosternon flavescens* were examined in this study (see Specimens examined), 768 of which were used in the numerical analyses. No attempt was made to examine every museum specimen in existence, nor was an attempt made to correct literature or museum identifications (but see Iverson, 1978*b*, 1979*a*, 1979*b*; Conant and Berry, 1978; Iverson and Berry, 1979 for such corrections). Instead, specimens from as much of the geographic range of the species as possible were examined, with emphasis on specimens from marginal populations or those of particular systematic importance.

Populations

Studies of geographic variation in *Kinosternon* turtles have effectively used major river systems as populations for the purpose of numerical analysis (Berry, 1978; Berry and Legler, 1980; Iverson, 1978*a*, 1979*b*, 1982; Houseal et al., 1982). *Kinosternon flavescens* tend to be somewhat more terrestrial than many *Kinosternon* species, but previous studies of *K. flavescens* as well as other, similarly terrestrial *Kinosternon* species (Berry, 1978; Berry and Legler, 1980; Iverson, 1982) have suggested the utility of the use of samples from major river systems as biological populations. To maintain validity of the numerical analyses, no population was analyzed unless it consisted of at least three measurable adult specimens of each sex. It was necessary to pool samples from some adjacent river systems to achieve this minimum number (for example, Table 1, population 20 consists of specimens from four adjacent river systems in northeastern Mexico). In other instances, large samples from segments of a single drainage permitted partitioning into two or more populations (for example, Table 1, populations 13 and 14 are samples from the Upper and Lower Rio Grande respectively). The populations sampled, abbreviations, and numbers of specimens examined are given in Table 1.

Characters

The numerical analyses used in this study are based on 28 mensural and four meristic characters, which have been shown to be geographically variable in other kinosternid studies (Berry, 1978; Iverson 1977, 1978*a*, 1979*b*, 1982; Houseal et al., 1982; Seidel et al., 1981; Reynolds and Seidel, 1983). All linear measurements were taken by the author with a dial caliper to the nearest 0.1 mm. Details on techniques of measurement (excluding reflectance) are given by Berry (1978).

The characters and their abbreviations are as follows: maximum length of carapace (CL); maximum width of carapace (CW); length of each scute seam at the midline, gular (GUL), humeral (HUL), pectoral (PEL), abdominal (ABL), femoral (FEL), anal (ANL), and the depth of the anal notch (NOT); the width of the plastron at the gular scute (GUW), anterior lobe at the humeral-pectoral seam (HPW), anterior hinge at the pectoral-abdominal seam (AHW), posterior hinge at the abdominal-femoral hinge (PHW), transfemoral scutes (TFW), and width at the femoral-anal seam (FAW); height of the shell from mid-abdominal scute (ventral) to mid-third central scute (dorsal) (SHT); length of the bridge on the left side (BRL); maximal width of the head (HW); length of the first central scute at the midline (C1L), width of C1 at its anterior extremity (C1A), and width at its contact with C2 (C1P), length and width of C3 (C3L and C3W), and length and width of C5 (C5L and C5W); maximum length of the axillary (AXL) and inguinal (ING) scutes on the left side; and reflectance as described below (REF). Meristic characters included the following: marginal scute number at maximum carapace width (CWN); are axillary and inguinal scutes in contact on the right and/or left sides? (AIC); is the first central scute in contact with the second marginal on the right and/or left sides? (M2C); and is marginal scute 10 higher than marginal scute 11 on the right and/or left sides?

Table 1.—*Populations of* Kinosternon flavescens *utilized in numerical analyses as represented by river systems, with abbreviations, states, and numbers of specimens examined.*

Sample		State	Males	Females
		K. f. spooneri		
1. Illinois River	(ILL)	Illinois	11	7
2. Mississippi River	(MIS)	Illinois, Iowa, and Missouri	54	58
		K. f. flavescens		
3. Nebraska sandhills	(NEB)	Nebraska	21	18
4. Republican River	(REP)	Nebraska	3	3
5. Arkansas River and Smoky Hill River	(ARK)	Oklahoma, Kansas	26	40
6. Cimarron River	(CIM)	Kansas	31	33
7. Canadian River	(CAN)	Oklahoma, Texas, New Mexico	50	49
8. Red River	(RED)	Oklahoma, Texas	5	3
9. Brazos River	(BRZ)	Texas	9	4
10. Colorado River	(COL)	Texas	5	3
11. San Antonio River and Nueces River	(SAN)	Texas	8	5
12. Pecos River	(PEC)	Texas, New Mexico	57	48
13. Upper Rio Grande	(URG)	Texas, New Mexico, Chihuahua	16	4
14. Lower Rio Grande	(LRG)	Texas, Coahuila	5	8
15. Río Conchos	(CON)	Chihuahua	5	0*
16. Playa Lakes	(PLA)	New Mexico	13	8
17. Río Casas Grandes	(CAS)	Chihuahua	10	8
18. Río Santa Maria	(SMA)	Chihuahua	36	17
19. Río Salado	(SAL)	Coahuila	11	18
20. Río San Fernando, Río Soto la Marina, Río Tamesí (northeastern Mexico)	(NEM)	Tamaulipas, Nuevo Leon	6	4
		K. f. arizonense		
21. Río San Simón, Río Magdelena, Río Sonora, Río Yaqui (northwestern Mexico)	(NWM)	Arizona, Sonora	9	26
		K. f. durangoense		
22. Río Nazas and Bolsón de Mapimí	(DUR)	Durango, Chihuahua	8	7

* Not used in numerical analyses.

(M11). Coloration of the soft parts, the number and shape of gular barbels, and presence of epizoic algae were noted, but not used in the numerical analyses. Only data from adult specimens (carapace length 80 mm or more) were used for the numerical analyses, which is in agreement with the criteria used by Houseal et al. (1982) rather than Iverson's

(1979*b*) use of 75 mm or Seidel's (1978) use of 100 mm. Conant and Berry (1978) discussed the significant morphological differences between adults and juveniles of *Kinosternon flavescens.*

In general, only specimens from which a full complement of characters was available were used in the numerical analyses, but if only one or two characters were absent the missing data were estimated using computer program BMDPAM (Dixon, 1983), a linear regression approximation procedure.

Since the first published accounts of its existence (Cahn, 1931, 1937; P. W. Smith, 1948), and throughout its taxonomic history (P. W. Smith, 1951, 1961; Conant, 1975; Conant and Berry, 1978; Pritchard, 1979; Ernst and Barbour, 1972; Iverson, 1979*b*; Houseal et al., 1982), *Kinosternon flavescens spooneri* has been diagnosed as having a dark brown to black shell and soft parts. As analysis of the status of *K. f. spooneri* is a major objective of this study, a technique to measure objectively the relative "darkness" of *K. flavescens* specimens was developed. Since this technique is new and bears importantly on the results of the analyses, a detailed description is appropriate. Houseal et al. (1982) used a subjective, non-numerical color estimate to categorize *K. flavescens* specimens. In this study "reflectance," or the ratio of incident to reflected light (Bennett, 1966), was used as a measure of the relative lightness or darkness of the shell. Because darker specimens absorb more incident light, relatively less light is reflected than in lighter specimens. The apparatus used to measure reflectance utilized two standard photographic lamps with 100-watt incandescent bulbs, positioned 150 mm from the surface being measured. A photovoltaic light meter with an accurate photoelectric cell was positioned between the light sources, 150 mm away from the surface. A calibrating measurement was first made of a piece of flat black construction paper with a known reflectance of 17 footcandles. Minor adjustments were made in the distance from the lights to the paper until a measurement of precisely 17 footcandles was achieved. For reflectance measurement a *K. flavescens* shell replaced the black paper. As flat a surface as possible was presented to the apparatus—usually the third central scute (C3). If C3 was damaged, algae encrusted, discolored, or not flat, then an adjacent area was measured. Lower reflectance values indicated less reflected light (that is, more absorbed light) and a darker shell.

This technique, however, measures only relative lightness or darkness; it does not measure "color." Caution must be exercised to avoid several sources of error. It has been suggested to us by several museum curators that standard turtle preservation techniques (hardening with formalin and storage in ethanol or isopropanol) do not significantly alter color, even though Houseal et al. (1982) imply that such color alteration might occur. Our experience is that discoloration of carapacial scutes may result from excessive exposure to light, drying, or other mismanagement of specimens. If a specimen appeared to be discolored, it was excluded from the numerical analyses.

Epizoic algae or encrusted mud may discolor *Kinosternon* shells and hamper reflectance measurement. Superficial materials can usually be removed with careful scrubbing, but care must be used not to roughen the surface of the scutes and thus alter reflectance.

Numerical Techniques

The statistical analyses performed in the present study are "phenetic," based on the relative similarity or dissimilarity of individuals in populations with many characters considered simultaneously without *a priori* weighting (Jardine and Sibson, 1971; Sneath and Sokol, 1973). Such analyses have been used frequently and successfully in analyses of variation in kinosternid turtles (Iverson, 1977, 1978*a,* 1979*b,* 1982; Berry, 1978; Seidel et al., 1981; Houseal et al., 1982; Reynolds and Seidel, 1983). Cladistic analyses (Hennig, 1966; Eldredge and Cracraft, 1980; Wiley, 1981) of kinosternid turtles are those of Iverson (1982) and Seidel and Lucchino (1981). Mayr (1981) has compared phenetic and cladistic methodologies.

Univariate statistics (means, standard deviations, and various ratios) were generated using either program BMDP1D (Dixon, 1983), or programs of the author's development. Multivariate analyses are based on a stepwise multiple discriminant analysis (MDA) which utilized the program BMDP7M (Dixon, 1983), the output of which includes: (1) the variable added at each step of the analysis which added most of the separation of the populations; (2) the F-statistic on which the variables added are based, and which can be used as a test of significance; (3) the multivariate distance between population centroids D^2; (4) a canonical analysis which provides percent dispersion of each subsequent axis; and (5) a plot of each specimen and population centroids plotted on the first versus the second canonical axes (only centroids will be presented in this study). Finally, cluster analyses were performed with D^2 values using program BMDP2M (Dixon, 1983). Because of the extreme sexual dimorphism in *Kinosternon flavescens* (Seidel, 1978; P. W. Smith, 1961), all analyses were performed separately on males and females.

Data Standardization

The specimens of *Kinosternon flavescens* used in the analyses varied considerably in size (CL = 80–169 mm). To standardize data such that they are independent of size, ratios of each mensural character (exclusive of REF) divided by CL were used as input variables to the statistical analyses.

The use of ratios as input variables has been controversial (Atchley et al., 1975, 1976; Nussbaum, 1976; Corruccini, 1977; Atchley and Anderson, 1978; Atchley, 1978; Albrecht, 1978; Dodson, 1978; Hills, 1978). Elsewhere Berry (1978, manuscript) contrasted the use of ratios as input variables with residual values from regression (the alternative to ratios, but see Wood, 1983) in MDA analyses of variation in the *Kinosternon leucostomum* species group. Results were practically indistinguishable. Ratios have been used effectively as input variables in multivariate analyses of geographic variation in other kinosternid turtles (Berry, 1978; Iverson, 1977, 1978*a*, 1979*b*, 1982; Houseal et al., 1982). No statistical significance is associated with the output of the MDA in the present study, rather the output from the MDA are used as descriptive statistics only.

Finally, linear regression analysis using program BMDP2R (Dixon, 1983) was performed using reflectance (REF) values as dependent variables, and a series of environmental characteristics as independent variables. This analysis seeks to determine which environmental characteristics are most important in explaining the relatively dark (or light) shell of *Kinosternon flavescens* populations. Mean REF values were used from the following populations, males and females considered separately (see Table 1 for abbreviations): *K. f. spooneri*, MIS; *K. f. flavescens*, NEB, CIM, CAN, BRZ, SAN, PLA, SMA, and NEM; *K. f. arizonense*, NWM; and *K. f. durangoense*, DUR. Environmental variables used as independent variables in the multiple regression analyses were the following: (1) mean precipitation for March; (2) mean precipitation for September; (3) mean rainfall variability; (4) mean humidity for March; (5) mean humidity for September; (6) annual percent of sunshine; (7) mean temperature for January; (8) mean temperature for July; (9) average annual days with snowfall over 25 mm; (10) latitude; (11) longitude; (12) elevation; (13) natural vegetation type (for example, deciduous forest or prairie); and (14) natural soil type (for example, sand or loam). Sources for environmental data include Vivo Escoto (1964), Anonymous (1968, 1970), and a series of maps including the American Geographical Society topographic maps, and World Aero Chart maps.

RESULTS

Data reductions (mean, range, standard deviation) for nine characters or character ratios are given in Table 2. Values are presented for combined populations of each recognized subspecies, and separately for population NEB (Nebraska sandhills). Because ratios may not represent a normally distributed data set, standard deviations are intended only to demonstrate relative variability rather than statistical significance (Iverson, 1979*b*:15, 1982:20). Table 2 (univariate analyses) shows several interesting patterns. The relatively large size attained by *K. f. arizonense* and *K. f. durangoense* is apparent. The largest specimen measured in this study was an adult male (JBI A31) from Pima Co., Arizona with CL = 168.8 mm. Each of the characters or character ratios in Table 2 separates at least one taxon from the other three. ANT/CL suggests a north-south cline with the northernmost taxa (*K. f. spooneri,* populations 1 and 2, and Nebraskan *K. f. flavescens,* populations 3 and 4) generally having the shortest anterior lobes by comparison with the southernmost (*K. f. arizonense* and *durangoense*). Similar clines appear for each character presented, although values may decrease from north to south (ANT/CL, ANL/POS), increase from north to south (REF), or show major differences between the southern subspecies *K. f. durangoense* and *K. f. arizonense* (AHW/CW, TFW/CW, GUL/ANT, AIC, and M2C). Because of their importance in previous diagnoses of *K. f. spooneri* (Wermuth and Mertens, 1961; Ernst and Barbour, 1972; Seidel, 1978; Smith and Smith, 1979; Behler and King, 1979; Iverson, 1979*b*), the characters GUL/ANT and REF are of special significance. Table 2 suggests that these characters are of questionable diagnostic value.

Results of the multivariate analyses are presented in Table 3 and Figs. 1–4. Table 3 shows the first eight characters selected by the MDA for males and females and their F-values, which indicates the relative importance of each character in accounting for variability in the system. Figs. 1 and 2 are plots of population mean centroids along the first versus second canonical axes. These axes account for 38.2% and 16.8% (males), and 40.4% and 14.2% (females) of the total dispersion. The relative positions of the centroids to each other is an effective visual demonstration of the relative positions of population means based on all 32 characters considered simultaneously. The relative distances between population centroids can be represented numerically by the Mahalanobis distance measure "D^2." The D^2 values between each population mean centroid are used as the basis for the phenograms in Figs. 3 and 4. The closer two populations appear in the branching sequence, the closer their population centroids in hyperspace (that is, D^2 is smaller). This is a visual demonstration of the phenetic similarity among populations. The results of the multiple regression analyses appear in Table 4, males and females separate. For each analysis, the first six most important variables (those with the highest correlation coefficient = r^2) are listed in decreasing order.

Table 2.—*Characters and character ratios resulting from univariate analyses. Values for ratios are given as percents. CL is in mm. Each ratio includes ± one standard deviation, and the range.*

Sex and population CL	ANT/CL	AHW/CW	TFW/CW	GUL/ANT	ANL/POS	REF	AIC	M2C
Males								
K. f. spooneri (populations 1–2). N = 60								
123.9 ± 11.4 86.5–144.3	31.9 ± 1.8 28.3–34.2	67.3 ± 2.7 63.7–72.0	60.7 ± 2.4 57.7–65.1	48.3 ± 4.6 40.8–54.8	71.5 ± 10.4 61.1–101.0	9.8 ± 2.6 7–14	53/60 = 88.3%	52/60 = 86.7%
K. f. flavescens (population 3). N = 18								
121.5 ± 6.0 101.8–127.9	33.4 ± 1.2 31.7–36.1	69.9 ± 1.6 67.3–72.7	63.0 ± 1.1 61.4–64.5	47.9 ± 3.5 41.8–53.2	71.7 ± 2.6 67.6–75.2	15.2 ± 2.8 9–19	18/18 = 100%	7/18 = 38.9%
K. f. flavescens (populations 3–20). N = 311								
120.6 ± 15.7 83.8–144.3	32.3 ± 1.6 27.5–36.3	69.1 ± 2.6 61.4–74.7	61.1 ± 2.2 55.4–65.1	41.7 ± 8.2 14.2–65.3	70.1 ± 4.5 57.1–79.2	16.1 ± 3.0 8–23	283/311 = 91.6%	167/311 = 53.7%
K. f. arizonense (population 21). N = 7								
139.0 ± 23.2 97.8–168.8	32.8 ± 1.0 31.4–34.2	71.5 ± 2.4 67.5–74.4	60.6 ± 1.5 58.5–62.3	59.5 ± 2.9 56.9–65.3	59.8 ± 5.1 51.1–63.2	16.1 ± 3.2 13–23	4/7 = 57.1%	0/7 = 0.0%
K. f. durangoense (population 22). N = 8								
139.1 ± 13.4 118.3–157.7	31.3 ± 1.2 29.4–32.1	65.5 ± 1.8 63.8–69.0	56.8 ± 1.5 54.4–58.5	63.0 ± 2.6 59.7–65.7	57.7 ± 8.4 49.9–71.2	23.6 ± 6.1 15–31	6/8 = 75.0%	7/8 = 87.5%
Females								
K. f. spooneri (populations 1–2). N = 58								
102.2 ± 9.4 92.6–114.4	35.6 ± 1.1 34.3–37.8	72.1 ± 2.0 69.4–77.1	62.5 ± 1.4 60.6–65.8	47.8 ± 5.4 39.8–55.1	83.5 ± 2.3 80.4–87.2	7.9 ± 1.5 5–11	48/58 = 82.8%	51/59 = 87.9%
K. f. flavescens (population 3). N = 18								
102.7 ± 5.5 93.2–111.1	34.3 ± 1.1 32.5–36.4	72.2 ± 3.6 68.8–80.3	64.6 ± 2.4 61.5–70.2	44.3 ± 6.6 36.7–59.0	85.1 ± 0.7 84.0–86.3	14.7 ± 1.0 13–16	17/18 = 94.4%	4/18 = 22.2%

Table 2.—*Continued.*

Sex and population CL	ANT/CL	AHW/CW	TFW/CW	GUL/ANT	ANL/POS	REF	AIC	M2C
K. f. flavescens (population 3–20). N = 263								
107.8 ± 9.2	32.9 ± 1.5	70.3 ± 3.0	61.3 ± 2.8	40.1 ± 7.8	82.3 ± 3.8	16.8 ± 3.6	258/263	150/263
80.0–127.61	29.4–36.4	63.8–80.3	50.7–70.2	20.2–59.0	75.9–91.2	8–29	= 94.2%	= 57.0%
K. f. arizonense (population 21). N = 22								
134.0 ± 17.0	33.1 ± 1.1	75.5 ± 2.4	64.1 ± 1.9	51.9 ± 13.7	69.6 ± 9.5	14.1 ± 2.8	7/22	0/22
110.7–157.7	31.4–35.1	72.5–78.6	61.3–67.1	22.8–62.6	62.2–84.2	8–17	= 31.8%	= 0.0%
K. f. durangoense (population 22). N = 7								
119.7 ± 17.0	31.0 ± 1.1	66.1 ± 1.9	57.8 ± 2.0	60.1 ± 4.6	63.7 ± 8.3	21.4 ± 4.9	6/7	6/7
96.2–147.9	28.6–31.7	63.8–69.4	55.2–60.0	53.3–69.2	54.7–80.9	15–29	= 85.7%	= 85.7%

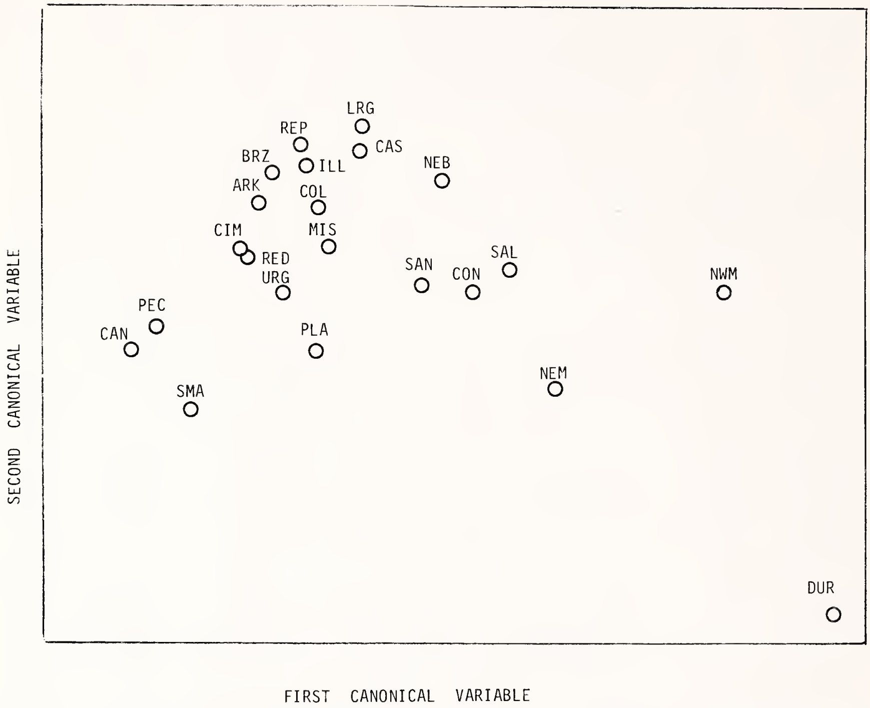

Fig. 1.—Plots of population centroids on first versus second canonical variables for males of *Kinosternon flavescens*. Population abbreviations are given in Table 1.

DISCUSSION

Univariate Analyses

Diagnoses of each subspecies of *Kinosternon flavescens* using the univariate analyses in Table 2 are given under *Taxonomic Recommendations* below.

Data for specimens from population 3 (NEB = Nebraska sandhills) are included for comparative purposes in Table 2. Specimens from this population are intermediate between *K. f. spooneri* and *K. f. flavescens* (or even closer to *spooneri*) in the characters CL, ANT/CL, ANT/CL (females), GUL/ANT, and REF. *Kinosternon f. spooneri* is more similar to *K. f. flavescens* (populations 3–20) than it is to population 3 alone in characters ANT/CL (males), AHW/CW, TFW/CW, ANL/POS, AIC, and M2C. This illustrates the uniqueness of specimens from the Nebraska sandhills (population 3), and the overall similarity of *K. f. spooneri* to the nominate subspecies. The characters used most fre-

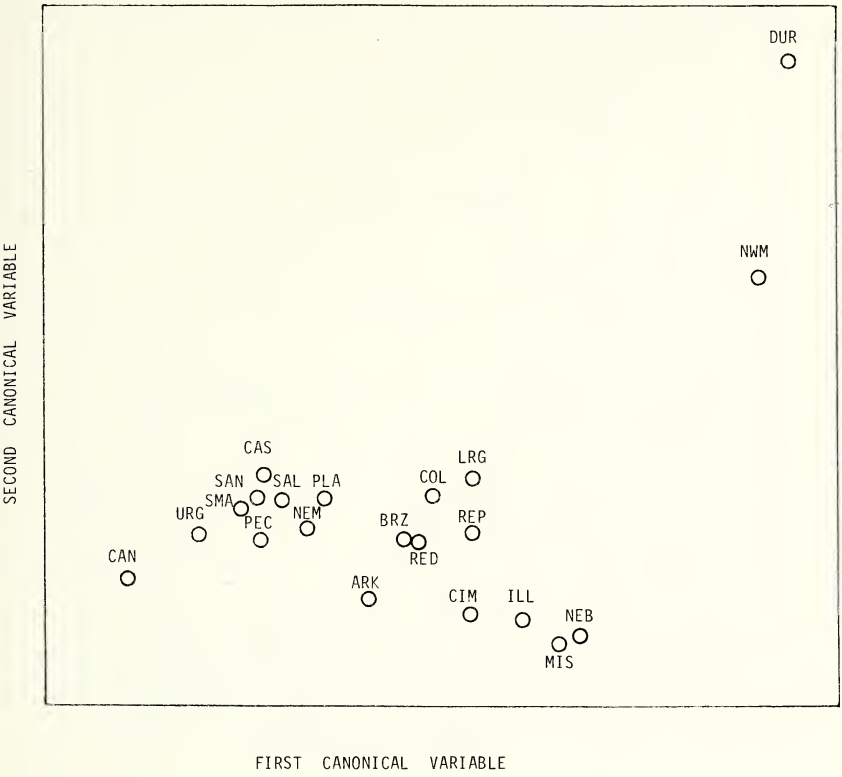

Fig. 2.—Plots of population centroids on first versus second canonical variables for females of *Kinosternon flavescens*. Population abbreviations are given in Table 1.

quently to diagnose *K. f. spooneri* (GUL/ANT and REF) are of questionable reliability. Based on the results of the univariate analyses, *K. f. spooneri* is more similar to *K. f. flavescens* than is either *K. f. arizonense* or *K. f. durangoense*.

In addition, Table 2 demonstrates sexual dimorphism in several characters (Seidel, 1978; Iverson, 1979*b*; Berry and Shine, 1980). Males are larger than females in mean and maximum CL in each group of populations. Females generally exceed males in ANT/CL, AHW/PW, and TFW/CW, indicating the proportionately larger plastron in females (Berry, 1977; Iverson, 1979*b*). Males generally exceed females in GUL/ANT and REF.

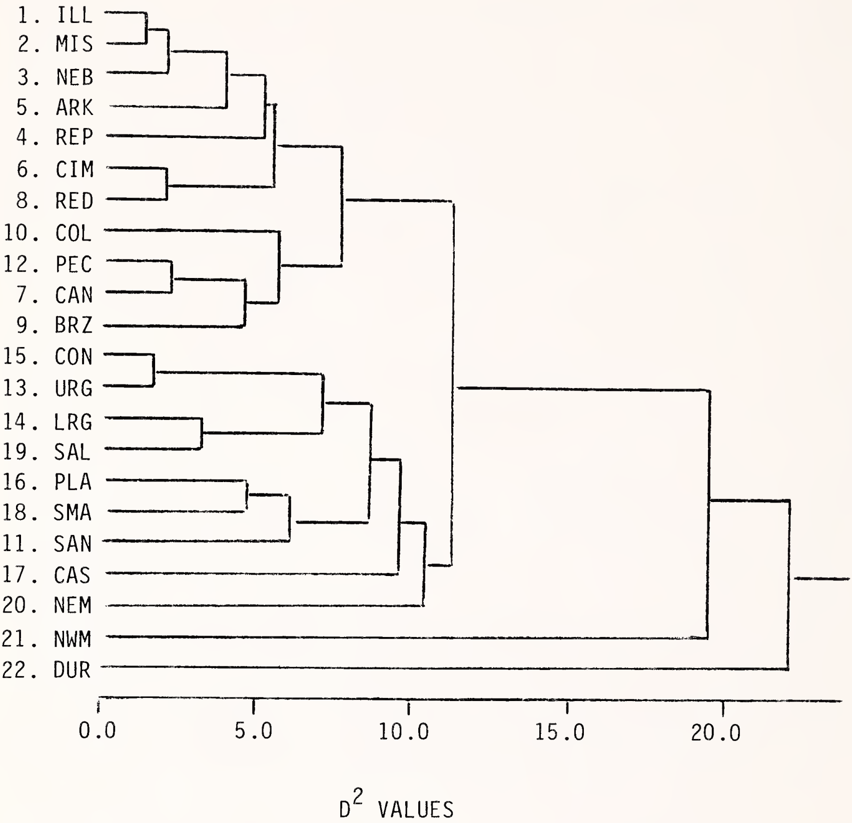

Fig. 3.—Dendrograph of D^2 values of males of *Kinosternon flavescens.* Population abbreviations are given in Table 1.

Multiple Discriminant Analyses

The characters GUL and REF on which most diagnoses of *K. f. spooneri* are based are among the first four selected by the MDA (1 and 2 in males, 1 and 4 in the female analysis; Table 3). This suggests these characters are important in accounting for variability among populations. Six of the first eight characters selected in both males and females relate to the shape of the plastron indicating that the plastron is a geographically variable structure in *Kinosternon flavescens* (Iverson, 1979*b*; Houseal et al., 1982).

Figs. 1–4 demonstrate recurrent phenetic distinctiveness of popu-

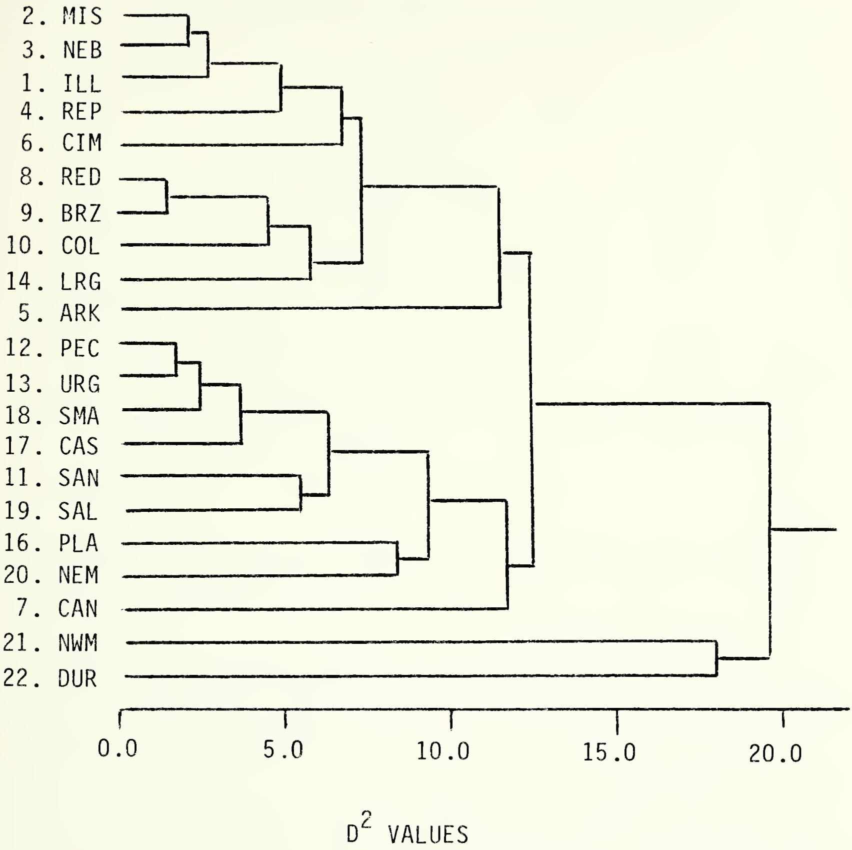

Fig. 4.—Dendrograph of D^2 values of females of *Kinosternon flavescens*. Population abbreviations are given in Table 1.

lations 21 (NWM, corresponding to *K. f. arizonense*), and 22 (DUR, corresponding to *K. f. durangoense*). Although the two populations cluster together in the female analysis (Fig. 4), it is only at a high level of similarity ($D^2 = 17.6$). The remainder of the populations form a more-or-less homogeneous group. In Fig. 1 population NEM (northeastern Mexico) is somewhat distinct, as is population CAN (Canadian River) in Fig. 2. However, Figs. 3 and 4 indicate that populations NEM and CAN are not consistently phenetically distinctive.

Of particular consequence to the objectives of the present study is the lack of phenetic distinctiveness of the two populations (MIS and ILL, populations 1 and 2 which correspond to the subspecies *K. f.*

Table 3.—*Summary of first eight steps of multiple discriminant analyses. Includes the variable selected at each step, and the appropriate F-statistic.*

Sex	Step number	Variable selected	*F*-statistic
Males			
	1.	AHW	28.936
	2.	GUL	21.032
	3.	REF	18.766
	4.	ANL	10.318
	5.	PHW	7.504
	6.	FEL	6.446
	7.	M2C	6.783
	8.	HPW	6.204
Females			
	1.	GUL	24.437
	2.	TFW	21.354
	3.	ANL	16.175
	4.	REF	9.270
	5.	AHW	6.570
	6.	FEL	5.226
	7.	AXL	5.043
	8.	SHT	4.813

spooneri). Instead, populations ILL and MIS cluster only at a very low level of phenetic similarity, and consistently with population NEB (Nebraska sandhills, population 3). This phenetic relationship is almost precisely that found by Houseal et al. (1982). Although we would not support such a partition in *Kinosternon flavescens,* the most logical and parsimonious division of populations 1–20 would put all populations from the Canadian River northward in one phenetic group, and populations from the Red River southward in another.

Multiple Regression Analysis of Reflectance

In their analysis of color in *Kinosternon flavescens,* Houseal et al. (1982) found a north-south cline with the highest proportion of dark individuals in the northern part of the range. In this study, mean reflectances (males and females combined) were determined for the following populations (arranged in order approximately from north to south): MIS = 7.93, NEB = 15.00, CIM = 18.44, CAN = 15.22, BRZ = 19.67, PEC = 13.89, PLA = 19.11, SMA = 16.56, NWM = 15.07, SAN = 17.44, NEM = 19.86, and DUR = 22.47. There is an increase in reflectance from north to south (r = .646, with 10 df, $P < .05$). Multiple regression analysis of reflectance against latitude and environmental variables suggests other factors which might affect darkness

Table 4.—*Environmental variables added to multiple regression on reflectance.*

Sex	Step	Variable added	r^2	Increase in r^2
Males				
	1.	Annual percent of sunshine.	.6600	.6600
	2.	Mean temperature for July.	.7918	.1318
	3.	Average days with snowfall.	.8803	.0884
	4.	Latitude.	.9380	.0577
	5.	Mean precipitation for September.	.9789	.0409
	6.	Mean temperature for January.	.9871	.0382
Females				
	1.	Mean temperature for January.	.7338	.7338
	2.	Latitude.	.8140	.0802
	3.	Annual percent of sunshine.	.8673	.0533
	4.	Mean temperature for July.	.9053	.0380
	5.	Average days with snowfall.	.9264	.0211
	6.	Rainfall variability.	.9570	.0306

of the shell. The results (Table 4) show that factors associated with temperature and/or sunshine are most highly correlated with reflectance.

Brown and Moll (1979) suggested that the dark coloration of *K. f. spooneri* is a cryptic adaptation to camouflage turtles in ponds covered with dark leaves, or where the water is stained darkly. This hypothesis fails to explain the populations of dark individuals that occur in clear-water ponds with sand or submerged vegetation on the bottoms, such as are found in Illinois and Nebraska (Kofron and Schreiber, 1982; authors' personal observations; J. B. Iverson, personal communication). It also fails in view of either the high between and within population variation, or the clinal nature of shell coloration in *K. flavescens*. As an alternative hypothesis, we suggest that the dark coloration of *K. f. spooneri* (as well as other dark populations) is an adaptation to the cooler conditions under which Illinois, Iowa, Missouri, and Nebraska populations must survive. The darker carapace could serve to heat the animal more quickly than a lighter carapace. P. W. Smith (1957) speculated that *Kinosternon flavescens* (like *Pseudacris streckeri* and *Heterodon nasicus*) is a relict species, having been isolated in pockets of sandy soil in Illinois and Iowa by a Pleistocene glacial event. The results of the reflectance analysis as well as the MDA tend to support this hypothesis. In fact, the phenetic similarity of Illinois and Iowa populations to those from the Nebraska sandhills suggests that the geographic range of *Kinosternon flavescens* was once continuous across the northern Midwest. A subsequent glacial event with associated cooling may have extirpated the intervening populations leaving relict populations in the sandy refugia they currently inhabit. The biogeography of *K. flavescens* has been reviewed by Houseal et al. (1982).

Taxonomic Recommendations

Based on both univariate and multivariate analyses, it seems clear that *K. f. arizonense* and *K. f. durangoense* are phenetically distinct from the nominate subspecies, and are therefore considered valid subspecies. Based on the multivariate analyses the remainder of *K. f. flavescens* populations (populations 1–20) are not further divisible into subspecies. As noted above, the most logical division would separate populations at the Canadian and Red rivers, but would not recognize populations 1 and 2 (ILL and MIS = *K. f. spooneri*) as distinctive. Brown and Moll (1979:21) suggested that *K. f. spooneri* might actually be a species distinct from *K. flavescens*. Iverson (1979*b*) recommended the continued recognition of *spooneri* as a subspecies of *Kinosternon flavescens*. Nevertheless, based on the univariate and multivariate analyses presented in this study we follow Houseal et al. (1982) in recommending that *Kinosternon flavescens spooneri* be placed in the synonymy of *K. f. flavescens*.

Kinosternon flavescens (Agassiz)
Yellow Mud Turtle

Platythyra flavescens Agassiz, 1857:430, Pl. V. Type-locality: "Texas, near San Antonio . . ."; incorrectly restricted by Smith and Taylor (1950) to "Waco, Texas" (Maslin, 1959:22). Lectotype: USNM 50, from "Rio Blanco, near San Marcos, Texas."
Cinosternum flavescens Agassiz, 1857:Pl. V.
Kinosternon hippocrepis Gray, 1858:289 (in part).
Cinosternon hippocrepis Strauch, 1862:41 (in part).
Kinosternum flavescens Cope, 1892:333.
Kinosternon flavescens Stone, 1903:540. First usage.

Kinosternon flavescens flavescens (Agassiz)
Yellow Mud Turtle

Kinosternon flavescens flavescens Hartweg, 1938:3. First use of trinomen.
Kinosternon flavescens spooneri P. W. Smith, 1951:195. Type-locality: "Henderson County State Forest, 7 miles north of Oquawka, Henderson Co., Illinois." Holotype: INHS 4244. Placed in synonymy by Houseal et al., 1982:579.

Diagnosis.—*K. flavescens flavescens* (populations 1–20): Carapace small (CL averages 120.6 mm and reaches a maximum of 144.3 mm in males, averages 107.8 mm and reaches 127.6 mm in females); plastron relatively wide at both anterior and posterior hinge (AHW/CW = 69.1% in males, 70.3% in females; TFW/CW = 61.1% in males, 61.3% in females); gular scute short (GUL/ANT = 41.7% in males, 40.1% in females); interanal seam long (ANL/POS = 70.1% in males, 82.3% in females); shell of medium darkness (REF = 16.1 in males, 16.8 in females); axillary and inguinal scutes nearly always in contact on both sides (AIC = 91.6% in males, 94.2% in females); and second marginal scutes in contact with first central in just over one-half of specimens (M2C = 53.7% in males, 57.0% in females).

Distribution.—*K. f. flavescens* occurs from the Republican River in Nebraska, south to coastal Mexico below the Río Pánuco in Veracruz, and west to the upper Río Yaqui in Arizona and the Río Conchos in Chihuahua. Isolated populations occur in the northern Nebraska sandhills (population 3); the Neosho River in southeastern Kansas, and adjacent Missouri and Oklahoma; and the Illinois and upper Mississippi rivers in Illinois and adjacent Iowa and Missouri (populations 1 and 2). Range maps are in Iverson (1979*b*), Smith and Smith (1979), and Houseal et al. (1982).

Kinosternon flavescens arizonense Gilmore
Arizona Mud Turtle

Kinosternon arizonense Gilmore, 1922:2. Type-locality: "Benson Locality Quarry, 3.2 km S Benson, Cochise Co., Arizona." Holotype: Blancan fossil USNM 10463. Placed in synonymy by Iverson, 1979*a*:176–177.

Kinosternon flavescens stejnegeri Hartweg, 1938:1 (in part). Type-locality: "Llano, Sonora, Mexico." Holotype: UMMZ 72235. Placed in synonymy by Iverson, 1979*a*: 176–177.

Kinosternon flavescens flavescens Stebbins, 1954:162 (in part).

Kinosternon flavescens arizonense Iverson, 1979*a*:177. First use of trinomen.

Diagnosis.—*K. flavescens arizonense* (population 21): Carapace large (CL averages 139.0 mm in males, and reaches 168.8 mm; CL averages 134.0 mm in females, and reaches 157.7 mm): anterior plastral lobe relatively long (ANT/CL = 32.8% in males, 33.1% in females); anterior hinge wide (ANT/CL = 71.5% in males, 75.5% in females); but posterior hinge moderate in males (TFW/CW = 60.6%) and wide in females (TFW/CW = 64.1%); gular scute short (GUL/ANT = 59.5% in males, 51.9% in females); interanal seam short (ANL/POS = 59.8% in males, 69.6% in females); shell of medium darkness (REF = 16.1% in males, 14.1% in females); axillary and inguinal scutes in contact on both sides in only about one-third to one-half of specimens (AIC = 57.1% in males, 31.8% in females); and second marginals do not contact first central scutes (M2C = 0.0% in both males and females).

Distribution.—*K. f. arizonense* ranges from the San Simon Valley in southern Arizona, south to the Río Yaqui and Río Matape in southern Sonora, Mexico. Range maps are in Iverson (1979*b*), Smith and Smith (1979), and Houseal et al. (1982).

Kinosternon flavescens durangoense Iverson
Durango Mud Turtle

Kinosternon flavescens stejnegeri Hartweg, 1938:1 (in part).

Kinosternon flavescens durangoense Iverson, 1979*b*:219. Type-locality: "8 km from Ceballos in Lagos de los Palomas, Durango, Mexico." Holotype: UF/FSM 16180.

Diagnosis.—K. flavescens durangoense (population 22): Carapace large (CL averages 139.1 mm and reaches 211.0 mm in males; CL averages 119.7 mm and reaches 147.9 mm in females); anterior plastral lobe short (ANT/CL = 31.3% in males, 31.0% in females); plastron relatively narrow (TFW/CW = 56.8% in males, 57.8% in females; AHW/CW = 65.5% in males, 66.1% in females); gular scute long (GUL/ANT = 63.0% in males, 60.1% in females); interanal seam short (ANL/POS = 57.7% in males, 63.7% in females); carapace light (REF = 23.6 in males, 21.4 in females); axillary and inguinal scutes usually in contact on both sides (AIC = 75.0% in males, 85.7% in females); and second marginal scutes usually in contact with first central (M2C = 87.5% in males, 85.7% in females).

Distribution.—K. f. durangoense occurs in the lower Río Nazas and the Bolsón de Mapimí in Durango, Chihuahua, and Coahuila, Mexico. Range maps are in Iverson (1979*b*), Smith and Smith (1979), and Houseal et al. (1982).

SPECIMENS EXAMINED

Museum acronyms are as in Duellman et al. (1978) except as follows: JFB is James F. Berry (CM); JBI is John B. Iverson (UF/FSM); JLC is James L. Christiansen, JAC is J. A. Cooper, and AJQ is A. J. Quinn, all of Drake University. Specimens marked with an asterisk (*) were examined but were not included in the numerical analyses.

Population 1 (ILL), Illinois River: (Illinois) CM 62022–23. FMNH 37992. UIMNH 2252–53, 2255–56. INHS 5587–89, 5987–89, 6010–11, 7164–66, 4991*, 7920*.

Population 2 (MIS), Mississippi River: (Illinois) INHS 4244–45, 7937*, 3220–22*. (Missouri) JLC 4408. (Iowa) JLC unnumbered (3 specimens), 3560, 3822–31, 3945–46, 4049–50, 4277, 4362, 4545–47. JAC 9–10, 14, 17, 19–25, 27–30, 33–34, 44–46, 54–58, 64, 67–69, 76–84, 89, 177–98, 203–06. AJQ 78, 80–89, 110. TAW 58, 66–68, 75. Murphy and Corn unnumbered (4 specimens).

Population 3 (NEB), Nebraska Sandhills: (Nebraska) UF/FSM 40567–72, 40591*, 40594*, 52627–43, 52652, 52655–59, 52904–08, 53380–81, 55393–412, 55414. JBI 380–85*, 416–521*, 748–50*.

Population 4 (REP), Republican River: (Nebraska) JBI 284–89.

Population 5 (ARK), Arkansas and Smoky Hill rivers: (Oklahoma) CM 58806*, 88639*. (Kansas) FMNH 211706. KU 3032, 3753–54, 3761, 14108–12, 18379, 18383, 18386, 18388, 18391–93, 19480, 19594–95*, 20520–21, 41712–38, 46862, 50304, 50307–09, 51450, 69986–70009. UMMZ 130149.

Population 6 (CIM), Cimarron River: (Kansas) CM 50802a–g, 50803. UF/FSM 11023.1–.2, 11072. INHS 5952–53. KU 2791–97, 3037–51, 46899, 49632*. UMMZ 89633*, 96076*, 106672–73*, 127242–64, 155091–98*, 127065–66. UNM 13277–79.

Population 7 (CAN), Canadian River: (Oklahoma) CM 58827, 60402. UF/FSM 3453, 11022.1–.2. FMNH 8317, 8325–26*, 16896. KU 18128. (Texas) TU 14517–17.2, 14525–25.4, 14535. (New Mexico) FMNH 51919. UMMZ 13283–86, 13290–99, 14188–90, 20575–90, 20685–92, 20694–98, 20700–01, 21167, 23180–82, 23189. UNM 20511–12, 20516–19, 20525, 20554, 22388, 22392, 23750–51, 31949–52, 31954–69.

Population 8 (RED), Red River: (Oklahoma) CM 42855–56, 44722*, 88637–38, 88641–42. UMMZ 77579*. FMNH 28508*. INHS 8035*. (Texas) CM 42857. TU 16676–76.1.

Population 9 (BRZ), Brazos River: (Texas) FMNH 46293, 46295–96, 55083. INHS 5958, 6015. KU 3130–31. UMMZ 70825–26*, 92726. TU 16675. UU 17416–17, 17418–27, 17428–37, 17501, 17591–97. JFB 15292–305.

Population 10 (COL), Colorado River: (Texas) CM 3020, 3071. FMNH 1830. INHS 6392. LACM 7976, 61110, 66709*–10, 66712*–13*, 74392. UMMZ 50153*.

Population 11 (SAN), San Antonio and Nueces rivers: (Texas) CM 13483*, 21120*–21*, S8336–43. FMNH 28302, 37473. KU 44945. TU 10834–35. INHS 9451*.

Population 12 (PEC) Pecos River: (New Mexico) UF/FSM 40550–54. KU 51153. LACM 7971–75, 105358–59. UMMZ 65378*, 121895*–96*, 123516*, 123550*, 123689*, 134177–78, 134275–79. UNM 7519–20, 11257, 12506–09, 13014, 14489, 14612–13, 14741–42, 15563–68, 16695, 17208–09, 19449, 20535, 20604–08, 20686. TU 17176. UU 8355–56, 8358–75, 8377–85, 8390–94, 8396–408, 8410–11, 8413–16, 8418.

Population 13 (URG), Upper Rio Grande (above the Pecos River): (New Mexico) UF/FSM 30366–68. UNM 16695, 17192. (Texas) FMNH 27763–65, 27839–40, 37468*. UMMZ 85079, 101291–93, 114356–58, 116579*–80*. UNM 8170, 17191. (Chihuahua) KU 45018, 51082. USNM 10519.

Population 14 (LRG), Lower Rio Grande (below the Pecos River): (Texas) UF/FSM 11024*–25*, 15926–38, 30369. UMMZ 96631*–33*. (Coahuila) FMNH 46135.

Population 15 (CON), Río Conchos: (Chihuahua) UNM 31943, 31945–48.

Population 16 (PLA), New Mexico Playa Lakes: (New Mexico) UNM 4041, 20513–15, 20520–23, 20526, 20531–34, 20553, 20599–603, 23753–54.

Population 17 (CAS), Río Casas Grandes: (Chihuahua): UF/FSM 39103. USNM 19058–59. UU 8441–43, 8445–53, 8455–56, 8459–60.

Population 18 (SMA), Río Santa Maria: (Chihuahua) KU 44496–98. UMMZ 118272–83. USNM 104976–105013.

Population 19 (SAL), Río Salado: (Coahuila) UIMNH 48534–43, 62779–81. FMNH 28840, 47355–65.

Population 20 (NEM) Río San Fernando, Río Soto la Marina, and Río Tamesí: (Tamaulipas) UMMZ 103184. UNM 30809. USNM 108588. TU 15971–71.10*. UU 9857. (Nuevo León) UMMZ 125565.

Population 21 (NWM), Río San Simón, Río Magdalena, Río Yaqui, and Río Sonora: **(Arizona) INHS 8650. UIMNH 41218*. LACM 105407*. JBIA01–A03, A31. (Sonora) UF/FSM 52780–81, 52784–85, 52787–96, 52809–13, 52849–52. UIMNH 23919–20, 72495–97. UU 7956.

Population 22 (DUR), Río Nazas and Bolsón de Mapimí: (Chihuahua) CM 59376. (Coahuila) FMNH 1535, 1537. (Durango) UF/FSM 16180. FMNH 112996–98, 123666, 179224*. UIMNH 19338–39. USNM field 60987–91, 60999.

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** Specimen UNM 17663 from 3 miles East of Mazatlán, Sonora, México, which was included in the numerical analyses of Houseal et al. (1982), is not *K. flavescens*; it is a female *Kinosternon alamosae* Berry and Legler (1980).

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DISTRIBUTION OF AMPHIBIANS AND REPTILES ON ISLANDS IN THE GULF OF CALIFORNIA

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Abstract

The distribution records and updated nomenclature for the amphibians and reptiles on the islands in the Gulf of California are presented. Five new populations of lizards, and 14 previously unrecorded populations of snakes are reported. Nomenclatorial problems are noted for about 20% of the species complexes of reptiles.

Resumen

Se presentan los registros de distribución y se ponen al dia los nombres científicos para los anfibios y réptiles de las islas del Golfo de California. Se anuncian cinco poblaciones nuevas de lagartijas y 14 poblaciones de culebras que no había sido documentados previamente. Se notan problemas con la taxonomía de los complejos de especies de réptiles.

Introduction

The herpetofauna on the islands in the Gulf of California has received considerable attention from taxonomists, systematists, biogeographers, and ecologists within the past 15 years; Case (1975, 1983) reviewed the colonizing ability and community structure of the lizards, Wilcox (1978) and Wright et al. (in prep.) examined the effect of island age in determining the number of species on islands, and Murphy (1983*a*,

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1983*b*) and Wright et al. (in prep.) examined the evolutionary origin of the insular populations. Moreover, there have been several significant taxonomic revisions of particular groups, for example, Ballinger and Tinkle (1972), Dixon (1966), and Murphy (1983*a*). In light of the considerable attention now given to this particular insular herpetofauna by researchers, this updated checklist has been prepared.

In their checklist, Soulé and Sloan (1966) noted the occurrence of about 260 populations of amphibians and reptiles on the islands in the Gulf of California. Their list included 33 genera with about 60 species divided into 109 subspecies. Subsequently, about 50 new populations have been found and many nomenclatorial changes have been made. In this checklist, we report 311 populations composed of 34 genera including 85 species and 143 subspecies. Soulé and Sloan (1966) provided insular records for 45 islands; our list is expanded to include data for 49 islands. Records for islands off the Pacific Coast of Baja California are provided by Savage (1967) and Wilcox (1980).

The annotated list of reptiles and amphibians of the islands in the Gulf of California (Table 1) is based on Soulé and Sloan (1966) with taxonomic and distributional updating from Ballinger and Tinkle (1972), Campbell and Christman (1982), Dixon (1966), Etheridge (1961), Gehlbach (1971), Goodrich et al. (1978), Grismer (1984), Hall (personal communication to R.W.M. regarding *Sceloporus magister sensu lato*), Hall and Smith (1979), Harris and Simmons (1978), Klauber (1972), Montanucci et al. (1975), Murphy (1974, 1975, 1983*a*), Murphy and Ottley (1980), Ottley et al. (1980), Ottley and Tanner (1978), Phelan and Brattstrom (1955), Powers (1974), Powers and Banta (1973, 1974, 1976), Radcliffe and Maslin (1975), Rau and Loomis (1977), Robinson (1974), Ruth (1974), Seib (1978), Smith (1972), Smith and Larsen (1973), Smith and Smith (1976), Smith and Tanner (1974), Tanner (1966, 1981), Walker et al. (1966), and Wilson (1970, 1973), and unpublished records from recent collections. The localities of most islands referred to in this report are shown in Figs. 1 and 2 and/or in Case and Cody (1983). It should be noted that our undocumented, preliminary version of this checklist (Murphy and Ottley, 1983) contains errors introduced in typesetting. *Coleonyx* (*Anarbylus*) *switaki* is incorrectly listed as occurring on Isla Tortuga (it occurs on Isla San Marcos) and *Sauromalus ater ater* is incorrectly listed as occurring on Isla Cerralvo. Herein we add *Eridiphas slevini* to the herpetofauna of Isla Coronados.

In order to provide a testable classification to those unfamiliar with the systematic and taxonomic problems of the Gulf herpetofauna, we base our nomenclature on the presumed sequence of cladogenic events. We believe the classification and taxonomy should reflect the evolutionary history of the organisms, and thus contain the greatest information content. As a basis for taxonomic decisions, the testable principles of holophyly (Hennig, 1966; Farris, 1979) are utilized; two taxa must have shared the same common ancestor to be assigned to the same taxonomic level. For example, if three populations, A, B, and C, are related, and A and B shared the same most recent common ancestor (thus being more closely related to each other than either is to C), then if populations A and C are considered conspecifics, population B must also be considered conspecific with both A and C. Similarly, if population A is accorded a taxonomic rank (e.g., species) higher than B and C (conspecific subspecies), then both B and C also must be elevated to a rank equivalent to A; populations B and C cannot be contained within the same lower taxonomic rank conspecific because population B is genealogically closer to A.

Strict application of the principles of holophyly to the Gulf insular herpetofauna involves one problem. Historically, the land bridge islands were formed at essentially the same time (Fig. 3). Thus, polychotomous relationships likely reflect geologic and thus phylogenetic reality of herpetofaunal populations on islands in the Gulf of California. Because polychotomous relationships exist, how are the principles of holophyly applied to the nomenclature of insular populations? The nomenclature should contain the maximum amount of information about the phylogenetic relationships of various insular populations. Clearly no nomenclatorial problem would exist if all terminal branches were accorded identical taxonomic rank; nor would any problem exist if all of the polychotomous terminal branches (island populations and the peninsular population) were considered to be unique, endemic taxa at the same taxonomic level (all subspecies or species, etc.). It is acceptable, although not necessarily preferable, to consider some of the terminal branches to represent endemic taxa and others to be the same as the peninsular population; it is possible to invoke the hypothesis that the unique populations are older. However, it is unacceptable to consider two or more insular populations as belonging to the same taxon exclusive of the peninsular population unless it can be demonstrated by cladistic methods that one population was derived from the other via overwater dispersal, or that the insular populations were contiguous after separation from their respective peninsular populations. This latter situation does occur; Isla Mejia, for example, is a land bridge island to Isla Angel de la Guarda, and vice versa, but neither of these islands were connected with the peninsula during the last glaciation (Fig. 3; Murphy, 1983*a*). However, some taxa are considered to be restricted to multiple Gulf land bridge islands and in these cases major nomenclatorial problems exist because the taxonomy does not reflect evolutionary relationships. Taxonomic groups having taxonomic problems by these criteria are so noted in Table 1.

Table 1.—*Distribution of reptiles and amphibians on islands in the Gulf of California. "Status" symbols are: C = on peninsula of Baja California; E = of peninsular origin and endemic to one island; R = of peninsular origin and restricted to multiple islands; N = mainland Mexico taxon; S = mainland Mexico origin and endemic to one island; M = mainland Mexico origin and restricted to multiple islands; U = unidentified and/or unassigned in last revision; X = sight record.*

Taxon	Status	Insular distribution
Class Amphibia		
Family Bufonidae		
Bufo punctatus	C	Cerralvo, Espiritu Santo-Partida Sur, Tiburon
Family Pelobatidae		
Scaphiopus couchi	C	Cerralvo, Espiritu Santo-Partida Sur
Class Reptilia		
Subclass Anapsida		
Order Testudines		
Family Testudinidae		
Gopherus agassizi	N	Tiburon
Subclass Lepidosauria		
Order Squamata		
Suborder Sauria (Lizards)		
Family Gekkonidae		
Coleonyx switaki	C	San Marcos
Coleonyx variegatus peninsularis	C	Coronados, Espiritu Santo-Partida Sur, San Jose
Coleonyx variegatus slevini[1]	R	San Marcos, Santa Ines
Coleonyx variegatus sonoriensis	N	Tiburon
Coleonyx variegatus subsp.	X	Angel de la Guarda, Danzante
Phyllodactylus angelensis	R	Angel de la Guarda, Mejia, Pond
Phyllodactylus apricus[1]	E	Las Animas
Phyllodactylus bugastrolepis	E	Santa Catalina
Phyllodactylus homolepidurus nolascoensis	S	San Pedro Nolasco
Phyllodactylus nocticolus acorius[1]	E	San Diego
Phyllodactylus nocticolus angulus	R	Salsipuedes, San Lorenzo Norte, San Lorenzo Sur
Phyllodactylus nocticolus circus[1]	E	San Ildefonso
Phyllodactylus nocticolus coronatus[1]	E	Coronados
Phyllodactylus nocticolus estebanensis[1]	R	Pelicano, San Esteban, Tiburon
Phyllodactylus nocticolus nocticolus[1]	C	Carmen, Cayo, Coyote, Danzante, La Ventana, Monserrate, Piojo, San Francisco, San Jose, San Marcos
Phyllodactylus partidus	E	Partida Norte
Phyllodactylus santacruzensis	E	Santa Cruz

Table 1.—*Continued.*

Taxon	Status	Insular distribution
Phyllodactylus tinklei[1]	E	Rasa
Phyllodactylus tuberculosus saxatilis	N	Farallon
Phyllodactylus unctus	C	Ballena, Cerralvo, Espiritu Santo-Partida Sur, Gallina
Family Iguanidae		
Callisaurus draconoides carmenensis	C	Carmen, Coronados, San Francisco, Santa Ines, San Jose, San Marcos
Callisaurus draconoides draconoides	C	Cerralvo, Espiritu Santo-Partida Sur
Callisaurus draconoides inusitatus	N	Tiburon
Callisaurus draconoides rhodostictus	C	Encantada Grande, Smith
Callisaurus draconoides splendidus	E	Angel de la Guarda
Crotaphytus collaris dickersonae	S	Tiburon
Crotaphytus insularis insularis	E	Angel de la Guarda
Ctenosaura hemilopha conspicuosa	M	San Esteban, Lobos
Ctenosaura hemilopha insulana	E	Cerralvo
Ctenosaura hemilopha nolascensis	S	San Pedro Nolasco
Dipsosaurus dorsalis carmenensis[1]	R	Carmen, Coronados
Dipsosaurus dorsalis catalinensis	E	Santa Catalina
Dipsosaurus dorsalis dorsalis	C	Angel de la Guarda, Encantada Grande, San Marcos
Dipsosaurus dorsalis lucasensis	C	Cerralvo, Espiritu Santo-Partida Sur, Monserrate, San Jose
Gambelia wislizenii wislizenii	N	Tiburon
Petrosaurus mearnsi mearnsi	C	El Muerto
Petrosaurus mearnsi slevini	R	Angel de la Guarda, Mejia
Petrosaurus thalassinus repens	C	Danzante
Petrosaurus thalassinus thalassinus	C	Espiritu Santo-Partida Sur
Phrynosoma solare	N	Tiburon
Sator angustus	M	San Diego, Santa Cruz
Sator grandaevus	S	Cerralvo
Sauromalus ater ater[1]	R	Danzante, Espiritu Santo-Partida Sur, San Diego, San Francisco, San Jose, Santa Cruz
Sauromalus ater shawi	E	San Marcos
Sauromalus hispidus[2]	R	Angel de la Guarda, Cabeza de Caballo, Granite, La Ventana (X), Mejia, Piojo, Pond, Smith, San Lorenzo Norte, San Lorenzo Sur
Sauromalus klauberi	E	Santa Catalina
Sauromalus obesus townsendi	N	Tiburon
Sauromalus slevini[1]	R	Carmen, Coronados, Monserrate

Table 1.—*Continued.*

Taxon	Status	Insular distribution
Sauromalus varius[3]	R	Lobos (X), Pelicano, San Esteban
Sceloporus clarki clarki	N	San Pedro Nolasco, Tiburon
Sceloporus hunsakeri	C	Ballena, Espiritu Santo-Partida Sur
Sceloporus lineatulus	E	Santa Catalina
Sceloporus magister magister	N	Tiburon
Sceloporus monserratensis	C	Carmen, Coronados, Monserrate, San Jose
Sceloporus orcutti	C	Carmen, Coronados, San Francisco, San Ildefonso, San Jose, San Marcos, Tortuga
Sceloporus zosteromus	C	Espiritu Santo-Partida Sur
Urosaurus microscutatus	C	Carmen, Coronados, Danzante, Espiritu Santo-Partida Sur, Las Animas, San Francisco, San Jose, San Marcos
Urosaurus nigricaudus	C	Ballena, Espiritu Santo-Partida Sur, Gallina, Gaviota
Urosaurus ornatus schotti	N	Tiburon
Uta antiqua	R	Salsipuedes, San Lorenzo Norte, San Lorenzo Sur
Uta nolascensis	S	San Pedro Nolasco
Uta palmeri	E	San Pedro Martir
Uta squamata	E	Santa Catalina
Uta stansburiana elegans	C	Ballena, Calaveras,[4] Carmen, Cayo, Cholludo, Coloradito, Coronados, Coyote, Danzante, Encantada Grande, Espiritu Santo-Partida Sur, Las Galeras, La Ventana, Piojo, San Francisco, San Ildefonso, San Jose, San Marcos, Smith, Tortuga
Uta stansburiana taylori	N	Angel de la Guarda, Granite, Mejia, Partida Norte, Pond, Rasa, San Esteban, Tiburon
Uta stansburiana subsp.	U	El Muerto, Patos, Pelicano
Uta sp.	E	Monserrate
Family Teiidae		
Cnemidophorus catalinensis	E	Santa Catalina
Cnemidophorus ceralbensis	E	Cerralvo
Cnemidophorus estebanensis	S	San Esteban
Cnemidophorus hyperythrus danheimae	E	San Jose

Table 1.—*Continued.*

Taxon	Status	Insular distribution
Cnemidophorus hyperythrus hyperythrus	C	Espiritu Santo-Partida Sur, Carmen, Coronados, San Francisco, San Marcos
Cnemidophorus hyperythrus pictus	E	Monserrate
Cnemidophorus martyris	E	San Pedro Martir
Cnemidophorus tigris bacatus	S	San Pedro Nolasco
Cnemidophorus tigris canus	R	Salsipuedes, San Lorenzo Norte, San Lorenzo Sur
Cnemidophorus tigris celeripes	R	San Francisco, San Jose
Cnemidophorus tigris dickersonae	R	Angel de la Guarda, Partida Norte, Pond
Cnemidophorus tigris gracilis	N	Tiburon
Cnemidophorus tigris maximus	C	Espiritu Santo-Partida Sur
Cnemidophorus tigris rubidus	C	Carmen, Coronados, Danzante, San Marcos
Cnemidophorus tigris tigris	C	Smith
Suborder Serpentes		
Family Leptotyphlopidae		
Leptotyphlops humilis boettgeri	C	Cerralvo
Leptotyphlops humilis humilis	C	Danzante
Leptotyphlops humilis levitoni	E	Santa Catalina
Leptotyphlops humilis lindsayi	E	Carmen
Family Boidae		
Lichanura trivirgata trivirgata	C	Cerralvo, San Marcos, Tiburon
Lichanura trivirgata subsp.	R	Angel de la Guarda, Mejia
Family Colubridae		
Chilomeniscus cinctus	C	Monserrate, San Jose, San Marcos
Chilomeniscus punctatissimus[1]	E	Espiritu Santo-Partida Sur
Chilomeniscus savagei	E	Cerralvo
Elaphe rosaliae	C	Danzante
Eridiphas slevini marcosensis	E	San Marcos
Eridiphas slevini slevini	C	Cerralvo, Coronados, Danzante
Hypsiglena torquata catalinae	E	Santa Catalina
Hypsiglena torquata klauberi	C	Angel de la Guarda, Mejia
Hypsiglena torquata gularis	E	Partida Norte
Hypsiglena torquata ochrorhyncha	C	Cerralvo, San Francisco, San Jose, San Lorenzo Sur
Hypsiglena torquata tiburonensis[1]	M	San Esteban, Tiburon
Hypsiglena torquata tortugaensis	E	Tortuga
Hypsiglena torquata venusta	C	Carmen, Danzante, San Marcos
Hypsiglena torquata ssp.	E	Monserrate
Lampropeltis getulus californiae	C	Angel de la Guarda, Cerralvo, Monserrate, Salsi-

Table 1.—*Continued.*

Taxon	Status	Insular distribution
		puedes, San Lorenzo Norte, San Lorenzo Sur, Tortuga
Lampropeltis getulus catalinensis	E	Santa Catalina
Lampropeltis getulus nigrita	N	San Pedro Martir
Masticophis barbouri[1]	E	Espiritu Santo-Partida Sur
Masticophis bilineatus bilineatus	N	Tiburon
Masticophis bilineatus slevini	S	San Esteban
Masticophis flagellum fuliginosus	C	Carmen, Cerralvo, Coronados, Danzante, Espiritu Santo-Partida Sur, Monserrate, San Ildefonso, San Jose, San Marcos
Masticophis flagellum cingulum	N	Tiburon
Phyllorhynchus decurtatus arenicolus	E	Monserrate
Phyllorhynchus decurtatus decurtatus	C	Cerralvo, San Jose, San Marcos
Phyllorhynchus decurtatus perkinsi	C	Angel de la Guarda
Pituophis melanoleucus affinis	N	Tiburon
Pituophis melanoleucus bimaris	C	San Jose
Rhinocheilus lecontei lecontei	C	Cerralvo
Salvadora hexalepis hexalepis	N	Tiburon
Salvadora hexalepis klauberi	C	San Jose
Sonora semiannulata	C	San Jose, San Marcos
Tantilla planiceps planiceps	C	Carmen
Trimorphodon biscutatus lyrophanes	C	Cerralvo, Danzante, San Marcos
Family Elapidae		
Micruroides euryxanthus euryxanthus	N	Tiburon
Family Viperidae		
Crotalus atrox	N	San Pedro Martir, Santa Cruz, Tiburon
Crotalus catalinensis	E	Santa Catalina
Crotalus cerastes cercobombus	N	Tiburon
Crotalus enyo cerralvensis	E	Cerralvo
Crotalus enyo enyo	C	Carmen, Espiritu Santo-Partida Sur, San Francisco, San Jose, San Marcos
Crotalus mitchellii angelensis	E	Angel de la Guarda
Crotalus mitchellii mitchellii	C	Carmen, Cerralvo, Espiritu Santo-Partida Sur, Monserrate, Salsipuedes, San Jose
Crotalus mitchellii muertensis	E	El Muerto
Crotalus mitchellii pyrrhus	C	Piojo, Smith
Crotalus molossus estebanensis	S	San Esteban
Crotalus molossus molossus	N	Tiburon

Table 1.—*Continued.*

Taxon	Status	Insular distribution
Crotalus ruber lucasensis	C	Danzante, Monserrate, San Jose
Crotalus ruber lorenzoensis	E	San Lorenzo Sur
Crotalus ruber ruber	C	Angel de la Guarda, Pond, San Marcos
Crotalus tigris	N	Tiburon
Crotalus tortugensis	S	Tortuga

[1] Taxon of questionable status because of holophyly and/or biogeographic problems.

[2] Distributions on islas Smith, Cabeza de Caballo, La Ventana and Piojo probably the result of Indian activity (Aschmann, 1959).

[3] Distributions on islas Pelicano and Lobos probably the result of Indian activity.

[4] The record for this island is listed as "a small islet just south of Isla Smith" and we assume this to be Isla Calaveras.

Aside from the application of the principles of phylogenetic systematics to the determination of taxonomic categories, the problem of the species concept must be considered. In working with insular populations, we have not found either the "Biological Species Concept" (Mayr, 1963) or the "Evolutionary Species Concept" (Wiley, 1978) to be universally applicable. To gain some degree of consistency, however, populations on land bridge islands were considered to be accorded subspecific rank at most, except where such considerations would create new nomenclatorial combinations. We believe this approach is justified because 1) land bridge island populations have not been isolated for a long period of time, 2) the land bridge islands were formed at least four times, once with each advance of the Laurentide Glacier, apparently without formation of "new" species, and 3) there is a general consensus among systematists who have worked with land bridge island populations that the subspecific rank is the highest appropriate rank. The former ideas are supported by electrophoretic studies (Murphy, 1983*a*, unpublished data; Murphy and Ottley, 1980), which failed to resolve unique alleles in island populations, suggesting that recontact would result in interbreeding.

Following the guidelines outlined above we encountered several additional taxonomic problems in our review and in a few cases the taxonomic ranks of populations have been shifted from the species to subspecies level and vice versa; however, in doing so we have intentionally avoided creating new nomenclatorial combinations pending detailed evaluation. Moreover, it was occasionally necessary to list populations as "subsp." for unidentified or undescribed subspecies, and "sp." for species pending further revisionary work and/or evaluation (Table 1).

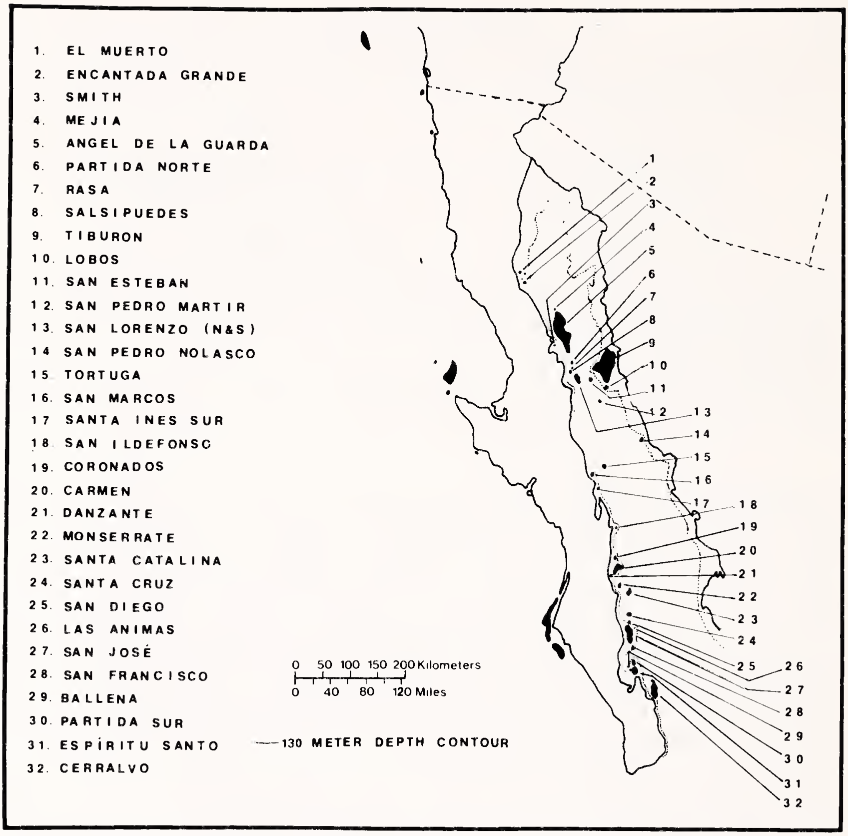

Fig. 1.—The major islands in the Gulf of California referred to in this report.

NEW AND PROBLEMATIC INSULAR RECORDS

Voucher specimens for the new insular records are deposited in the collections of the M. L. Bean Life Science Museum, Brigham Young University (BYU), Provo, Utah, the California Academy of Sciences (CAS), San Francisco, California, the San Diego Museum of Natural History (SDSNH), San Diego, California, the Los Angeles County Museum of Natural History (LACM), Los Angeles, California, the University of Arizona (UAZ), Tucson, Arizona, and the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania.

Lizards

Coleonyx switaki (Murphy)

A population of barefoot geckos was found on Isla San Marcos in 1978. The lizards were observed on north-facing slopes of Arroyo de la Tanaria, usually in steep, boulder-strewn regions and small, adjoining

Fig. 2.—The land bridge islands in the Gulf of California in the region of Bahia de Los Angeles.

arroyos, from May through July. Specimens were found to be most active between 45 min after sundown and midnight. No *C. switaki* were found in the flat portions of the main arroyo where *C. variegatus slevini* is very abundant. Synpatry between the two species is apparently

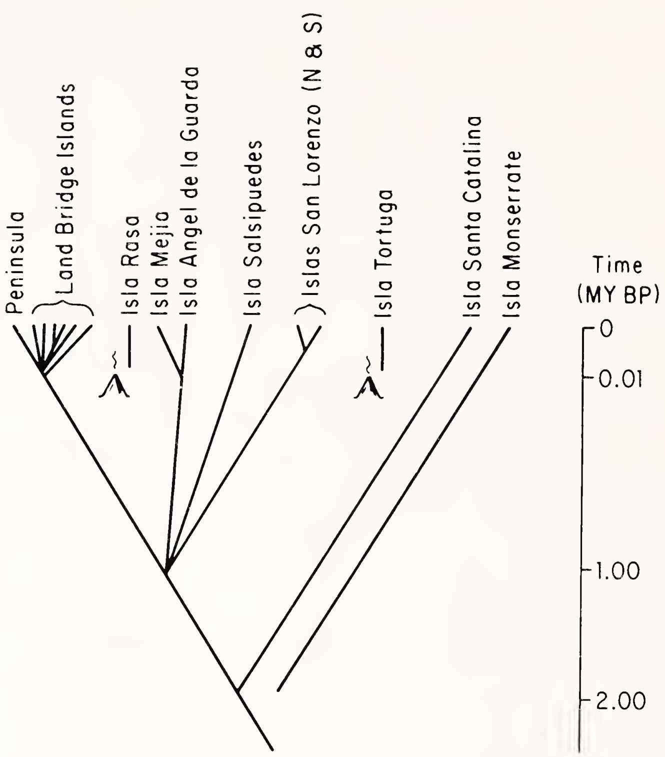

Fig. 3.—A vicariogram depicting the relationships and relative ages of many of the islands in the Gulf of California. The multiple formations of land bridge islands are not depicted for clarity. Note that if this history were used to imply phylogenetic relationships of populations on the various islands, polychotomous cladogenic branching points would result.

confined to the ecotone between the floor of Arroyo de la Taneria and a few meters up the slopes. The parapatric distributions may result in part from *C. switaki* feeding upon the smaller *C. variegatus*; we have observed this behavior after placing specimens of both species in a 10 l bucket shortly after capture.

A morphometric summary of three specimens was reported by Fritts et al. (1982); the specimens were listed as being from the "vicinity of Santa Rosalia." Based on those three specimens (CAS 147349, 147351–52), and three specimens from Isla San Marcos (BYU 34501, CM 95398, LACM 135946), a series including three adult females and three adult males, we report the following variation: body length 72–85 mm, postnasals 2, granules in contact with nasals 10 ± 1.9 (mean ± 95%

confidence limits and range), scales of eye fringe 42.1 ± 4.6 (38–45), enlarged supralabials 10 ± 1.9 (9–11), infralabials 13.4 ± 1.8 (12–15), midbody transverse tubercles 16.7 ± 2.0 (15–18), preanal pores 6.8 ± 2.3 (6–9), subdigital lamellae on fourth finger 14.3 ± 1.0 (14–15), subdigital lamellae on fourth toe 18.3 ± 1.2 (17–19), yellow pattern bands from forelimbs to caudal constriction 11.4 ± 1.3 (10–12). Our counts for supralabials are lower than those reported by Fritts et al. (1982); we restricted our counts to enlarged scales.

Coleonyx variegatus (Baird) subsp.

Two adult specimens were collected at Puerto Refugio on the north end of Isla Angel de la Guarda by John Ottley on 20 June 1974 between 2100 and 2200 hours. Both specimens were taken on desert hardpan among clumps of thick, low (< 1 m) brush. Unfortunately, both of these specimens were apparently lost in transit.

A second new insular record for the banded gecko is Isla Danzante. Steve Strand (UCLA) found a single adult individual on 28 July 1976 at the north end of Isla Danzante; the individual was released after identification. Because no voucher specimen is available, subspecific assignment is not possible.

Phyllodactylus angelensis Dixon

This leaf-toed gecko, previously restricted to islas Angel de la Guarda and Pond, is known from a single specimen (BYU 41103) from Isla Mejia. This immature female, measuring 32 mm snout–vent length, was found beneath a large rock at 1445 hours on 15 April 1973 by John Ottley.

Sauromalus ater ater Duméril

Seven adult specimens of this subspecies (BYU 34494–34495, 34740–34744), collected on 27–28 June 1978 by J. Cram, M. Mahlstedt and us, represent the first chuckwalla record for Isla Danzante. These chuckwallas have a gray-brown ground color, heavily mottled with small, brown spots. Four specimens have a fourth transverse band that is typical of the subspecies, but two specimens have only a single band at the shoulders, and one lacks bands entirely. This population is assigned to the subspecies *S. a. ater* due to similarity of meristic characters (see Shaw, 1945). Specimens most closely approximate *S. a. ater* in the number of caudals (27.4 ± 2.7; mean ± 95% confidence limits), dorsals (29.0 ± 7.9), and ventrals (137.6 ± 29) (one specimen [BYU 34740] has a high ventral count [170] with all others ranging between 125 and 137). However, humeral counts (35.3 ± 3.5) are much closer to those given for *S. slevini.*

Uta Baird and Girard

The Isla Monserrate population of side-blotched lizards has been referred to *U. stansburiana elegans,* a peninsular and land bridge island subspecies (Ballinger and Tinkle, 1972). Electrophoretic investigations of this group have yielded the surprising result that this population is biochemically well differentiated from peninsular populations. Indeed, the Monserrate Island population and *Uta squamata* from Isla Santa Catalina are electrophoretically the most unique populations in the genus in terms of allozyme characteristics (Murphy, 1983*a*). These data suggest that both the Isla Santa Catalina and the Isla Monserrate populations have been isolated for a period of time greater than that of any other insular population of *Uta.* If this is true, then the Isla Monserrate population must also be considered a distinct species to maintain a holophyletic phylogeny and classification, especially if one accepts the taxonomy of Ballinger and Tinkle (1972). Hence, this population is listed as "*Uta* sp." in this checklist (Table 1).

Snakes

Leptotyphlops humilis humilis Baird and Girard

A female blind snake (BYU 34730) was collected on the north end of Isla Danzante by John Ottley on 28 June 1978 at 2130 hours. The specimen was found crawling in an open area near a rock outcropping about 20 m above sea level. The total length is 223 mm, tail length 9 mm. There are 14 scale rows at midbody, 13 subcaudals, 253 scales between the rostral and spine of the tail, 12 rows around the tail, and 7 dorsal rows with a medium brown pigment. The specimen has a lower number of dorsal scales between the rostral and tail spine than other members of the subspecies (see Murphy, 1975); however, there is a highly significant positive correlation ($P < .01$) between the number of dorsal scales of individual snakes and latitude of collecting site (Murphy, unpublished data). This specimen represents the southernmost record for this subspecies and thus a lower number of dorsal scales is expected.

Chilomeniscus stramineus (Cope)

Although Powers and Banta (1974) report this snake as being taken from Isla Cerralvo, their description of the aberrant specimen precludes definite assignment to this species; therefore, for the moment, the record is excluded from Table 1.

Elaphe rosaliae (Mocquard)

Two specimens of this rare rat snake have been collected from Isla Danzante by Steve Strand (UCLA). The first specimen, a "large" snake, was found on 2 August 1975 on the northern portion of the island and then released. The second specimen, documented by a complete shed skin (BYU 37106), was collected on 26 October 1977, also on the northern region of the island. In November 1979, it measured approximately 1004 mm total length with a 149 mm tail. There are 287 ventrals, 78 caudals (divided), and smooth dorsals that number 30 behind the head, 33 at midbody, and 23 just anterior to the tail. The anal plate is divided. Preoculars are 1-1 (left-right), postoculars 2-2, suboculars 6-6, supralabials 10-10, and infralabials 12-13. The snake is rust-colored above and cream below (see Ottley and Jacobsen, 1983). This rat snake appears very similar to other Baja California peninsula specimens (Dowling, 1957).

Eridiphas slevini (Tanner)

A new insular record of this species is reported herein for Isla Coronados through the courtesy of Francisco Reynoso (Universidad Autonoma de Baja California Sur, La Paz, Mexico); the voucher specimen is in the UABCS collection.

Eridiphas slevini marcosensis Ottley and Tanner

This subspecies, restricted in distribution to Isla San Marcos, was recently described (Ottley and Tanner, 1978) on the basis of two specimens. An additional specimen (BYU 37642), an adult female, was collected on 21 July 1979 at about 2300 hours on a high, steep slope on the south side of Arroyo de la Taneria. It was found crawling among gypsum boulders. Meristic characters are as follows: 195 ventrals, 57 subcaudals, 23 scale rows (at 100th ventral), 8-8 supralabials, 10-10 infralabials, 1-1 preoculars, 2-2 postoculars, 1-1 loreal, 1+2-1+2 temporals, dorsal blotches 65, 426 mm total length, 73 mm tail length, and 16.7 mm head length (in 70% ethanol). There are fewer ventrals than previously reported for the subspecies (Ottley and Tanner, 1978); however, the number is greater than reported for peninsular specimens and, along with the relatively small head and large number of dorsal blotches, remains diagnostic of the subspecies.

Hypsiglena torquata klauberi Tanner

An adult female (BYU 41285) containing three developing eggs was collected from Isla Mejia on 15 April 1973 by Thomas Cozens beneath a rock on the south side of the island in late afternoon. This specimen measures 341 mm including the 48 mm tail. Ventral count is 190, with 45 subcaudals, and 21 scale rows at midbody. The nape blotch is greatly enlarged posteriorly (6 scale rows across, 3–5 longitudinally), contacting the lateral blotches. The anterior projection from the nape blotch is unusual in that it misses the parietals by one scale, and the posterior half is less than half a scale wide. The general pattern is typical of *H. t. klauberi* except in having a very light ground color.

A single specimen also represents the first record of the San Diego night snake on Isla Angel de la Guarda. The subadult female (BYU 33207) was collected on Isla Angel de la Guarda during December 1969 by Benjamin H. Banta. The specimen measures 287 mm in length, with a 46 mm tail. Ventrals number 177, subcaudals 51, with 21 dorsal scale rows at midbody. The anal scale is divided. There are 71 dorsal blotches on the body, but the tail is irregularly patterned with a pinpoint stipling and minute irregular blotches. The nape pattern is greatly enlarged posteriorly, as in the specimen from Isla Mejia, and is well separated from the left lateral blotch but contacting the right. The anterior projection of the nape blotch is 3 scales long and 2 wide, the length of which is composed of one complete scale row with a bissected row at each side. The stomach of this specimen contained an adult side-blotched lizard (*Uta stansburiana taylori*).

Hypsiglena torquata ochrorhyncha Cope

A spotted night snake was found on 23 March 1967 by Wilmer W. Tanner and Ronald Morris coiled beneath a boulder at about midmorning on the south end of Isla San Lorenzo Sur. The subadult female (BYU 30214) is 232 mm in length including the 44 mm tail. There are 180 ventrals, 48 subcaudals, 21 dorsal scale rows at midbody. The anal plate is divided. Loreals are 1-1, parietals are separated from lower postoculars. The gular scales, although not as large as those of *H. torquata gularis,* are substantially larger than those of other known insular populations. The blotches number 20 on the tail and 62 on the body. There are 3 rows of lateral spots. The nape pattern is fairly typical of this subspecies; it is not enlarged posteriorly and does not contact the lateral head blotches. However, there are two small round spots, one on each side of the anterior projection of the nape blotch creating a rather unique pattern. This specimen is tentatively assigned to the subspecies *H. t. ochrorhyncha* until additional material becomes available. Although most characters are within the range of variation ascribed to this subspecies by Tanner (1966), the number of dorsal blotches is higher, the gular scales are larger, and the nape pattern appears to be distinctive.

Hypsiglena torquata venusta Mocquard

An immature female (BYU 33659) was collected by us on 29 June 1978 at 2300 hours when it fell from the top of the cliff into our path along the beach on the northwest side of Isla Danzante. It is 244 mm in total length; the tail is 35 mm long. There are 181 ventrals, 48 subcaudals, and 21 scale rows at midbody. The specimen lacks distinct separation of the dorsal blotches, although it is similar to *H. t. venusta* in the other characters.

Hypsiglena torquata Gunther subsp.

Michael D. Robinson collected a male night snake on the northwest side of Isla Monserrate at Ensenada de las Galitas on 18 June 1970. The specimen (UAZ 32959) has 197 ventrals, 54 subcaudals, 8-8 supralabials, 10-10 infralabials, 2-2 preoculars, 2-2 postoculars, 1-2 loreals, and 21 scale rows at midbody. The anal scale is divided. There are 75 dorsal blotches on the body excluding the tail; the first 10 are distinctly separated dorsally.

Phyllorhynchus decurtatus decurtatus (Cope)

Six specimens of this subspecies (BYU 33682--33686, 34765) were collected from Arroyo de la Taneria on Isla San Marcos as previously reported (Murphy and Ottley, 1980). The first five specimens were found by John C. Cram and John Ottley during 1–2 June 1978 on warm nights between 2030 and 2300 hours; a sixth was collected on 20 July 1979 at 2100 hours by Larry E. Hunt. Most were found lying motionless beneath bushes or along the edges of the arroyo. There are three juveniles and three adults. The following meristic and pattern variability was found (mean ± 95% confidence limits; bilateral counts are grouped): ventrals in males (n = 4) 163.5 ± 3.8, in females (n = 2) 174–175; subcaudals in males 33.5 ± 1.1, in females 26–27; scale rows at midbody 19.2 ± 0.8; supralabials 6.3 ± 0.9; infralabials 8.9 ± 0.6; oculars 8.2 ± 0.8; loreals 2.2 ± 0.8; body blotches 28.5 ± 7.2, split body blotches 3.3 ± 4.6; tail blotches 6.5 ± 1.6.

As noted above, five of the six specimens have their dorsal blotches split and thus resemble *P. decurtatus arenicolus* from Isla Monserrate. However, none of these specimens fall within the range of number of blotches set by Savage and Cliff (1954) for *P. d. arenicolus*. By meristic characters and coloration the Isla San Marcos specimens are most similar to the subspecies *P. d. decurtatus*, the only exception being slightly higher subcaudal counts in the females.

Pituophis melanoleucus bimaris Klauber

A single adult female Baja California gopher snake, LACM 23234 (originally UCLA 16408) was collected on 1 September 1964 by Kenneth K. Asplund on Isla San Jose. The specimen has 256 ventrals, 61 divided subcaudals, and a divided anal scale. There are 9 supralabials with the 5th contacting the eye, 12 infralabials, single loreals, 31 scale rows behind the head, 33 at midbody and 26 just proximal to the tail, 2-2 (left-right) preoculars and 3-5 postoculars. Body blotches number 37 plus 9 on the tail; the first 7 and last 30 blotches are blackish-brown in color (in 70% ethyl alcohol) with the cream interspaces being narrower than the blotches; there are 9 less dense brown blotches between the anterior and posterior blackish-brown blotches with the lighter cream interspaces being approximately equal in width. The ventral scales are cream anteriorly becoming progressively more pigmented posteriorly. The specimen is readily assigned to *P. m. bimaris* on the basis of the blackish-brown anterior body blotches. The Baja California gopher snake has previously been recorded from islas Santa Margarita and Magdalena on the Pacific Coast of Baja California del Sur (Klauber, 1946).

Sonora semiannulata Baird and Girard

An adult female (BYU 34766) was collected on 20 July 1979 by John Ottley in front of the commissary in the mining town on the southwest region of Isla San Marcos. Apparently it had been killed several days earlier and consequently was found in poor condition; the posterior one fourth of the body is missing. Fragments of two developing eggs remained in the body cavity. Despite the poor condition of the specimen the coloration appears typical; the dorsal scales are drab-brown with lighter edges. Black stippling appears to be more concentrated on the dorsal scales than usual but we are uncertain if this is due to individual variation or specimen condition.

Trimorphodon biscutatus lyrophanes (Cope)

Two specimens were collected in the vicinity of Arroyo de la Taneria on the southwest portion of Isla San Marcos. The first, a subadult female (BYU 33673), was collected on 3 June 1978 at 2300 hours by John C. Cram near the top of the steep, north-facing slope of Arroyo de la Taneria about 1 km from the western beach. This snake measures 508 mm overall with a tail 78 mm in length. There are 29 body blotches and 15 tail blotches. Ventrals number 236, subcaudals 65, midbody dorsal scale rows 23. The anal scale is undivided. The second specimen, an adult female (BYU 33674), was collected on 18 June 1978 by Robert Murphy. It was found at 2040 hours crawling in an area of sparse low brush about 200 m from the west shoreline on the south side of Arroyo de la Taneria. Measurements for this snake are 818 mm total length including the 120 mm tail. Body blotches number 32; the tail has 15. There are 237 ventrals, 63 subcaudals, and 24 scale rows at midbody. The anal plate is undivided. Both specimens are easily recognized as being typical of the subspecies *T. b. lyrophanes* which is known from the adjacent peninsula. However, the parietals on both snakes are heavily sutured, nearly divided diagonally.

A second new insular record for the Baja lyre snake is documented by a single specimen (CAS 153841) collected on Isla Danzante about 1 km south of the north end of the island at about 23 m elevation on flat desert hardpan near *Perognathus* (pocket mouse) burrows. The snake was found at 2100 hours on 30 August 1977 by Steve Strand (UCLA). In meristic pattern it appears to be typical of *T. biscutatus lyrophanes* (see Gehlbach, 1971). There are 33 body blotches plus 18 on the tail, about 222 ventrals, 66 caudals, and 22 scale rows at midbody. The snake measures about 560 mm with the tail comprising 83 mm. The specimen is in poor condition making the total length and number of ventrals only estimates. The anal plate is not divided.

Crotalus enyo enyo (Cope)

Three specimens (BYU 34604–34606), all males, were collected in Arroyo de la Taneria on Isla San Marcos. The first was collected on 2 June 1978 at 2130 hours by John C. Cram at the edge of a trash dump. The second specimen was taken by us on 17 June 1978 after it had fallen into a water well at the goat corral and drowned. The third rattlesnake was found by Robert Murphy on 18 June 1978 at 2200 hours as it lay in a resting coil on a pile of rubbish near the center of the arroyo about 1.5 km from the western shoreline.

These specimens fall within the range of variation of the subspecies *C. e. enyo* as defined by Klauber (1931:363) in meristic characters and coloration. The following counts were taken from BYU 34604–34606, respectively: ventrals 165, 172, 169; subcaudals 28, 29, 27; scale rows at midbody 25, 25, 25; supralabials 13-13, 14-14, 14-14; infralabials 14-14, 15-14, 14-15; scales bordering rattle 10, 10, 10; scale rows at midtail 13, 13, 13; body blotches 33, 36, 31. Contrary to the general trend of dwarfism in insular snake populations commented on by Soulé and Sloan (1966), these rattlesnakes are quite large; two are in excess of 800 mm, and one (BYU 34606) is only 49 mm from matching Klauber's (1972) record of 895 mm for the subspecies.

Crotalus mitchellii mitchellii (Cope)

An adult male (SDSNH 44359) was collected on Isla Salsipuedes by the Vermillion Sea Expedition on 23 March 1962. It measures 807 mm in total length with a tail of 67 mm; rattle width is 15.7 mm; head is contained in the total length 24 times. There are 33 body blotches and 4 tail rings. Ventrals number 170, subcaudals 25, supralabials 17-17, infralabials 17-15, rattle segments 8 and equal in width to each other. The last supralabials are about twice as long as the preceding scales. Coloration (in alcohol) is a light cream-yellow background with blotches composed of black to dark brown stippling that frequently run together to form larger spots, a few of which are greater than 1 mm in diameter; the tail is light grayish-white in background with rings darkest dorsally blending to gray laterally; the ventrals are immaculate cream-yellow. Thus all characters of this specimen agree with the description of *C. m. mitchellii* (Klauber, 1972).

Crotalus ruber Cope

Although Harris and Simmons (1978) described the Isla Monserrate population of red diamond rattlesnakes, *Crotalus ruber,* as an endemic subspecies, we concur with McCranie and Wilson (1979) in not recognizing the incomplete "preliminary" description of the population. Consequently, the subspecific notation should be considered a *nomen suspectum* (and not a *nomen nudum* as McCranie and Wilson [1979] stated). The Isla Monserrate population of red diamond rattlesnakes is accordingly referred to as *C. ruber lucasensis.* Moreover, Harris and Simmons (1978) revived *C. ruber elegans* for the red diamond rattlesnake population on Isla Angel de la Guarda. However, we feel that their justification is inadequate, necessitating further investigation before their recommendation can be seriously considered.

COMPLETENESS OF THE DISTRIBUTIONAL RECORDS

This review summarizes and increases the known insular populations of lizards by only nine new populations, seven of which are for nocturnal geckos in the genera *Coleonyx* and *Phyllodactylus.* We believe that even though a few populations of geckos remain to be discovered, the distributional data base for lizards is better than 90% complete; this view is supported by lizard distribution patterns on Gulf islands (Murphy 1983*b*). In contrast, this review summarizes and increases the known insular populations of snakes by 30% over that of Soulé and Sloan (1966). Even though this increase is substantial, the records are undoubtedly incomplete; but just how incomplete are they? If we find a strong correlation between the number of snake species and any independent variable on the various Gulf islands, we may make an estimation of completeness of our records, predicting the number of insular snake populations which remain to be discovered. In the course of this investigation, the number of snakes was found to be significantly correlated with the number of lizards on the various Gulf islands ($P < .01$).

All islands have not received equal collecting effort. As evidence in support of this assertion, this checklist increases the snake fauna of Isla San Marcos by 100%, and Isla Danzante by 130% since Soulé and Sloan (1966). Because there is no unbiased method to identify poorly collected islands, we simply defined well collected islands as those having received at least 10 man-nights of collecting. On two such islands, Tortuga and Monserrate, one more species of snake than lizard is found, and on islas Danzante, San Pedro Martir, and San Marcos the number of species of snakes equals the number of species of lizards. On Isla San Marcos we have spent substantial efforts collecting yet expect to find at least one additional species of snake, the blind snake, *Leptotyphlops humilis,* and possibly the Baja California rat snake, *Elaphe rosaliae,* which occurs on the peninsula opposite this island. Therefore, the maximum number of species of snakes on the islands may equal the number of species of lizards plus 1 or 2, except on very small islands. It is thus possible to estimate the total number of snake populations, and therefore estimate the completeness of the distributional records. From these data we may estimate the snake distributional records to be roughly 50% complete.

One of us (Ottley) has spent considerable time collecting on one small island, Isla Mejia. Although four species of lizards have been recorded from this island only two snake species have been found. This finding of a lower number of snake species may be true for many very small islands; that is, the number of snake species on the small islands may not exceed the number of lizard species by one or two. Indeed, this would not be surprising considering that many snake species occupy a higher trophic level and consequently would be expected to occur in lower densities; small islands may be too small to support snake populations large enough to survive environmental bottlenecks. Moreover, many small islands do not provide appropriate habitat for many small, burrowing snake species. If we consider the number of snake species to equal the number of lizard species on the Gulf islands, and not to exceed them by one or two, our estimation of completeness is about 70%.

Because distributional records for snakes are likely only 70% complete we caution against their use in statistical analyses attempting to discern causative factors limiting the number of species of reptiles on Gulf of California islands (Case, 1983). Inasmuch as the distributional data for the lizards are far more complete we urge only these distributional data be used for such analyses; the predictive equations derived for the lizards (Wright et al., in preparation) should be generally applicable for the snakes as well because the number of lizards and snakes on the various Gulf islands are highly significantly correlated.

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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 5. GEOLOGY AND BIOSTRATIGRAPHY OF THE UPPER PART OF THE WIND RIVER FORMATION, NORTHEASTERN WIND RIVER BASIN

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Abstract

Stratigraphic studies in the Red Creek–Deadman Butte and Buck Spring areas of the northeastern Wind River Basin, central Wyoming, result in revised interpretations of the Eocene geology of these areas and the relations of the vertebrate fauna from the Lost Cabin Member (and equivalent units) of the Wind River Formation. Minor faulting and folding of Wind River strata complicate stratigraphic correlation between exposures; a possible south and east continuation of the Cedar Ridge Fault is mapped into the southwestern quarter of T.38N., R.87W. The Wind River Formation is divided into two lithostratigraphic units in the area of study: (1) the term Red Creek Facies is proposed for the lowermost sequence of strata of the Wind River Formation in this area which lies unconformably on, and is principally composed of clastic materials derived from, Mesozoic strata; the Red Creek Facies is exposed only along the southern flank of the Bighorn Mountains; (2) the Lost Cabin Member is exposed in most of the remaining parts of the study area and is composed principally of variegated and gray sequences of strata. A brown-colored volcaniclastic sequence overlies the Lost Cabin Member of the Wind River Formation and represents a remnant of either the Wagon Bed Formation or the Aycross Formation.

The suggestions of Granger (1910) and Guthrie (1971) that the vertebrate fauna from the Lost Cabin Member is restricted to either the same horizon or a narrow interval of strata are shown to be in error. In the upper part of the Wind River Formation (including both the Red Creek Facies and the Lost Cabin Member) the stratigraphic range of *Lambdotherium popoagicum* does not overlap that of *Palaeosyops* (=*Eotitanops*) *borealis, Hyrachyus* sp. cf. *H. eximius, Antiacodon,* and *Trogosus.* On the basis of these restricted ranges, two biostratigraphic zones are defined in the upper part of the Wind

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River Formation—the *Lambdotherium* Range Zone and the *Palaeosyops borealis* Assemblage Zone. The *Lambdotherium* Range Zone is Lostcabinian in age and the *Palaeosyops borealis* Assemblage Zone is Gardnerbuttean in age. A number of new taxonomic records are reported for the Wind River Formation. The term lithosympatric is used to indicate those species that come from the same fossiliferous horizon.

INTRODUCTION

The vertebrate fauna of the Wind River Formation of central Wyoming has long been used as the basis for defining and zoning middle to late early Eocene (middle and late parts of the Wasatchian Land Mammal Age) mammalian fauna of western North America. Since the first description of mammals from the formation (Cope, 1880, 1881), paleontologists have recognized that the fauna was intermediate or transitional in composition between the greater part of the Wasatch (early Eocene) and Bridger (middle Eocene) formation faunas. Subsequent biostratigraphic (for example, Osborn and Wortman, 1892; Osborn, 1909, 1929; Granger, 1910; Sinclair and Granger, 1911; Wood et al., 1941) and systematic studies (for example, Osborn, 1902; Kitts, 1956; Radinsky, 1963; Gingerich and Simons, 1977) of mammals from the Wind River Formation have documented the transitional nature of the fauna.

Two faunas, associated with different lithological units, have been generally recognized in paleontological studies of the Wind River Formation—an older Lysite Member fauna and a younger Lost Cabin Member fauna (Guthrie, 1967, 1971). These have been used, respectively, as the basis for defining the middle (Lysitean) and late (Lostcabinian) Wasatchian Land Mammal Age (Wood et al., 1941; Gazin, 1952, 1962; Robinson, 1966; Korth, 1982). Although mammals of Bridgerian aspect have been known to occur in the Wind River Formation for some time (Tourtelot and Thompson, 1948; see also Black, 1969; West and Atkins, 1970), the stratigraphic relations of these mammals have not been well understood.

Purpose and Scope

The purpose of this study is to clarify the lithostratigraphic and biostratigraphic relations of the upper part of the Wind River Formation in the northeastern Wind River Basin, Wyoming. A complete revision of the Wind River Formation vertebrate fauna is now in progress and some changes in taxonomy are necessary (Stucky and Krishtalka, 1982, 1983; Korth, 1982, 1984; Krishtalka and Stucky, 1983*a*, 1983*b*). These taxonomic changes, many of which are incorporated here, do not significantly alter the major biostratigraphic conclusions presented, which are based on the first appearances of exotic and easily identified taxa that have been used previously as biostrati-

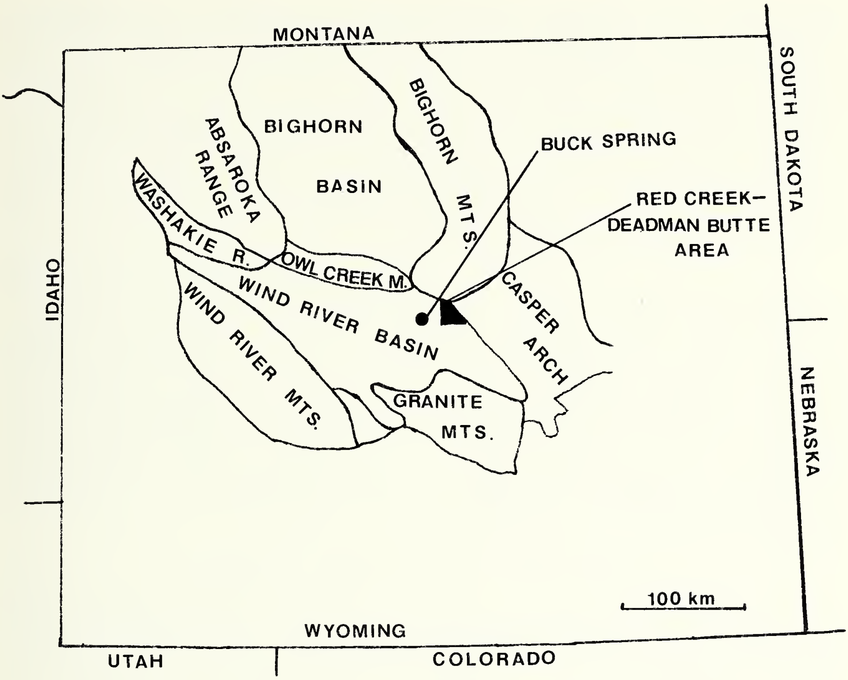

Fig. 1.—Wind River Basin, central Wyoming, showing the Red Creek–Deadman Butte, Buck Spring (type area of Lost Cabin Member, Wind River Formation) and other areas discussed in the text (after Seeland, 1978).

graphic indicators. This contribution is directed toward developing a well documented set of data for the Wind River Formation to be used in recording the history of vertebrate life and understanding the evolution and ecology of early Tertiary vertebrate faunas in the Wind River Basin (Stucky and Krishtalka, 1982).

This research focuses on the geology and mammalian paleontology of the Red Creek–Deadman Butte and Buck Spring (type area of the Lost Cabin Member, see Tourtelot, 1948) areas in the northeastern Wind River Basin (Fig. 1). The mammalian fauna from this area, as a whole, is equivalent to the Lost Cabin Member fauna of Sinclair and Granger (1911) and Guthrie (1971).

The principal results of this study are the documentation of the stratigraphic distributions of approximately 120 mammalian species in the upper part of the Wind River Formation, the mapping of hitherto unrecognized lithostratigraphic units, and the definition of concepts that allow a more objective approach to biostratigraphy, paleoecology, and systematics. Preliminary faunal lists of each classic fossil vertebrate locality in the Lost Cabin Member (see Guthrie, 1971) are provided for the first time. The assumption that these localities occur within the same fossiliferous horizon or a narrow interval of strata is shown to be false (contra Granger, 1910; Sinclair and Granger, 1911; Guthrie, 1971; but see Osborn, 1909) as recently suggested by Korth (1982, but see below for a modified interpretation).

Two zones are recognized as valuable biostratigraphic units in the upper part of the Wind River Formation: the *Lambdotherium* Range Zone and the *Palaeosyops borealis* Assemblage Zone. Use of these two zones clarifies the stratigraphic relations of fossil vertebrate localities in the Lost Cabin Member of the Wind River Formation. Recognition of these two zones also clarifies biostratigraphic relations with Eocene strata of similar age lying outside of the Wind River Basin, thus providing a more concrete basis for the definition of the Wasatchian-Bridgerian boundary in continental rocks throughout the western interior region of North America (Stucky, 1984*b*).

Geographical and Geological Setting

The Wind River Basin in central Wyoming is a large trapezoidal depression encompassing approximately 8500 square miles of land surface area (Fig. 1). It is bounded on the north by the Bighorn and Owl Creek Mountains, on the northwest by the Washakie Range, on the west by the Wind River Mountains, on the south by the Granite Mountains and Rattlesnake Hills and on the east by the Casper Arch. The western two-thirds of the basin are drained to the north by the Wind River into the Bighorn Basin, and the eastern third is drained to the east by the Powder and North Platte rivers. Tributaries of these rivers with headwaters in the mountains surrounding the basin have cut through and exposed Tertiary and older sediments throughout the basin.

During the Laramide orogeny, from late Cretaceous through early Eocene time, the highland and mountain areas were uplifted to form the Wind River Basin. Consequent basin subsidence and faulting near the basin margin resulted in stratal displacements of as much as 30,000 ft (9100 m) (Keefer, 1965*a*). The basin floor, however, remained at a relatively constant elevation of not more than a few thousand feet. Erosion of Mesozoic, Palaeozoic, and Precambrian strata from mountain and highland areas resulted in the deposition of alluvial fan and braidplain deposits around the basin margin, and lacustrine, stream channel and overbank deposits in the basin interior (Keefer, 1965*a*; Soister, 1968; Korth, 1982; this report). Importantly, Paleozoic limestones provided an abundant carbonate source, which resulted in the formation of abundant calcareous mineral deposits within the Wind River Formation. The paleo-Wind River developed and drained the Wind River Basin to the east (Seeland, 1978). After the early Eocene, aggradation continued until many mountainous areas were covered with volcaniclastic and terrigenous clastic debris (Love, 1978). Beginning in the late Pliocene or early Pleistocene the mountains were exhumed by erosion, revealing the paleolandscape of the early Eocene. The modern landscape reflects the topographic complexity of the early and middle Eocene during the time the Wind River Formation was deposited (Woodward, 1957).

Tectonic, erosional, and depositional events varied from place to place throughout the Wind River Basin (Keefer, 1965*a*, 1970). Love (1978) outlined these events in the Badwater area just to the west of the Red Creek–Deadman Butte area. Love indicates that abrupt uplift and southward thrust of the Bighorn Mountains resulted in the overturn of Paleocene strata just after the beginning of the Eocene. Continued uplift and correlated erosion of the highland deposits resulted in deposition of coarse grained alluvial fan deposits near the mountain fronts in the Badwater area and, more basinward, flood plain and channel deposits. The Red Creek–Deadman Butte area illustrates the variable effects of tectonic and depositional events when compared to the Badwater area during the early and middle Eocene. At the same time that the Bighorn Mountains were being uplifted and alluvial fans were being deposited in the Badwater area, braidplains were deposited near their southern front in the Red Creek–Deadman Butte area, where comparatively little tectonic activity was occurring.

History of Investigations

Nace (1936), Tourtelot (1948), Keefer (1965*a*), and Soister (1968) have outlined the history of investigations of the geology of the Wind River Formation and Wind River Basin. Keefer (1965*a*) has provided excellent summaries of pre-Wind River Formation strata and the general geologic history of the Wind River Basin since the Cretaceous. Seeland (1978) has presented a depositional model for the Wind River Formation and Korth (1982) has provided one for exposures of the formation in the north central part of the Basin. The general geologic history of the northeastern Wind River Basin was given by Tourtelot (1953) and Woodward (1957). The most recent geologic maps of the area were prepared by Keefer (1970) and Love et al. (1978). The most important discussions of Wind River Formation geology in the northeastern part of the basin are those of Tourtelot (1948) and Love (1978). Preliminary observations on the area of this report were provided by Stucky and Krishtalka (1982). The biostratigraphic history of the Wind River Formation is detailed below.

Abbrevations and Symbols

Abbreviations used in the text are: ACM, Amherst College Museum (Amherst); AMNH, American Museum of Natural History (New York); CM, Carnegie Museum of Natural History (Pittsburgh); DMNH, Denver Museum of Natural History (Denver); FMNH, Field Museum of Natural History (Chicago); JHU, Johns Hopkins University (Baltimore); LACM, Los Angeles County Museum (Los Angeles); MPM, Milwaukee Public Museum (Milwaukee); PU, Princeton University (Princeton); TTU, Texas Tech University (Lubbock); UCB, University of California, Berkeley (Berkeley); UCM, University of Colorado Museum (Boulder); UM, University of Michigan Museum of Paleontology (Ann Arbor); USGS, United States Geological Survey (Denver); USNM, United States National Museum (Washington); UW, University of Wyoming (Laramie); YPM, Yale Peabody Museum (New Haven). Loc., locality; MS, Measured Section; U, unit or stratigraphic horizon.

STRUCTURAL GEOLOGY—WIND RIVER FORMATION

The major geologic structures of the Wind River Formation in the Red Creek–Deadman Butte area have been well documented by Tourtelot (1948, 1953), Woodward (1957), Gard (1969), Keefer (1970), and Love (1978). Few researchers have, however, documented structural features within the Wind River Formation in the area of this report.

In practically all exposures of the Wind River Formation, minor faulting and changes in dip occur, making correlation difficult, even in continuous exposures (Fig. 2). Correlation of exposures separated by covered areas is extremely difficult and often unwarranted unless nearly identical sets of strata occur. Reliability of lithostratigraphic correlation of the Wind River Formation decreases substantially as the distance between exposures increases because of potential intervening but unknown geologic structure and lateral variation in lithology. Biostratigraphic correlations proposed on the basis of attitudinal and elevational relations should be supported by faunal data. In these instances, only general correlations can be made.

General structure.—Attitudes of Wind River Formation strata are structurally determined by their proximity to uplifted strata of the southern Bighorn Mountains and Casper Arch and to the Dry Fork and Cedar Ridge Faults. Compared to the structural relations of Wind River strata in the Badwater area (Love, 1978), these relations in the Red Creek–Deadman Butte area are less complex (Tourtelot, 1953; Woodward, 1957).

Wind River strata along the southern flank of the Bighorn Mountains strike uniformly east–west and dip between 6 and 8 degrees south. In this area the Wind River Formation generally lies with angular unconformity of approximately 10 degrees on Mesozoic strata. However, occasional small wedges of Mesozoic strata are completely surrounded by sediments of the Wind River Formation with angular relations of as much as 60 degrees in the central portion of T.38N., R.87W. (Tour-

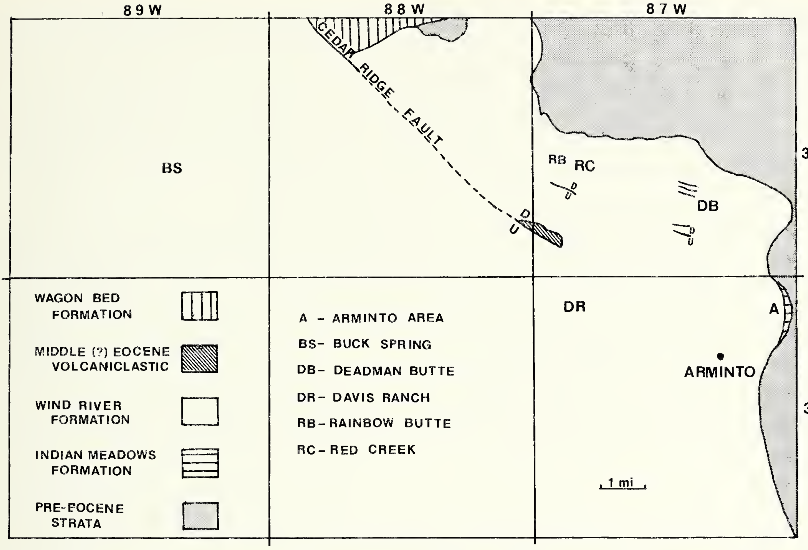

Fig. 2.—General geologic map of northeastern Wind River Basin, Wyoming (modified from Keefer, 1970).

telot, 1953). These data suggest an erosional surface of considerable relief between the Wind River Formation and underlying Mesozoic strata (Woodward, 1957). North and west of Arminto in Secs. 2 and 12, T.37N., R.86W., Wind River Formation strata strike north–south and dip at approximately 6 degrees west. Further to the south on the western limb of the Casper Arch in the SE ¼ of T.37N., R.87W., E ½ of Sec. 1, T.36N., R.87W., and NW ¼ of T.36N., R.86W., extensive exposures of the Wind River Formation lie with approximately 45 degrees angular unconformity on the Paleocene Fort Union Formation and dip to the west at 45 degrees. These attitudinal relationships of Wind River strata in the Red Creek–Deadman Butte area suggest a broad synclinal fold with a northeast trend that folds down to the south toward the basin axis between the southern front of the Bighorn Mountains and western edge of the Casper Arch (see Keefer, 1965*a*).

Cedar Ridge Fault.—Tourtelot (1953) mapped the Cedar Ridge Fault in the Badwater Creek area. This fault extends from the southern part of the Owl Creek Mountains eastward to the eastern part of Cedar Ridge in Secs. 4 and 5, T.38N., R.88W.

A possible continuation of the Cedar Ridge Fault was mapped in Sec. 25, T.38N., R.88W., and Sec. 30, T.38N., R.87W. (see Fig. 2). This continuation has greater than 80 ft (24 m) of displacement, as suggested by the fault contact of the Wind River Formation and the Middle(?) Eocene volcaniclastic sequence (Fig. 2). Areas between the easternmost mapped extent of the Cedar Ridge Fault and this fault are grass covered, making direct relations between the two faults impossible to determine without subsurface data. A continuation of the trends of the Cedar Ridge Fault to the southeast and this fault to the northeast suggests that they are the same.

Dry Fork Fault.—The Dry Fork Fault has been fully mapped in the Red Creek–Deadman Butte area by Woodward (1957). Minor normal faults in the NW ¼, SW ¼ of Sec. 17, N ¼ of Sec. 19, S ½ of Secs. 19 and 20, N ½ of Sec. 30, S ½ of Sec. 22 and S ½ of Secs. 27 and 28 of T.38N., R.87W. (Fig. 2) of less than 25 ft (8 m) displacement trend parallel to Dry Fork Fault, suggesting some structural relationship. The downthrown side is to the north of each of these faults. Displacement of each fault is easily determined in outcrop by repeated sequences of strata.

Other faults.—1) A normal fault of indeterminate displacement was mapped in the S ½ of Sec. 27, T.38N., R.87W. To the north, on the upthrown side of the fault, variegated sediments of the Lost Cabin Member of the Wind River Formation were exposed; to the south, gray mudstones and sandstones were exposed. UCM Loc. 81010 was found just to the south of the fault and cannot be directly placed in the Deadman Butte stratigraphic section. Based on its location to the south of the fault, UCM Loc. 81010 is higher stratigraphically than localities (UCM Locs. 80062, 80089, 80090, 81008, 81009) that are directly located in the Deadman Butte stratigraphic section (Stucky, 1984*a,* Measured Sections 16 to 20).

2) Biostratigraphic and structural relations of the Davis Ranch and Wolton localities (Locs. 1 and 2, respectively, of Guthrie, 1971) suggest that a fault may be present in the vicinity of Alkali Creek in T.37N., R.87W. Wind River strata at Davis Ranch dip to the south at approximately 4 degrees. Although both localities are at nearly the same elevation (6000–6200 ft), the fauna at the Wolton locality is within the older *Lambdotherium* zone, whereas the fauna at Davis Ranch is used to define the younger *Palaeosyops borealis* zone. If no faults occurred in this area, trigonometric calculation indicates that the Wolton locality should be at least several hundred feet above Davis Ranch (see Korth, 1982), and thus would be younger than Davis Ranch, contradicting the faunal evidence. In addition, the nearly straight course of Alkali Creek and subsurface data suggest a fault controlled valley (J. D. Love, verbal communication to P. Robinson, 1982).

3) On the northern side of the exposures at the Buck Spring locality (Locality 3 of Guthrie, 1971; probable type area of the Lost Cabin Member, see Tourtelot, 1948 and below), in Sec. 15, T.38N., R.89W.,

strata of the Lost Cabin Member are folded into a monocline with the limb of the monocline dipping to the north at approximately 12 degrees. In the next set of exposures to the north of this area, strata are flat lying, suggesting that an unmapped fault is present. To the south in Sec. 22, T.38N., R.89W., minor faulting has also been recognized which does not, however, complicate stratigraphic relations in this area.

4) Love et al. (1978) have mapped an *en echelon* fault system in the general vicinity of T.38N., R.91W. Each of these faults has an east–west trend. Sediments of the Lysite Member and Lost Cabin Member are in fault contact along a major fault in this system in the center of Sec. 35, T.38N., R.91W. Sediments of the Lysite Member are exposed on the north side of this fault and sediments of the Lost Cabin Member are exposed on the south, downthrown side. According to a field label of L. and D. Kelley (Field No. 1951–L31, Amherst College Museum) this is the area where a specimen of *Lambdotherium* was reported to have been recovered from the Lysite Member of the Wind River Formation (Guthrie, 1967).

LITHOSTRATIGRAPHY

Wind River Formation

The Wind River Formation was first called the "Wind River Valley deposits" by Meek and Hayden (1861), who believed they were developed between the early Tertiary "lignite deposits" (=Paleocene Fort Union Formation) and the "White River Tertiary Deposits" of Oligocene age. In 1878, Hayden suggested that these deposits represented the Wasatch group of southwestern Wyoming. Two years later, fossil mammals were discovered by Jacob L. Wortman in the Wind River Formation, which indicated that these deposits were intermediate in age between the Wasatch and Bridger beds (Cope, 1880, 1881).

Sinclair and Granger (1911, also see Granger, 1910) described and named the Lysite and Lost Cabin formations of the Wind River group in the Badwater Creek area of the northeastern Wind River Basin. The Lysite and Lost Cabin were lowered in rank to members of the Wind River Formation by Tourtelot (1948), who emended the criteria of Sinclair and Granger for recognizing them. Keefer (1965*a*, 1965*b*, and 1970) reviewed the geology of the Wind River Basin and discussed the Wind River Formation in detail. In 1968, Soister described a unit exposed in the south central part of the Wind River Basin as the Puddle Springs Arkose Member of the Wind River Formation.

Stratigraphic Terminology for the Wind River Formation

Significant confusion has resulted from the use of similar terms for stratigraphic units and faunas in the Wind River Formation and from the application of these terms to deposits outside of the Wind River Basin. The unfortunate result has been the *a priori* assumption that the age and identification of a fossil assemblage within the Wind River Formation is determined by the lithologic unit in which it is preserved. This assumption is clearly false; similar lithologies simply suggest similar depositional and diagenetic conditions. Because the Wind River Formation has been used as the basis for defining the middle to late Wasatchian Land Mammal Age (Lysitean and Lostcabinian) in western North America (see for example, Wood et al., 1941; Gazin, 1952, 1962; Robinson, 1966; Guthrie, 1967, 1971; Bown, 1979; Schankler, 1980), age relations of "late Wasatchian" faunas have been obscured by the lack of a rigorous terminology. Table 1 clarifies the terminology used here for the Wind River Formation and its faunas.

Lithology

The Wind River Formation in the area of this report is divided into the Red Creek Facies and the Lost Cabin Member (Fig. 3). The name "Red Creek Facies" is here applied to a mappable lithologic unit of homogeneous lithology exposed only along the northern portion of the Red Creek–Deadman Butte area to the south of the exposures of Mesozoic strata in T.38N., R.87W. The Lost Cabin Member occupies most of the rest of the area of this report.

The Lost Cabin Member exhibits a heterogenous lithology. In addition, correlations from one exposure to the next are often hampered by intervening covered areas or structural complexity. As aptly pointed out by Soister (1968:A9), lateral and vertical lithologic variation of the Wind River Formation is "so pronounced that composite stratigraphic sections, when applied to large areas, can give a false picture of the formation." His observations are especially pertinent to the Lost Cabin Member. Because of the lithologic variation, each major area of exposure of the Wind River Formation is discussed separately to clarify the local lithostratigraphic sequences and to point out vertical and horizontal variations in lithology as they apply to biostratigraphy. While this is not conventional practice, it is done here to emphasize that although lithologies of Wind River Formation rocks may be quite similar in different areas, they are not necessarily direct correlates.

The Lost Cabin Member has long been recognized for its diverse and interesting vertebrate fauna. Vertebrate paleontologists have suggested that the fauna was recovered from a narrow interval of strata (Granger, 1910; Guthrie, 1971). This generalization was based primarily on the assumption that prominent marker beds in exposures separated by some 20 mi (32 km) were the same fossiliferous horizon (Granger, 1910). This conclusion led to the lumping of faunal lists from widely separated localities. The lithologic descriptions presented here and the stratigraphic sections (Fig. 4; Stucky, 1984*a*) provide evidence

Table 1.—*Terminology used in this report for rocks and faunas of the Wind River Formation. Abbreviations are in parentheses.*

FORMAL LITHOSTRATIGRAPHIC UNITS

Lysite Member.—Lithostratigraphic unit of member rank of the Wind River Formation as defined and mapped by Tourtelot (1948, 1953).

Lost Cabin Member.—Lithostratigraphic unit of member rank of the Wind River Formation as defined and mapped by Tourtelot (1948, 1953) and emended by Keefer (1965*a*).

Wind River Formation.—Lithostratigraphic unit of formation rank limited to the Wind River Basin as characterized by Keefer (1965*a*).

INFORMAL LITHOSTRATIGRAPHIC UNIT

Red Creek Facies.—Mappable lithostratigraphic unit of the Wind River Formation exposed in central part of T.38N., R.87W.

BIOSTRATIGRAPHIC UNITS (UPPER PART OF WIND RIVER FORMATION ONLY)

Lambdotherium range zone (Lambdotherium zone).—Biostratigraphic unit of the Wind River Formation defined on the basis of the stratigraphic occurrence of *Lambdotherium popoagicum* in the Red Creek, Deadman Butte and Buck Spring stratigraphic sections. The *Lambdotherium* Range Zone is fully defined in text.

Palaeosyops borealis assemblage zone (Palaeosyops borealis zone).—Biostratigraphic unit of the Wind River Formation defined on the basis of the stratigraphic occurrence of *Palaeosyops borealis, Trogosus* sp., *Hyrachyus* sp., cf. *H. eximius, Microsyops lundeliusi* and *Antiacodon* in the Red Creek, Deadman Butte, Buck Spring and Davis Ranch stratigraphic sections. The *Palaeosyops borealis* Assemblage Zone is fully defined in text.

INFORMAL BIOCHRONOLOGIC UNITS

Lysitean Land Mammal Subage (Lysitean).—Informal biochronologic Land Mammal Subage which denotes the middle Wasatchian Land Mammal Age for faunas in western North America. Defined on the basis of the Lysite Member fauna, exclusive of the occurrence of *Lambdotherium* (Guthrie, 1967). Korth (1984) has listed several rodent species of value in determining the Lysitean. See Stucky (1984*b*).

Lostcabinian Land Mammal Subage (Lostcabinian).—Informal biochronologic Land Mammal Subage which denotes the late Wasatchian Land Mammal Age in western North America. Defined originally on the basis of the Lost Cabin Member fauna. In this report the Lostcabinian Land Mammal Subage is defined on the basis of the occurrence of *Lambdotherium* in an assemblage.

Gardnerbuttean Land Mammal Subage (Gardnerbuttean).—Informal biochronologic Land Mammal Subage which denotes early Bridgerian in western North America. Defined on the basis of the upper Huerfano Formation fauna of the Huerfano Basin (Robinson, 1966). As used in this report the Gardnerbuttean is also defined by localities in the Huerfano Basin and elsewhere from which *Palaeosyops borealis* is known (see text).

Wasatchian Land Mammal Age (Wasatchian).—Informal biochronologic Land Mammal Age in western North America, defined by the first occurrence in the fossil record of Perissodactyla, Artiodactyla, Adapidae (=Notharctidae) and Hyaenodontidae (Rose, 1981) at its lower boundary and the first occurrence of Brontotheriidae, Trogosinae and *Hyrachyus* above its upper boundary; early Eocene.

Bridgerian Land Mammal Age (Bridgerian).—Informal biochronologic Land Mammal Age in western North America, defined by the first occurrence of Brontotheriidae, Trogosinae and *Hyrachyus* at its lower boundary and the first occurrence of Lagomorpha, Agriochoeridae and Merycoidodontidae above its upper boundary (West et al., in press); early to middle Eocene.

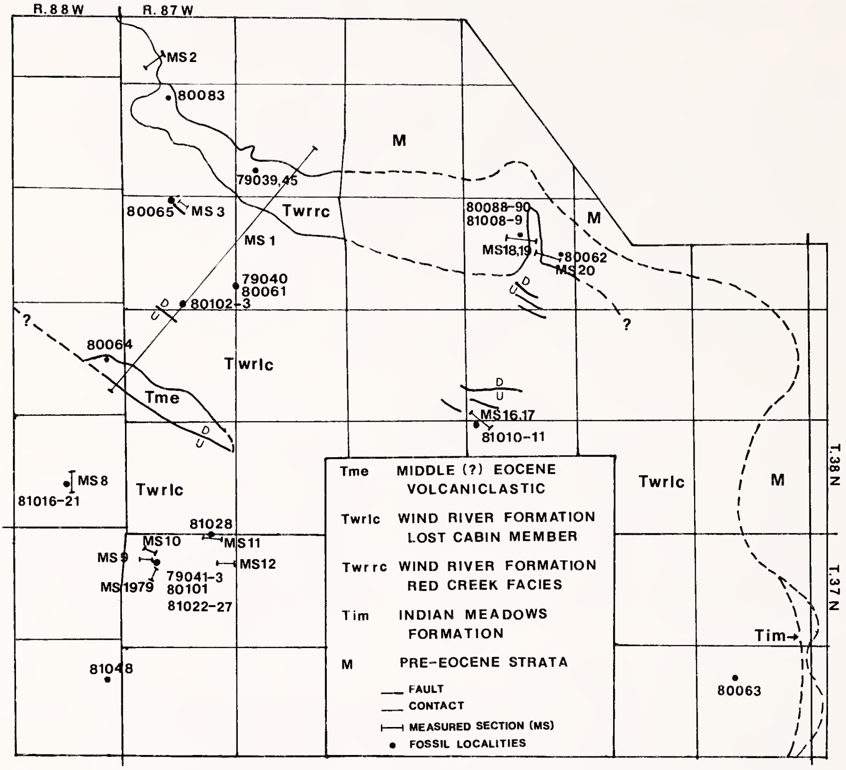

Fig. 3.—Geologic map of Eocene strata in the Red Creek–Deadman Butte area, Natrona County, Wyoming (base map from Arminto, Badwater SE and Waltman NW 7½ quadrangles and modified from Keefer, 1970).

that rejects the supposed long distance correlation of two key fossiliferous horizons—the "dark red stratum" (Granger, 1910) or "maroon shale" layers (Guthrie, 1971) at Davis Ranch and Buck Spring. The two localities are quite different in faunal composition.

Red Creek stratigraphic section (Stucky, 1984*a*; MS-1 and MS-2).—The Red Creek stratigraphic section was measured from the contact of the Wind River Formation with Mesozoic strata in Sec. 17, T.38N., R.87W., to the contact with an overlying volcaniclastic sequence in the SE ¼, Sec. 25, T.38N., R.88W. Total thickness of the Wind River Formation in the Red Creek section varies from a wedge edge at the unconformable contact on Mesozoic strata to several thousand feet in the subsurface (Keefer, 1965*a*). Measured thickness in surface outcrop is 655 ft (200 m). Sediments of the Wind River Formation measured in this stratigraphic section are divided into a lower gray sequence of

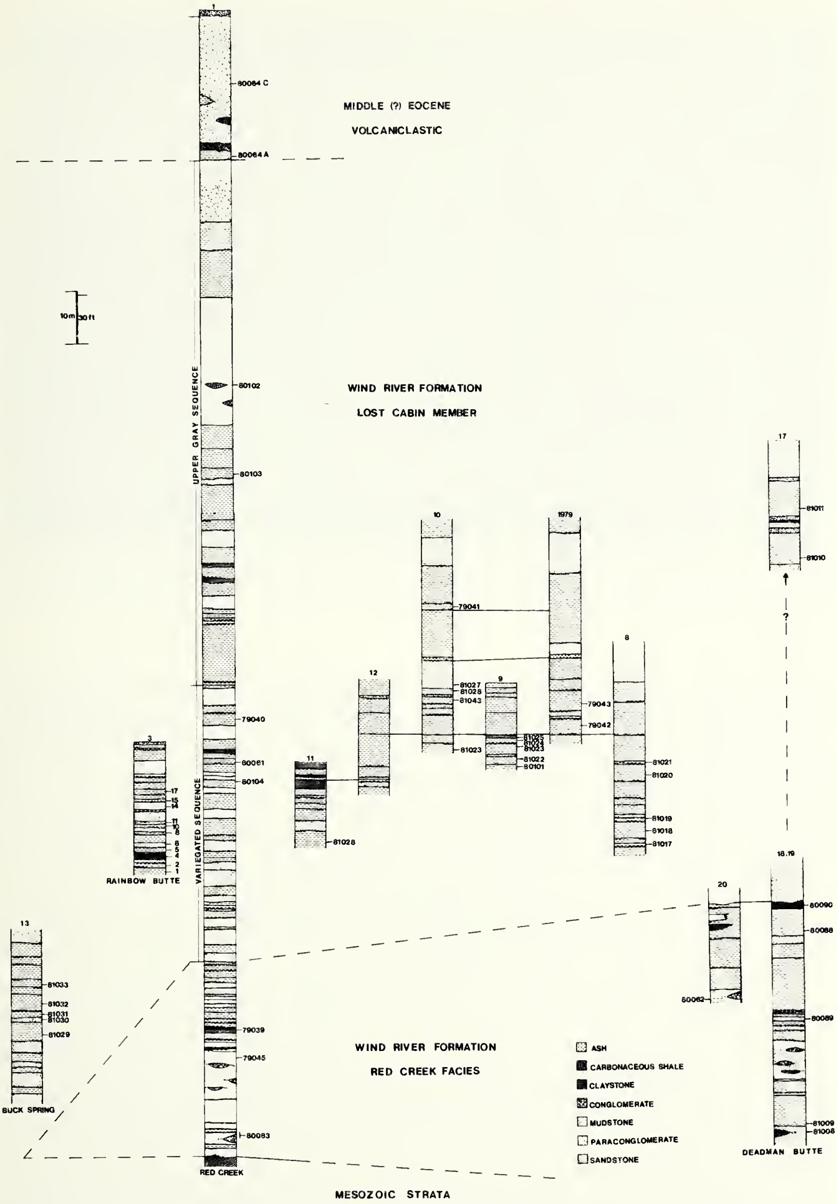

Fig. 4.—Stratigraphic correlation of the Wind River Formation in the northeastern Wind River Basin, Wyoming. Solid horizontal lines are direct correlations of specific horizons; dashed horizontal lines are inferred lithostratigraphic correlations; number at top of each stratigraphic column refers to measured sections in Stucky (1984*a*).

Fig. 5.—Exposures of Red Creek Facies, Wind River Formation (NE ¼, Sec. 20, T.38N., R.87W., Natrona County, Wyoming).

strata which, together with sediments in the lower part of the Deadman Butte stratigraphic section (see below) define the Red Creek Facies of the Wind River Formation, and a variegated and upper gray sequence, both of which are mapped as the Lost Cabin Member.

The *Red Creek Facies* is a maximum of 131.5 ft (40 m) thick and unconformably overlies Mesozoic strata. This unit is characterized by tabular grayish green tuffaceous sandstones and mudstones, with occasional tabular dark grayish green claystones and lenticular carbonaceous shales (Fig. 5). Conglomerates are of local importance and occur as lenticular units within sandstones.

Sandstones make up 58% of the unit and vary between 2.0 (0.6 m) and 31.0 ft (9.5 m) in thickness. Most sandstones are quartz arenites and have a tabular geometry. Sandstones may be followed in outcrop for up to several kilometers (total extent of exposures). The sand particles are predominantly well rounded, fine to medium, quartz grains derived from sandstones of the Cloverly and Morrison Formations. Isolated bones and teeth of fossil vertebrates are found in some sandstones (UCM Loc. 79045). Conglomeratic beds are clast supported and occur as lenses within sandstone units (Fig. 6). The matrix of these conglomerates is a well sorted fine to medium sand. These conglomerates are composed of pebble- to cobble-sized clasts derived princi-

Fig. 6.—Lenticular conglomerate in sandstone of Red Creek Facies, Wind River Formation (SW ¼, Sec. 17, T.38N., R.87W., Natrona County, Wyoming).

pally from Mesozoic strata (subangular and angular porcelanite from the Mowry shale; subrounded chert pebbles and rounded sandstone and conglomerate rock fragments from the Morrison and Cloverly Formations; chert and fossil fragments from the Sundance Formation; and sandstone and chert fragments from the Chugwater Formation), but also contain some Paleozoic rock fragments (subrounded limestone fragments). Rounded fragments of the belemnite *Pachyteuthis,* a common fossil of the Sundance Formation (Jurassic), are occasionally found in conglomerates. Within a single sandstone unit, as many as eight lenticular conglomeratic lenses separated by sandstone matrix were recorded in a thickness of 31 ft (9 m). These lenses vary from 0.66 ft (0.2 m) to 2.0 ft (0.6 m) in thickness and 2.0 ft (0.6 m) to 8.0 ft (2.4 m) in lateral extent. Boundaries between sandstones and conglomerates are sharp, as are boundaries of sandstones on mudstones.

Gray, probably tuffaceous mudstones represent 38% of the Red Creek Facies. Mudstones vary between 0.5 ft (0.2 m) and 4.0 ft (1.2 m) in thickness. Most mudstones are siltstones with a very low percentage of sand and a high percentage of clay. Pedotubules, calcareous glaebules, coprolites and articulated fossil vertebrates occur in association in some gray mudstones which generally have a bluish-gray cast when seen from a long distance (UCM Loc. 79039). Some mudstone units contain abundant gypsum crystals and occasional petrified wood and invertebrate shell fragments.

Dark grayish green claystones and carbonaceous shales are a minor constituent of the Red Creek Facies in the Red Creek section, comprising 4% of the sequence thickness. Claystones vary from 0.5 ft (0.2 m) to 3.0 ft (0.9 m) in thickness but are laterally quite extensive. One claystone unit was mapped for one kilometer (unit 15, Red Creek section, Stucky, 1984*a*). This unit was easily recognized in outcrop by its dark gray color band and proved to be useful in local correlation. Claystones are thinly laminated and preserve occasional burrows approximately 3 to 4 mm in diameter. Both color and lithologic contacts with lower and upper units are sharp; occasional intraclasts of these claystones are incorporated into overlying units.

Carbonaceous shales weather dark brown and are lenticular in overall morphology. Leaf and stem fragments occur locally. No fossil vertebrates are known from either the claystones or carbonaceous shales in the Red Creek Facies.

The Lost Cabin Member in the Red Creek–Deadman Butte area is divided into a lower variegated sequence and an upper gray sequence. The variegated sequence lies conformably on the Red Creek Facies. Thickness is 176.5 ft (53.8 m). The lower boundary of this variegated sequence is defined as the lowest sandstone unit that contains abundant rock fragments, and calcareous cement. This boundary coincides with the lower boundary of the Lost Cabin Member (see Tourtelot, 1948; Korth, 1982). The variegated sequence of the Lost Cabin Member is characterized by channel sandstones and alternating mottled red-gray and gray mudstones. Claystones are rare and carbonaceous shales absent.

Sandstones represent 47% of the variegated sequence. These sandstones have apron-channel, shoestring channel, and tabular geometries (see Bown, 1979). Shoestring channel sandstones are most common and are prominent linear features on the landscape surface. Most sandstones are crossbedded and have calcium carbonate cement. Calcareous, preferentially cemented cannonball concretions up to one foot in diameter are common in some sandstone units. Grains are generally subrounded, very fine to coarse, quartz and rock fragments. Pebble conglomerates are rare but occur at the base of some sandstones. Pebbles in these conglomerates are derived from Precambrian sources.

Alternating mottled red-gray and gray mudstones make up 48% of the variegated sequence. Mottled red-gray mudstones often contain calcareous pedotubules and glaebules, coprolites, eggshell fragments, and fossil vertebrates in abundance (UCM Loc. 79040). Gray mudstones may contain these as well (UCM Loc. 80061) but are generally not bioturbated and not fossiliferous. Mudstones generally do not show

Fig. 7.—Upper gray sequence of Lost Cabin Member, Wind River Formation (road cut in SE ¼, Sec. 19, T.38N., R.87W., Natrona County, Wyoming). Note that the horizons are separated by sharp contacts.

primary structure in hand samples. This variegated sequence represents a basinward facies of the Wind River Formation.

The upper gray sequence lies conformably on the variegated sequence and represents the uppermost part of the Lost Cabin Member. The lower boundary of the upper gray sequence is arbitrarily defined at the conformable base of a gray mudstone that lies on the uppermost mottled red-gray mudstone in the variegated sequence. This unit is conformably overlain by a volcaniclastic sequence which is inferred to represent a Wagon Bed or Aycross formation equivalent (see below). The upper gray sequence is characterized by thick crossbedded sandstones, gray mudstones and dark gray claystones which contrast with the alternating red and gray bands of the variegated sequence (Fig. 7). Thickness is 334 ft (101.8 m).

Sandstone units in the upper gray sequence vary between 4 ft (1.2 m) and 82 ft (25 m) in thickness and represent 46% of the total thickness of the sequence. These sandstones are crossbedded, micaceous, and have a calcareous cement. Preferentially cemented calcareous cannonball concretions are common. The thickest sandstone in this sequence contains carbonaceous shale plugs and silicified fossil logs. The sand grains are medium to coarse quartz and rock fragments. Conglomeratic lenses occasionally occur at the base of sandstones and are composed primarily of pebble-sized, rounded, Precambrian rock fragments.

Gray mudstones represent 53% of the upper gray sequence. These mudstones have sharp color and/or lithologic contact boundaries with adjacent units and generally show graded bedding. Bioturbation structures are uncommon or absent. Many of these mudstones are channeled into underlying units and often have mudstone, calcareous glaebule, and claystone intraclasts at their base. Many contain biotite(?) flakes which decrease in size toward the top of the unit. All mudstones are micaceous and are probably tuffaceous. A roadcut along the Arminto-Lost Cabin Road in Sec. 19, T.38N., R.87W. best exhibits mudstones and claystones of the upper gray sequence.

Dark gray claystones nearly identical in structure to dark gray claystones in the Red Creek Facies are important marker beds. These units are laterally persistent and vary between 2 ft (0.6 m) and 3 ft (0.9 m) in thickness. Dark gray claystones are thinly laminated and have sharp contacts with adjacent units. As is true for dark gray claystones in the Red Creek Facies, these claystones often have burrows that are filled with sediment similar to that found in the overlying unit.

Fossil vertebrates are extremely rare in the upper gray sequence of the Red Creek section, being represented only by several lepisosteid scales and turtle shell fragments.

Deadman Butte stratigraphic section (Stucky, 1984*a*, MS-16 to MS-20).—The Deadman Butte stratigraphic section was measured in Sec. 22, T.38N., R.87W. Here, the Wind River Formation lies unconformably on Mesozoic strata (Tourtelot, 1953). The top of the formation is not preserved in this area. Measured thickness is 160 ft (48.8 m) in this section.

Both the Red Creek Facies and a variegated sequence of the Lost Cabin Member were measured in this stratigraphic section, which correlate directly with the same units in the Red Creek section. In addition, a sequence of gray mudstones and sandstones that outcrop south of the fault in the S ½ of Sec. 27, T.38N., R.87W. probably represent sediments that correlate with the upper gray sequence of the Lost Cabin Member in the Red Creek section.

The Red Creek Facies in the Deadman Butte section is 142 ft (43.3 m) thick. The sequence is characterized by thick tabular sandstones and tabular dark gray claystones and mudstones. Sandstones are as described for the facies in the Red Creek section, although some are extremely fossiliferous—Deadman Butte and *Viverravus* localities (Fig. 8, UCM Loc. 80062 and UCM Loc. 81008, respectively; Stucky and Krishtalka, 1982; Stucky, 1984*a*). Isolated teeth and limb elements of vertebrates are extremely common in these fossiliferous horizons.

Dark gray claystones and gray mudstones are similar to those de-

Fig. 8.— *Viverravus* locality (UCM Loc. 81008), Red Creek Facies, Wind River Formation (NW ¼, Sec. 22, T.38N., R.87W., Natrona County, Wyoming). Major fossiliferous horizon is the vertically weathering and light colored sandstone at base of exposure. Note the sharp contact of mudstone on this horizon. Pick is approximately 0.5 m in length.

scribed in the Red Creek section but carbonaceous shales are more common in the Deadman Butte section.

The variegated sequence of the Lost Cabin Member in the Deadman Butte section is truncated by faulting and surface erosion. The lithological change from the Red Creek Facies to the variegated sequence is more abrupt than occurs in the Red Creek section, suggesting a possible unconformity between the two units. A shoestring channel sandstone lies near the base of this sequence. Mottled red mudstones are brightly colored and sparsely fossiliferous. A dark gray claystone at the base of the variegated sequence contains the associated skeletal remains of *Coryphodon* sp., isolated teeth of *Paleosyops borealis* and other vertebrates (UCM Loc. 80090). Above this claystone is a tabular carbonaceous shale which is locally important in correlation.

A possible remnant of an upper gray sequence of the Lost Cabin Member, similar to the upper gray sequence of the Red Creek section, is preserved in the SE ¼ of Sec. 22, T.38N., R.87W., to the south of the major exposures in the Deadman Butte area. Covered section and several faults prevent conclusive lithostratigraphic placement, but, according to geologic structure, these sediments are higher than those exposed to the north. These rocks consist of 84 ft (25 m) of drab colored mudstones and sandstones. Mudstones have sharp lithologic and color contacts with adjacent units and are composed primarily of clay with some sand and silt particles. Sandstones are friable, tabular and very fine to medium grained. No fossil vertebrates were recovered from the sandstones. Gray mudstones in this sequence are more fossiliferous than recorded in gray mudstones of any other area in the Red Creek–Deadman Butte area. One of these fossiliferous horizons (*Palaeosyops* jaw locality, UCM Loc. 81010) preserves associate skeletal elements of *P. borealis,* numerous other mammals, but few lower vertebrates. This unit is unique in preserving calcified wood in some abundance.

Rainbow Butte stratigraphic section (Stucky 1984*a,* MS-3).—The Rainbow Butte section is 75 ft (23 m) thick and was measured in the center of the N ½ of Sec. 19, T.38N., R.87W. on the west side of Red Creek, opposite exposures of the variegated sequence of the Lost Cabin Member in the Red Creek section (Fig. 9). Direct correlation between the two sections is not possible, although faunal data suggest that they are similar in biostratigraphic position. Neither the base nor the top of the Wind River Formation is exposed. The strata in this section consist of alternating mottled red-gray and gray mudstones, which are similar in lithology to the variegated sequence of the Red Creek section, and drab colored sandstones, which differ from the sandstones of the variegated sequence in the Red Creek section in having basal conglomerates which contain a higher percentage of Paleozoic and Mesozoic rock fragments. Preliminary reconnaissance work to the west suggests that quartzite (? Flathead Formation) and Paleozoic limestone and dolomite pebbles and cobbles become common and dominate conglomerates in this direction (see Stucky 1984*a,* MS-21). Eleven of 25 stratigraphic horizons in the Rainbow Butte Section are fossiliferous.

Davis Ranch stratigraphic sections (Stucky, 1984*a,* MS-1979, MS-8 to MS-12).—The Davis Ranch stratigraphic sections were measured in Sec. 36, T.38N., R.88W. and Sec. 6, T.37N., R.87W. A composite thickness of 222 ft (68 m) of strata was measured. Strata of the Wind River Formation in these stratigraphic sections are well known for their abundant fossil vertebrates (Davis Ranch locality, AMNH; 5 mi north and west of Arminto, PU; Locality 1, Sullivan Ranch CM Loc. 34, of Guthrie, 1971). The lithology of the strata in these sections is quite similar to the lithology of the variegated sequence of the Lost Cabin Member in the Red Creek and Deadman Butte sections and is a probable lithostratigraphic equivalent. These strata have been classically referred to the Lost Cabin Member (Sinclair and Granger, 1911; Guthrie, 1971). The strata at Davis Ranch are characterized by brightly colored, variegated mudstones and abundant channel sandstones (Figs. 9, 10).

Fig. 9.—Rainbow Butte (UCM Loc. 80065), Lost Cabin Member, Wind River Formation (NW ¼, Sec. 19, T.38N., R.87W., Natrona County, Wyoming). Eleven of 25 horizons in this set of strata are fossiliferous (MS-3, Stucky, 1984*a*). Approximately 75 ft (23 m) of strata are exposed.

Sandstone units are prominent linear features and have a calcareous cement. Sandstone geometry in the Davis Ranch area is similar to sandstones from the variegated sequence of the Red Creek section but on a much larger scale. They are best described as apron-channel sandstones (Bown, 1979). Fossil vertebrates are rare in the main bodies of the sandstones, but laterally these grade into red, mottled red-gray and gray mudstones where calcareous glaebules and pedotubules, eggshell fragments, coprolites and invertebrates are common and vertebrate fossils are extremely abundant (for example, UCM Loc. 79043, see Stucky, 1984*a*).

One sandstone unit was followed for two kilometers in surface outcrop, which measures 60 ft (18 m) thick and extends laterally for 150 ft (46 m) (estimated). This sandstone is multistoried, well sorted, crossbedded and channeled into lower mudstone units. Occasional carbonaceous shales lie lateral to and contact the main body of the sandstone. This sandstone intertongues with mudstone units approximately halfway up from its base and cuts into the mottled red mudstone termed the "maroon shale" layer by Guthrie (1971).

The mottled red mudstone or "maroon shale" layer (UCM Loc. 79042; Fig. 11) is laterally persistent and important in correlating the

Fig. 10.—Davis Ranch, Lost Cabin Member, Wind River Formation (Sec. 6, T.37N., R.87W., Natrona County, Wyoming). The shoestring channel sandstone on left side of photo has an angular interface with dark colored horizon at base of exposures. Approximately 120 ft (40 m) of strata exposed.

Davis Ranch sections; it was traced 3 km in surface outcrop. Guthrie (1971:50) suggested that this layer was the same unit as a maroon shale layer exposed at the Buck Spring locality (Guthrie's Locality 3) in the type area of the Lost Cabin Member some 8 mi to the west. Granger (1910:242) implied the same correlation.

This mottled red unit is dark reddish brown (10 R 3/4) in color at its base and grades upward into a red-green-yellow-rust brown mottled mudstone. The brightly red colored part of this mudstone consists primarily of clay with some silt-sized particles; very little sand is present. Calcareous glaebules and pedotubules are abundant throughout, and fossil vertebrates are more abundant in this mudstone than in any other fossiliferous horizon studied. Teeth and jaw fragments of mammals are the most common fossils found. Calcareous glaebule masses often cover the dentition of jaw fragments. Bones from this horizon show an orange-white color and teeth are black or translucent gray and brown. Skeletal elements of individual mammals, turtles, and crocodiles are sometimes associated, and burrowing reptiles (snakes and amphisbaenids) are often partially articulated in life position. Fish remains are uncommon and are not certainly known to be articulated.

Most fossil vertebrates from the American Museum Davis Ranch

Fig. 11.—"Dark red stratum" or "maroon shale" layer (dark colored horizon in center of exposures) at Davis Ranch (UCM Loc. 79042; CM loc. 34), Lost Cabin Member, Wind River Formation (Sec. 6, T.37N., R.87W., Natrona County, Wyoming). Most fossils from the Davis Ranch Locality are recovered from this fossiliferous horizon. Horizon is approximately 15 ft (5 m) thick.

locality, Princeton Museum 5 mi north and west of Arminto locality, University of Colorado Museum Loc. 79042 and Carnegie Museum Sullivan Ranch locality (CM Loc. 34, all referred to as Locality 1 by Guthrie, 1971) come from this single fossiliferous horizon. Fossil vertebrates include abundant remains of *Palaeosyops borealis* and *Antiacodon* and less abundant remains of *Hyrachyus* sp., cf. *H. eximius.* No *Lambdotherium* material is known from this fossiliferous horizon. Specimens from this horizon labelled as *Lambdotherium* have been reexamined and found to be incorrectly identified.

Sediments below this mottled red mudstone differ in various exposures. Sediments below this horizon in the center of Sec. 36, T.38N., R.88W., are variegated and similar in lithology and fossil content to the mottled red mudstone and, in general, similar to the variegated sequences in the Red Creek and Deadman Butte sections. In the NE ¼ of Sec. 6, T.37N., R.87W., underlying sediments are primarily gray and poorly fossiliferous. However, in all areas of exposure a gray mudstone and sandstone lie below the mottled red horizon. Only the mottled red horizon and the channel sandstone can be traced between these two exposures.

Sediments above the mottled red mudstone are preserved in the NW ½ of Sec. 6, T.37N., R.87W. All of these upper strata are gray, probably tuffaceous, and intertongue with the large channel sandstone unit discussed above. A probable volcanic ash is preserved approximately 30 ft (9 m) above the mottled red mudstone and was traced to the butte at 6005 ft (1830 m) in elevation in the NE ¼ of Sec. 12, T.37N., R.88W. Fossil vertebrates and calcareous glaebules and pedotubules occur in gray mudstone units both above and below this ash bed. Fossils from these upper gray strata are better preserved than those from the mottled red mudstones. Associated remains of mammals are common, whereas crocodiles and turtles are less common.

Exposures north and east of Arminto.—Keefer (1965*a*:39, 1970, Plate I) has mapped both the Wind River and Indian Meadows formations in Secs. 1 and 12, T.37N., R.87W. for a 50 ft (15 m) thick "series of conglomerate beds containing sandstone, siliceous shale, and chert cobbles that unconformably overlie the Upper Cretaceous Cody Shale and underlie varicolored shales of the Wind River Formation." Strata in this area lie on the western limb of the Casper Arch and dip to the west at approximately 6 degrees. These conglomerates could represent the Red Creek Facies of the Wind River Formation although they are tentatively retained in the Indian Meadows Formation.

The "varicolored shales" in these exposures superficially resemble the variegated sequence of the Red Creek, Deadman Butte and Davis Ranch sections. Although mottled red mudstones are similar in surface exposure, they differ from other mottled red mudstones in other areas in containing dark brown iron oxide glaebules and pedotubules and in not preserving abundant fossil vertebrates. Sandstones are tabular, well sorted quartz arenites. One sandstone (UCM Loc. 80063) contains numerous fossil vertebrates, many of which are water-worn and show post-depositional cracking and distortion. More field studies are needed to clarify the lithostratigraphic relationships of this area. The "varicolored shales" most likely represent the Lost Cabin Member of the Wind River Formation, at least in the upper part of the exposures.

Buck Spring, type area of Lost Cabin Member (Stucky, 1984*a*, MS-13).—The Buck Spring area in Secs. 15 and 22, T.38N., R.89W. probably represents part of the type area of the Lost Cabin Member of the Wind River Formation as originally understood by Sinclair and Granger (1911). Sinclair and Granger (1911:105) indicated that the "type area of the Lost Cabin formation is to the east of Lost Cabin along Alkali Creek and on the divide between Alkali and Poison Creeks." No type section has ever been designated (contra West and Atkins, 1970). Tourtelot (1948) has, however, presented a convincing argument that the type area "east of Lost Cabin" is in fact the exposures at Buck Spring. Stratigraphic sections in this area measured by Tourtelot (in Keefer, 1965*a*) and Stucky (1984*a*) are nearly identical to a stratigraphic section measured by Granger (1910:242) "eight miles east of Lost Cabin." This is the same area figured by Osborn (1929, Fig. 47, Plate VI-B) as typical Lost Cabin exposures. The type area "on the divide between Alkali and Poison Creeks" probably lies along Frenchie Draw in Secs. 9, 10, 11, 14, 15 and 16, T.37N., R.90W. (east of the highway between Moneta and Lysite).

Neither the base nor the top of the Wind River Formation or Lost Cabin Member is exposed in the Buck Spring area. A total of 109.5 ft (33.4 m) of Lost Cabin Member sediments was measured in surface outcrop. However, Keefer (1965*a*) has suggested that the maximum thickness of the Lost Cabin Member could be as much as 2000 ft (600 m) in this area. Two lithologic sequences can be generally distinguished in surface exposures—a lower gray and a variegated sequence. Both of these sequences were included in the original description of the Lost Cabin Member (Sinclair and Granger, 1911).

The lower gray sequence of the Lost Cabin Member in the Buck Spring area, which is best exposed along Alkali Creek near the town of Lysite, on the divide between Alkali and Poison Creeks, and in Sec. 27, 28, 29, T.38N., R.89W., consists primarily of gray mudstones and yellow and gray sandstones. The sandstones generally have either an apron-channel or tabular geometry. Conglomeratic beds are very rare, and where they occur they contain primarily Precambrian clasts, intraformational mudstone clasts and occasional water-worn fossil teeth and bone fragments. Gray mudstones are siltstones and occasionally are purple-mottled. Some calcareous glaebules and pedotubules are present. Most gray mudstones are poorly fossiliferous but may have been the units from which well preserved specimens were obtained by Granger in the early 1900S. Intensified collecting efforts by Krishtalka and Stucky in 1983 in Sec. 27, T.38N., R.89W. resulted in the recovery of well preserved fossil vertebrates, including skull and articulated materials.

The variegated sequence of the Lost Cabin Member in the Buck Spring area is characterized by alternating mottled red and gray mudstones and apron-channel sandstones. Some variegated mudstone units have prominently banded alternating red and greenish gray mudstone horizons with each band having an undulatory appearance and varying between approximately one inch (0.02 m) and one foot (0.30 m) in thickness. These banded mudstones are laminated and contain a small percentage of sand and silt. These units were observed only in the Buck Spring area and occur directly above a mottled purple mudstone ("dark red stratum" of Granger, 1910, and "maroon shale" of Guthrie, 1971).

Locally they contain abundant calcareous glaebules and extremely well preserved and associated remains of fossil vertebrates. A partial articulated skeleton of *Palaeictops multicuspis* (UCM 46284) and associated dentary and fragmentary skull of *Notharctus* sp. cf. *N. venticolus* (UCM 47674) were recovered from these banded mudstones.

Of particular importance is the mottled purple mudstone exposed near the base of most exposures in the Buck Spring area (UCM Loc. 81029). Granger (1910), Keefer (1965*a*), and Guthrie (1971) have commented on this horizon because of its lateral persistence and abundant fossil vertebrates.

Granger (1910:242) referred to this horizon as the "dark red stratum" which "could be identified for twenty miles along Alkali Creek, partly by its peculiar coloring and partly by the presence, always, of numerous fragmentary fossils; wherever seen it was resting on the thick gray stratum." Guthrie (1971:50) referred to this horizon as the "maroon shale" which he believed was the same horizon as a dark red unit exposed at his Locality 1 (discussed above, Davis Ranch stratigraphic sections), and Locality 2. He also suggested that this "maroon shale" correlated with gray strata at his Locality 4. These relations suggested to Guthrie that "nearly all [fossil] material from these localities was collected in a vertical interval of no more than 40 feet."

At Buck Spring, the "dark red stratum" or "maroon shale" unit can be followed and traced in all exposures. This horizon is between 8 and 15 ft (2.4–4.6 m) thick and is a poorly sorted mottled grayish red (10 R 4/2) mudstone with anastomizing very pale green (10 G 8/3) striae. These striae may be remnants of rhizoliths (see Klappa, 1980). The unit contains a relatively high percentage of fine to medium quartz grains and is micaceous. Calcareous glaebules are locally important, but pedotubules are rare. These lithologic characters occur throughout its thickness and lateral extent. The unit is cut into by a light green colored apron-channel sandstone in Sec. 15, T.38N., R.89W. Farther to the south in Sec. 22, the unit is overlain by banded mudstones. Fossil vertebrates are extremely common, dominated in order of abundance by turtle shell fragments, crocodile scutes and isolated teeth of mammals. Mammal jaws are extremely rare in this unit, with a ratio of isolated teeth of mammals to jaw fragments greater than 50:1. No associated skeletal elements of a single mammal individual were observed. Isolated teeth and bone fragments from this horizon are always black or very dark brown in color and often have a thin veneer of an iron oxide mineral. Rare jaw fragments of mammals preserving more than one tooth (less than ten specimens known) are distorted by postdepositional crushing. Identified mammalian remains are typical of mammals recovered from the *Lambdotherium* zone in the Red Creek and Deadman Butte stratigraphic sections. *Lambdotherium* is abundant. No remains of *Palaeosyops borealis* or *Hyrachyus* sp., cf. *H. eximius* are known from this fossiliferous horizon. Osborn (1929) did, however, report that the type specimen of *P. gregoryi* was found 100 ft (30 m) above this unit and Dawson (personal communication, 1982) found associated teeth of *Hyrachyus* in the upper part of the exposure at Buck Spring. Osborn (1929) also reports that the type specimens of *P. borealis* and *L. popoagicum* came from this area. Because these were collected in 1880, when no precise locality data were kept, this conclusion must be viewed with some circumspection.

Supposed Correlation of Granger's "Dark Red Stratum" and Guthrie's "Maroon Shale" Layer in the Lost Cabin Member

As described above, the "dark red stratum" or "maroon shale" measured in the Davis Ranch stratigraphic sections differs in a number of criteria from the "dark red stratum" or "maroon shale" in the Buck Spring area, the designated type area of the Lost Cabin Member (this report and Sinclair and Granger, 1911; sensu Granger, 1910; Tourtelot, 1948). Criteria apparently used by both Granger (1910) and Guthrie (1971) to correlate these two distinctive horizons include: 1) dark red color; 2) high fossil content; and 3) superposition above a dark gray stratum. The following observations suggest that the hypothesis that the "dark red stratum" or "maroon shale" at Guthrie's Locality 1 and Locality 3 represent the same fossiliferous unit is false:

1) The sediments of the two units in these different areas are different in color pattern, particle content, and the relative distribution of calcareous glaebules and pedotubules;

2) Fossil vertebrates from the two horizons were diagenetically altered in different ways (crushing, coloration and probably mineralogical content of encrustation);

3) The two units preserve a fossil vertebrate assemblage that was subjected to differing taphonomic histories (bone element preservation, associated skeletal parts of individuals, and proportions of lower vertebrate and mammal taxa, see Stucky, 1984*a*);

4) Almost all red units in the Wind River Formation are underlain by dark gray strata; and

5) The two fossiliferous horizons are in different biostratigraphic zones of the Wind River Formation.

These observations suggest that these two horizons differ lithostratigraphically, biostratigraphically and chronostratigraphically and do not represent the same horizon in any sense (Hedberg, 1976:14). The Davis Ranch strata lie some 8 mi (13 km) from the Buck Spring type area of the Lost Cabin Member, where the intervening area is grass covered. Any lithostratigraphic correlation of the two fossiliferous mudstone units must be done by subsurface sampling. The erroneous assumption that these two units were the same has resulted in a misunderstanding of the mammalian biostratigraphy of the upper part of the Wind River Formation.

Summary of Lithostratigraphic Correlation of the Wind River Formation, Red Creek–Deadman Butte and Buck Spring Areas

The Red Creek Facies, measured at the base of the Red Creek and Deadman Butte stratigraphic sections, is a mappable unit of the Wind River Formation (see Stucky and Krishtalka, 1982). It was deposited on an erosional surface of considerable relief on Mesozoic strata (Tourtelot, 1953; Woodward, 1957). As far as known, this facies occurs only at the base of the Wind River Formation in the central part of T.38N., R.87W. from Secs. 18 to 25. The facies becomes somewhat thicker to the east and is characterized in all sections by gray tabular sandstones and mudstones, occasional tabular dark gray claystones and rare tabular and lenticular carbonaceous shales. The sandstones are quartz arenites and consist primarily of well rounded to rounded, fine to medium, quartz, sand grains (presumably eroded from the Morrison and Cloverly Formations). Conglomerates commonly occur in sandstones as well separated lenses. Clasts in conglomerates consist of angular to rounded fragments of sandstones, limestones and chert, derived primarily from Mesozoic formations exposed just to the north of the study area. The sandstones are more fossiliferous than the mudstones. The mudstones are primarily siltstones, many of which contain abundant gypsum crystals. Some mudstones contain bioturbation structures and calcareous glaebules. Dark gray claystones are laminated and are useful marker beds.

The Red Creek Facies differs from the Lysite and Lost Cabin Members in the following characteristics (compare criteria established for the Lost Cabin and Lysite Members by Tourtelot, 1948): 1) Clasts in sandstones and conglomerates are derived principally from Mesozoic rocks; 2) Sandstones are tabular in geometry, laterally extensive, and contain well separated sets of conglomeratic lenses; 3) Fossil vertebrates (isolated teeth and bone fragments) are a common constituent of sandstones; and 4) Mudstones are almost exclusively gray in color; mottled red or red mudstones are almost entirely absent. This facies probably intertongues with variegated strata of the Lost Cabin Member to the east and south, as suggested by biostratigraphic data. The Red Creek Facies is within the *Lambdotherium* Range Zone throughout its exposures (Lostcabinian).

The *Lost Cabin Member* of the Wind River Formation apparently lies conformably on the Red Creek Facies in the Red Creek–Deadman Butte area, although a slight unconformity between the two units may be present in Sec. 22, T.38N., R.87W. The Lost Cabin Member in these areas is composed of a lower variegated sequence and upper gray sequence. In the Buck Spring area the member consists of a variegated sequence overlying a gray sequence of strata (see Sinclair and Granger, 1911), whereas north and east of Arminto only a variegated sequence is exposed. At Davis Ranch, the Lost Cabin Member is represented by a set of prominently colored variegated beds which intertongue with a gray sequence in the lower part of the section and are overlain by a gray sequence of strata.

Strata of the Lost Cabin Member are characterized by apron-channel and shoestring channel sandstones and both variegated and gray mudstone sequences of strata. Sandstone bodies often cut into and intertongue with mudstones, and are prominent linear features. Sandstones are principally composed of fine to coarse, subangular to rounded quartz and rock fragments. Conglomerates are uncommon in the member in the Red Creek–Deadman Butte and Buck Spring areas, but where they occur they are composed primarily of rounded Precambrian rock fragments and intraclasts. Upsection and basinward sandstone bodies trend toward larger size (see Seeland, 1978). These large scale channel sandstones are prominent linear features which are crossbedded and occasionally associated with carbonaceous shales.

Mudstone sequences vary from variegated to gray sets of strata throughout the Lost Cabin Member. Mottled red mudstones are commonly more fossiliferous than are gray mudstones and often contain abundant calcareous glaebules and pedotubules. Mottled red mudstones are often laterally persistent and can be used as marker beds within local exposures.

Gray mudstone sequences of the Lost Cabin Member are preserved both above and below variegated sequences. Gray mudstone sequences are less fossiliferous than are variegated sequences of the Lost Cabin Member. Poorly fossiliferous and unfossiliferous gray mudstone units often have sharp lithologic lower contacts, show graded bedding, and seldom show bioturbation structures in hand samples. Gray mudstones that are fossiliferous generally have calcareous glaebules and pedotubules.

In the Lost Cabin Member both variegated and gray sequences are of only local significance and cannot be used for lithostratigraphic correlation on a regional scale. Interregional correlations of colored sets of strata must be supported either by subsurface data or by detailed field studies of both lithostratigraphy and biostratigraphy.

Within the Red Creek–Deadman Butte area the variegated and upper gray sequences in the Red Creek, Deadman Butte, and Davis Ranch stratigraphic sections are lithostratigraphic and biostratigraphic equivalents. Variegated sequences in the Buck Spring area and north and east of Arminto are lithologically equivalent to the variegated sequence but are not biostratigraphically equivalent. The biostratigraphic zonation presented below suggests that the variegated sequences of the Lost Cabin Member in the Buck Spring and general Arminto areas and the Red Creek Facies in the Red Creek–Deadman Butte area are Late Wasatchian (Lostcabinian) in age, whereas the Lost Cabin Member in the Red Creek–Deadman Butte area is probably early Bridgerian (Gardnerbuttean) in age (Stucky, 1984*b*).

Depositional Environment

Keefer (1965*a*), Soister (1968), Seeland (1978), Korth (1982), and others have discussed the depositional environments of the Wind River Formation. Love (1978) has recently reviewed the tectonic background necessary for understanding the depositional environments of the Wind River Formation in the Badwater area. The present topography of the mountain fronts nearly represents the fossil topography and erosion surface during the deposition of the Wind River Formation in the Red Creek–Deadman Butte area (Woodward, 1957). Interpretations of the climatic conditions during the time of Wind River Formation deposition have been reviewed by Soister (1968) and Seeland (1978). Botanical evidence indicates the climate was "warm-temperate" (Berry, 1930:60), "humid, subtropical" (Leopold and MacGinitie, 1972:161), or "between paratropical and subtropical" (MacGinitie, 1974:40). Most researchers agree that the climate was not tropical.

Two facies can be distinguished in the Wind River Formation, a mountainward and a basinward (Keefer, 1965*a*). The mountainward facies is represented by the Lysite and Lost Cabin Members close to their source areas in the Badwater Creek area (Tourtelot, 1948; Korth, 1982) and by the Red Creek Facies in the Red Creek–Deadman Butte area. The Red Creek Facies, however, differs somewhat in its depositional environment as a result of differences in paleotopography and the amount of tectonic activity in its source area. The basinward facies is represented by typical deposits of the Lost Cabin Member in the Red Creek–Deadman Butte area, at Buck Spring and throughout most of the interior of the basin (Keefer, 1965*a*).

The Lysite and Lost Cabin Members in the Badwater area, close to their sources and near areas of major tectonic activity (Love, 1978), are dominated by interbedded sandstones and conglomerates which become less common basinward (Tourtelot, 1948; Keefer, 1965*a*; Korth, 1982). Korth (1982) has interpreted these near-source sediments as alluvial fan deposits. Seeland (1978) indicates that alluvial fans in the Wind River Formation are steep, do not show a radial pattern, and thus did not extend far into the basin interior.

Angular relations of the Red Creek Facies on Mesozoic strata in the Red Creek–Deadman Butte area suggest that dip slopes of the paleolandscape were moderate in this area (approximately 10 degrees, but in some areas up to 45 degrees, Tourtelot, 1953; Keefer, 1965*a*). Practically all sand and larger sized clasts in the Red Creek Facies are derived directly from these Mesozoic strata. This facies is dominated by laterally extensive tabular sandstones with interbedded conglomeratic lenses and lacks any evidence of debris flow. These characters suggest that the Red Creek Facies represents a braidplain off the gently dipping highland areas where Mesozoic strata were exposed (see Rust, 1979). Streams coming off of the highland areas that deposited the sandstones and interbedded conglomerates were variable in competence as indicated by varying clast and fossil sizes (Stucky and Krishtalka, 1982). These streams probably had catchment areas near the size of small semipermanent streams presently draining the area (for example, Red Creek), principally because of the landscape similarities between then and now.

Tabular mudstones and claystones suggest occasional deposition of sediment load deposits during overbank flooding. Some mudstones preserve bioturbation structures (burrows and rhizoliths) and pedogenic structures (calcareous glaebules) that indicate they were subareally exposed for substantial periods of time. These mudstones represent probable paleosols (see Bown, 1979; Bown and Kraus, 1981*a,* 1981*b*).

Sandstone and mudstone units in the Lost Cabin Member in the Red Creek–Deadman Butte and Buck Spring areas represent a shift in depositional environment to the basinward facies. Sediments in these areas were deposited basinward from the mountainward alluvial fan deposits of the Lost Cabin and Lysite Members and braidplain deposits of the Red Creek Facies.

Sandstones of the Lost Cabin Member in more basinward areas have primarily apron-channel and shoestring channel geometries, contain fewer conglomeratic lenses, and are composed of clasts from more distant Precambrian sources. These sandstones are often prominent linear features that intertongue with and cut and grade laterally into mudstones. These criteria suggest that the Lost Cabin Member in these areas was deposited by streams on broad flood plains with greater catchment areas than streams in the Red Creek Facies (see Walker and Cant, 1979). These streams were relatively straight, as shown by a lack of high sinuosity (Seeland, 1978).

A trend in larger size of apron-channel sandstones toward the central part of the basin suggests that streams were much larger toward the basin axis. Intertonguing of sandstones with mudstones and relatively large vertical and horizontal intervals between channel sandstone bodies with intervening mudstones suggest that channel movement occurred by avulsion.

Mudstones of the Lost Cabin Member reflect the overbank deposits of these streams on a relatively broad floodplain. Mudstones that have sharp subjacent lithologic contacts, show graded bedding and basal intraclasts, and are laterally persistent, indicate that floodplains were indeed quite broad. Short intervals of time between depositional events are indicated for these mudstones by the presence of these primary structures and a general lack of bioturbation or pedogenic characteristics.

However, many mudstones in the basin proper do suggest long periods of time between depositional events. This is indicated by bioturbation structures (calcareous pedotubules, burrows), pedogenic characteristics (rhizoliths, calcareous glaebules, and color mottling in some of these), and lack of primary depositional structures in hand samples. Often, these mudstones preserve abundant and diverse fossil vertebrates, coprolites, eggshell fragments, invertebrate fossils and silicified and occasionally calcified wood and plant fragments. Some fossil bones show subareal pre-burial weathering and evidence of carnivore or rodent gnawing. Both large and small bodied vertebrates are preserved together as are aquatic and terrestrial vertebrates. Some terrestrial and semiterrestrial species are represented by associated remains of single individuals (mammals, lizards, snakes, crocodiles), whereas completely aquatic vertebrates (fish) are rare and represented almost exlusively by isolated scales, jaw fragments and vertebrae. These data all suggest that these mudstones may be remnants of paleosols, although detailed chemical analyses are needed to confirm this (Bown, 1979; Bown and Kraus, 1981*a,* 1981*b*).

These data fit well with Seeland's (1978) model for the Paleo–Wind River drainage system, where the Red Creek–Deadman Butte sediments reflect tertiary and secondary stream tributaries draining into the Paleo-Wind River. The topography of the Wind River Basin during the deposition of the Wind River Formation was very similar to what it is today—highland and mountainous regions surrounding a broad, relatively flat, plain with numerous meandering tributaries of the Paleo–Wind River flowing toward what is now the basin axis or the actual stream valley of the Paleo–Wind River (Seeland, 1978). The major differences between then and now are that during the deposition of the Wind River Formation the periphery of the basin was variably shaken by tectonic activity and the central portions of the basin were being rapidly filled by sediments eroding off of the highlands. The vast central plain was also covered by a paratropical to subtropical forest (MacGinitie, 1974).

Middle (?) Eocene Volcaniclastic Sequence

A dark brown colored volcaniclastic sequence that is exposed in the SW ¼ of Sec. 30, and NE ¼ of Sec. 31, T.38N., R.87W. lies conformably on top of the Lost Cabin Member of the Wind River Formation. Thickness of this unit is 91 ft (28 m). The top of the sequence is unconformably overlain by Quaternary gravels. No detailed lithologic or petrographic studies have been done for this unit.

Three horizons were found throughout the exposures of the sequence. The lowermost horizon is 7 ft (2 m) thick and is a pale olive green mudstone with high clay content and some coarse subangular quartz grains. The surface of this unit is littered with euhedral gypsum and calcite crystals and spheroidal barite crystal clusters. Aquatic fossil vertebrates are common, dominated by fish, turtles and crocodiles. No mammals are known.

The middle horizon is a carbonaceous shale 4.5 ft (1.5 m) thick. The unit is yellowish-brown in color and is thinly laminated. Well preserved leaf and seed fossils were found in some outcrops of this horizon. The lower contact of this carbonaceous shale with the lower mudstone unit is sharp.

The upper unit is a massive volcaniclastic paraconglomerate which is 80 ft (25 m) thick, and poorly sorted. Clasts in this unit vary in size from very fine sand to cobble size. Pebble to cobble sized clasts consist of brown claystone balls and well rounded volcanic (red, green, and brown basalt) rock fragments. Pebbles and cobbles are sand matrix supported. Some lenticular carbonaceous shales and mudstone units with bedding planes parallel to strike are enclosed within the volcaniclastic paraconglomerate. Seeland's (1978) paleocurrent data would suggest these deposits were derived from the northwest. This unit is conformable on the lower carbonaceous shale unit.

Fossil vertebrates are rare. Several mammal tooth fragments were found in the volcaniclastic paraconglomerate including *Hyopsodus paulus* and a tooth fragment of an equid which most closely resembles *Hyracotherium vasaccience* (UCM Loc. 80064-C). These taxa together suggest an early or middle Eocene age. The base of this unit lies 325 ft (99 m) above UCM Loc. 79040 in the Lost Cabin Member of the Wind River Formation which preserves an early Bridgerian fauna that compares favorably with the vertebrate fauna of the Aycross Formation (Bown, 1982; Stucky, 1984*b*). This suggests that the volcaniclastic sequence is middle Eocene or younger in age.

The volcaniclastic nature of this sequence suggests that it is a lithostratigraphic equivalent of either the Wagon Bed Formation exposed along Beaver Rim and north of the Cedar Ridge Fault in the Badwater area (Van Houten, 1964; Love et al., 1978) or the Aycross Formation of the Absaroka Range (Love, 1939; Bown, 1982). Love (written communication, 1982) will map this unit as part of the Wagon Bed Formation on the USGS Wyoming geological map.

BIOSTRATIGRAPHIC ZONATION—UPPER PART OF THE WIND RIVER FORMATION

Two biostratigraphic zones are defined on the basis of the occurrence of key mammalian taxa in the Red Creek, Deadman Butte and Buck Spring (type area of the Lost Cabin Member) stratigraphic sections: the *Lambdotherium* Range Zone (*Lambdotherium* zone) and *Palaeosyops borealis* Assemblage Zone (*Palaeosyops borealis* zone). Faunal lists from previously reported fossil vertebrate localities of the Lost Cabin Member (Localities 1, 2, 3, and 4 of Guthrie, 1971) add additional support to the presence of these zones in the Wind River Formation.

The recognition of the *Lambdotherium* and *Palaeosyops borealis* zones allows for a more precise biostratigraphic correlation of the Wind River Formation with other formations in western North America that are of late early or early middle Eocene age.

Biostratigraphic Purpose

Biostratigraphic studies have proven invaluable for determining the relative age and time intervals during which a body of sedimentary strata was deposited. Relative proportions and occurrences of key taxa have allowed for broad based correlations between different mappable lithostratigraphic units. At present the relative ages of most formally recognized lithostratigraphic units in North America are well established. With the development and use of improved chronostratigraphic methods, such as magnetostratigraphy and radiometric dating, relative ages determined by biostratigraphic data have been corroborated and refined. With continued biostratigraphic and chronostratigraphic studies, a more accurate and precise time correlation of geologic, physical and biologic phenomena will be accomplished.

Recently the biostratigraphic record has been used to test, understand and develop evolutionary theory (see Kauffman and Hazel, 1977). Gingerich (1976, 1979*a*) has demonstrated the utility of a well documented biostratigraphic record for understanding evolutionary patterns in Eocene fossil vertebrates. While his systematic methods and results have not been without controversy, his basic biostratigraphic methodology for the study of fossil vertebrate evolution has influenced subsequent studies (for example, Bown, 1979; West, 1979; Rose, 1981). The essential feature of this methodology is the sequential ordering of fossil materials according to lithostratigraphic position (see also Kauffman, 1977; Savage, 1977). Once this has been done, the fossil materials can be analyzed through time, with a theoretical evolutionary framework in mind. Studies of fossil material that do not use time as a variable relate phenomena (species or material objects) only by their structural-functional relationships and are, thus, synchronic (cf., Radcliffe-Brown, 1952). It is when time and stratigraphy are incorporated that studies of the fossil record become diachronic and most useful to evolutionary theory.

Although the results of this research have been the documentation of biostratigraphic relations, the overall goal is to use these data for understanding evolutionary processes and patterns at both the species and assemblage levels.

Biostratigraphic Methodology

The biostratigraphic study of evolutionary patterns and processes begins with the concepts of *fossiliferous horizon, assemblage,* and *species.* These require operational definitions (Reynolds, 1971), which are derived from the general theories of stratigraphy (for example, American Commission on Stratigraphic Nomenclature, 1970; Hedberg, 1976), community ecology (for example, MacArthur, 1972; Whittaker, 1975), and biological systematics (for example, Simpson, 1961; Hennig, 1966). Uniformitarian principles posit a relation of the concepts of assemblage and species to the present living world, but in this study the concepts are defined solely upon the limits of their observation in the geological record.

A *fossiliferous horizon* is defined as a local fossiliferous stratigraphic unit that is minimally bounded by other stratigraphic units. The term horizon implies that this unit is a distinctive bed with a specific three dimensional location with lithologically defined boundaries (see Hedberg, 1976). An individual fossiliferous horizon is determined by its lithological continuity and distinctiveness in comparison to superjacent or subjacent horizons which are separated from the fossiliferous horizon either by sharp or gradational contacts. Thus a fossiliferous horizon is: 1) a lithostratigraphic unit that is bounded by sharp or gradational boundaries with adjacent, lithologically different units (including fossil *particle* content and observable physical features, Article 4, Code of Stratigraphic Nomenclature, 1970); 2) a biostratigraphic unit that contains fossils contemporaneous with the deposition and upper erosional surface of the lithostratigraphic unit (Article 19, Code of Stratigraphic Nomenclature, 1970); and 3) a chronostratigraphic unit that represents an interval of time (Article 26, Code of Stratigraphic Nomenclature, 1970).

The fossiliferous horizon would appear to be the minimal unit of study within biostratigraphy, faunal study and evolutionary analysis.

The definition of the fossiliferous horizon presumes that the fossil specimens recovered from it are at least penecontemporaneous with one another and are at the lowest level of resolution in the fossil record for determining variation and cluster pattern for assemblages and species. They are, thus, comparable to living assemblages at alpha and beta levels of species diversity. Taphonomic study of individual fossiliferous horizons may be useful in predicting the relative proportions of bias due to time, space, and accumulation environment that affect variation and cluster patterns in assemblages and species within and between fossiliferous horizons (see Behrensmeyer and Hill, 1980; Shipman, 1981; Bown and Kraus, 1981*b*; Gingerich, 1982).

A fossiliferous horizon is not determined on the basis of an arbitrary interval of strata, but rather on boundaries that are lithostratigraphically defined. The number of fossiliferous horizons within a given vertical thickness of strata is variable and will depend on the geologic character of the strata. A 10 m interval may contain many fossiliferous horizons such as occurs in some lacustrine deposits, or it may contain only one. Importantly, a particular fossiliferous horizon, when defined by lithostratigraphic criteria should be recognizable in subsequent research. Arbitrary intervals of strata, such as sets of exposures or metric intervals, are less precise and may include a number of fossiliferous horizons. Fossiliferous horizons, on the other hand, are defined by the characteristics of the geologic record independent of the measuring system, and can repeatedly be recognized by more than one paleontologist.

An *assemblage* is "a group of fossils that occur at the same stratigraphic level; often with a connotation also of localized geographic extent" (Bates and Jackson, 1980:38). An assemblage, then, is the set of specimens (usually reduced to a set of lithosympatric species, defined below) recovered from a *single* fossiliferous horizon. Tedford (1970) developed a heirarchical arrangement for the analyses of taxonomic and paleoecologic associations. The assemblage from a fossiliferous horizon is the basic unit within both of these schemes. Accordingly, patterns of the co-occurrence of taxa can be objectively defined simply by their presence in the assemblage from the same fossiliferous horizon(s).

The *species* concept in paleontology has been thoroughly discussed and defined (Sylvester-Bradley, 1956; Simpson, 1961; Van Valen, 1976; Wiley, 1978, 1979, 1981; Gingerich, 1979*b*; Lovstrup, 1979; Gould, 1981; Madden, 1981). Arkel (1956:99) points out that the species concept must be useful, and that "if too much weight is given to . . . the theoretical aspects of taxonomy . . . there is a tendency to rely and build on mere words and definitions instead of on the first-hand study of actual material."

Species are defined here as sets of specimens that show continuous morphologic variation and unique (homologous) character similarities as well as spatiotemporal continuity. This definition is selected primarily because it allows for hypotheses of morphologic variation, similarity and integrity that can be tested in the fossil record (see Gaffney, 1979; Eldridge, 1979; Eldridge and Cracraft, 1980).

The basic set of specimens from which species determinations are made is that recovered from a single fossiliferous horizon. This reduces the amount of morphologic variation due to time or geography. Specimens from two or more fossiliferous horizons from the same stratigraphic section or from geographically distant areas may be grouped into the same species on the basis of characters and similarity derived in common. What is then of interest is the variation within and between clusters of specimens (which may be grouped into species) both within and between fossiliferous horizons. Hypotheses of ancestor-descendent relations can thus be tested by the correlation of stratigraphic position with the polarity of derived character states, provided that the hypothesized ancestor has no independently derived characters; cladogenetic or immigration events can be recognized by the co-occurrence of two or more closely related species in the same fossiliferous horizon.

From the concepts of fossiliferous horizon and species follow the concepts of lithosympatry, lithoparapatry and lithoallopatry. *Lithosympatric* species are clusters of specimens divisible on morphological criteria that occur within the same fossiliferous horizon. *Lithoparapatric* species are clusters of specimens divisible on morphologic criteria that overlap in biostratigraphic occurrence but are not known to occur together within the same fossiliferous horizon. *Lithoallopatric* species are clusters of specimens divisible on morphologic criteria that do not overlap in biostratigraphic occurrence (if and only if the boundaries between the taxa are not arbitrarily defined by stratigraphic position). Any two or more species may be lithosympatric, lithoallopatric and lithoparapatric in different parts of their stratigraphic occurrence (Fig. 12).

Using the fossiliferous horizon as the basic unit in biostratigraphy will allow for a more precise biostratigraphic zonation of sedimentary rocks. Arbitrary sampling intervals or collections of fossils from areas which represent more than a single fossiliferous horizon are less precise and useful for either biostratigraphic or evolutionary studies. Systematic studies are more reliable when they focus on the assemblage of specimens from a single well represented fossiliferous horizon, simply because the defined species are less biased by variation due to geography and time. As Lamarck (1912; original 1809) and Darwin (1859) emphasized over a century ago, sorting out the patterns of variation of a species is more important than the category into which it is placed.

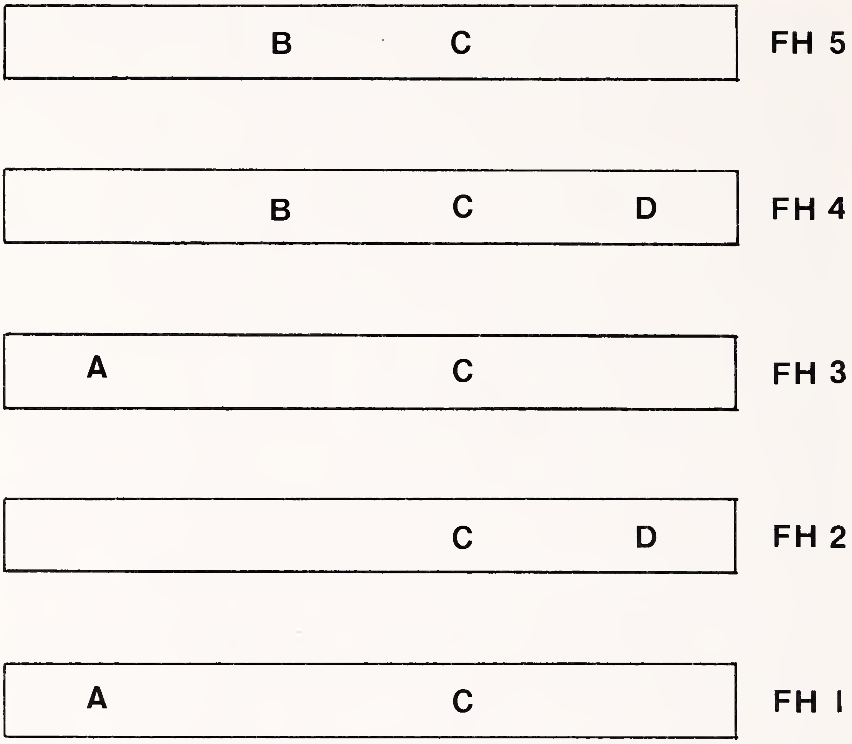

Fig. 12.—Stratigraphic distribution of four mammalian species (A, B, C, D) in five fossiliferous horizons (FH) to illustrate the concepts of lithosympatry, lithoparapatry and lithoallopatry. Species A and B are lithoallopatric in this stratigraphic record. Species A and D are lithoparapatric in FH2 and FH3, but lithoallopatric in FH1 and FH4. Species A and D also never occur in lithosympatry. Species B, C and D occur in lithosympatry only in FH4, but species B and C occur in lithosympatry in FH4 and FH5; whereas species C and D occur in lithosympatry in FH2 and FH4. Many other permutations are present. The terms lithosympatry, lithoparapatry and lithoallopatry apply to local stratigraphic sections. See text for definitions of fossiliferous horizon and species.

Repenning (1967), Tedford (1970), Woodburne (1977), Savage (1977), and Rose (1981) have recently reviewed the principles and practices of North American mammalian biostratigraphy. In following their recommendations, exotic taxa (species immigrants) are relied upon. The highest taxonomic rank held in common by an immigrant species with its closest lithosympatric sister group is an ordinal (in the statistical sense, see Siegel, 1956) measure of the potential utility of the species in biostratigraphy. As implied, an immigrant species has no apparent ancestral population (or species) below its first occurrence in the fossil record within the same geographic area. Extinction events and stages of evolution within species lineages are of secondary importance.

The extinction of a formerly widespread species generally involves disjunction prior to the last occurrence of the species. Following disjunction there does not seem to be any necessary correlation in evolutionary pattern or extinction among the fragmented populations of the species (MacArthur and Wilson, 1967; see also Endler, 1977). Thus it would be expected that not only will a species near extinction be rare, but also geographically restricted.

The stage of evolution of a sample within a lineage may be useful. However, stages of evolution are often arbitrarily defined, resulting in the identification of specimens to species by stratigraphic position rather than their morphology.

Fisher and Rensberger (1972), Lindsay (1972), Schankler (1980), Rose (1981), and Barry et al. (1982) provide excellent examples of biostratigraphic zonation techniques. As many stratigraphic sections as possible should be used to insure a consistent zonation. Poorly documented fossil collections should be used with extreme caution. Isolated fossiliferous horizons which contain abundant fossil remains can be employed to check for lithosympatric and lithoallopatric occurrences of key taxa. In the latter case, bias due to either taphonomic, ecologic or geographic variation should be considered. Lumping of specimens that come from a number of lithologically similar fossiliferous horizons or geographically isolated exposures (arbitrary sampling) tends to obscure relations and boundaries and lends confusion to age relations over broad geographic areas.

History of Upper Wind River Formation Biostratigraphy

The general historical development of the biostratigraphy of the Wind River Formation is presented in Table 2. Several key events are briefly reviewed to provide a background and basis for the biostratigraphic zonation that follows.

Osborn (1909) was the first to divide the Wind River Formation into biostratigraphic zones. Osborn (1909, fig. 5 and pp. 43–48; see Fig. 13, this report) recognized two zones, Wind River A and Wind River B, which were, in the modern sense, taxon range zones. He named these zones the *Lambdotherium* and *Bathyopsis* zones, respectively, and assumed that *Palaeosyops borealis* had been recovered from the *Bathyopsis* zone, although this was uncertain (see pp. 45 and 48). Although *Bathyopsis* was the namesake for the upper zone, Osborn reported this genus from the lower *Lambdotherium* zone as well (see p. 47). Osborn (1909, fig. 1, pp. 23 and 44), in his "Composite Section of the Tertiary Deposits of the West," suggested that the *Bathyopsis* zone or Wind River B was correlated, in part, with the upper Huerfano (see Robinson,

Table 2.—*History of Wind River Formation biostratigraphy.*

1880.	Cope first describes the "Wind River" vertebrate fauna consisting of 19 species of mammals collected by Wortman. Notes presence of Wasatch and Bridger taxa.
1881.	Cope emends the Wind River faunal list to include 45 species of vertebrates (three of which are now thought to have been collected in the Bighorn Basin, see Gazin, 1953). Compares a faunal list of the Wind River with the Wasatch and Bridger.
1892.	Osborn and Wortman begin revision of the Wind River fauna and refer the Wind River Basin fauna to the Bridger.
1899.	Matthew (1899:21) indicates "all the sediments of the Wind River Formation are later than the Wasatch and earlier than the Bridger."
1908–1918.	Systematic reviews of Wind River Formation taxa are reported in detail by Loomis, Granger, Sinclair and Matthew, based on collections in the AMNH and ACM.
1909.	Osborn suggests that two faunal horizons may be recognized in the Wind River: a lower "*Lambdotherium* zone" (Wind River A) and an upper "*Bathyopsis* zone" (Wind River B). Matthew divides the Bridger Formation into five units, Bridger A through E.
1910.	Granger "corrects" the error of Osborn and notes that two zones are present: a lower, newly recognized zone and an upper zone which includes both zones of Osborn.
1911.	Sinclair and Granger describe the Lost Cabin and Lysite Formations, formalizing Granger's 1910 observations.
1929.	Osborn recognizes 1909 "error" and presents a chart showing the stratigraphic distribution of important taxa. Records *Palaeosyops* and *Lambdotherium* as occurring together.
1933.	Simpson denotes the Wind River as "later lower Eocene, a part of the Eocene between the classic Wasatch and the Bridger," and recognizes the Lysite and Lost Cabin as formations.
1938.	Wilmarth recognizes the Lysite and Lost Cabin as faunal zones in the Wind River Formation.
1941.	Wood et al. note the lithologic distinctiveness of the Lysite and Lost Cabin members (or formations). Propose Wasatchian and Bridgerian as new provincial time terms. Wasatchian is "based on at least the upper part of the Wasatch group of southwestern Wyoming" and Bridgerian is "based on the Bridger formation of southwestern Wyoming." They indicate that, "if technical justification for assigning the Lost Cabin to Wasatchian time is required, it is supplied by the discovery of the La Barge local fauna (q.v., in the Glossary) in the type area of the Wasatch."
1945.	Van Houten reviews latest Paleocene and early Eocene mammalian faunas of North America. Provides comprehensive faunal lists for Lysite and Lost Cabin Members. Uses Lysite and Lost Cabin as terms for both faunas and beds.
1948.	Tourtelot formalizes and defines Lysite and Lost Cabin Members and provides faunal lists. Tourtelot and Thompson report Bridgerian-like species from the Wind River Formation.
1952.	White describes the Wind River Formation fauna from the Boysen Reservoir area. Gazin reviews Wasatchian faunas of southwestern Wyoming and refers to some of these as similar to the Lysite and Lost Cabin in age.
1954.	Kelley and Wood review Lysite Member fauna. Morris reviews Cathedral Bluffs Tongue of the Wasatch Formation fauna.

Table 2.—*Continued.*

1962.	Gazin revises the Wasatchian faunas of southwestern Wyoming in the type area of the Wasatch and refers to the Lostcabinian informally as an age.
1966.	Robinson proposes the Gardnerbuttean substage of the Wasatchian for the fauna from the upper Huerfano formation, which is similar in concept to the Lostcabinian of the Wind River Formation. He notes two faunal levels in the Lostcabinian faunal level of the Huerfano formation. Discusses many taxa recovered from the Lost Cabin Member.
1967.	Guthrie reviews Lysite Member fauna and notes the occurrence of *Lambdotherium* in upper beds of Lysite Member lithology.
1970–1971.	Guthrie reviews Lost Cabin Member fauna. Believes most fossils were recovered from narrow 40 ft (12 m) interval. McGrew and Sullivan describe the Bridger A fauna.
1973.	West reports New Fork–Big Sandy faunas from southwestern Wyoming and compares them to the Wind River fauna. West and Dawson present an augmented faunal list for the Cathedral Bluffs Tongue fauna.
1977.	Savage proposes the Wasatchian stage as worldwide in scope and *Lambdotherium* Concurrent Range zone for Western North America.
1980.	Schankler proposes biostratigraphic zonation for the Willwood Formation in the Bighorn Basin. Relates these zones to Wind River Formation as they were proposed by Guthrie.
1982.	Stucky and Krishtalka present preliminary faunal lists for two newly discovered fossiliferous horizons in a lithological unit unique from either the Lost Cabin or Lysite members. Korth discusses occurrence of specimens believed to represent *Lambdotherium* which were recovered from the Lysite Member. Bown presents a comprehensive faunal list for the Aycross Formation which he suggests is early Bridgerian.
1983.	*Trogosus* is reported from the Wind River Formation by Stucky and Krishtalka. They suggest that the uppermost part of the Wind River Formation is early Bridgerian (Gardnerbuttean) in age.

1966) and upper unfossiliferous "C" horizon or the "Wasatch of the Bighorn Basin" (see Bown, 1982).

The year following Osborn's biostratigraphic zonation, Granger (1910) revised Osborn's interpretations. He, as did Osborn, divided the formation into two zones. However, his upper zone included both the *Lambdotherium* and *Bathyopsis* zones (Fig. 14). The lower zone was a new concept which corresponds to the Lysite Member fauna of Guthrie (1967). This lower zone is not discussed here. Granger believed that *Lambdotherium* and *Palaeosyops* occurred together in the upper zone, but his reasons were not specifically stated. Granger suggested that a "dark red stratum" could be followed for some 20 mi (30 km) and apparently believed that the "dark red stratum" at Davis Ranch and Buck Spring were equivalent. As demonstrated above, the dark red strata at these localities are not the same unit. In 1911, Sinclair and Granger indirectly formalized the upper biostratigraphic zone by naming the Lost Cabin formation.

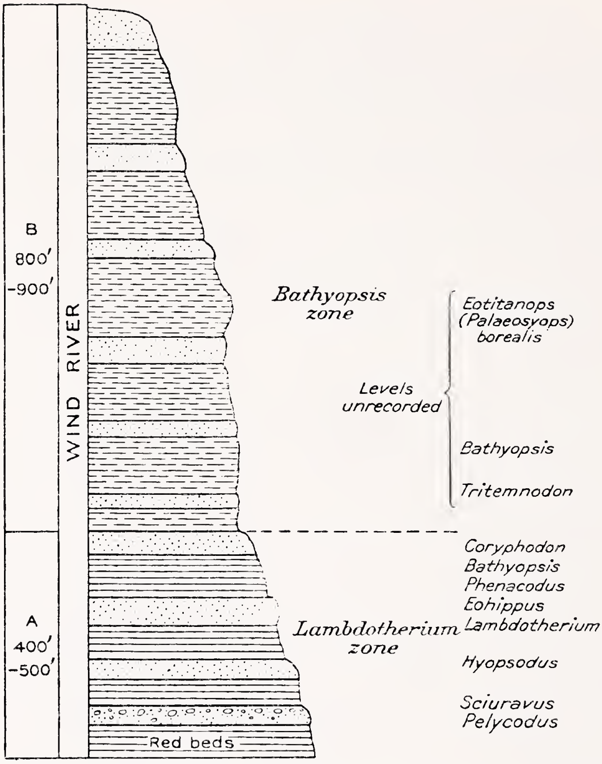

Fig. 13.—Osborn's interpretation of the biostratigraphy of the Wind River Formation proposed in 1909 (his fig. 5).

In 1929, Osborn presented a composite stratigraphic section for the Wind River Formation in which he recorded overlapping ranges of *Lambdotherium* and *Palaeosyops* (his fig. 48, reproduced here in Fig. 15). These overlapping ranges were apparently based on Granger's inference regarding the "dark red stratum" as a key lithostratigraphic marker. Osborn did, however, note that the type of *P. gregoryi* was recovered from the Buck Spring locality 100 ft (30 m) above the "dark red stratum." Importantly, *Lambdotherium* occurs in high abundance within this dark red stratum.

Guthrie (1971) presented the most recent revision of the Lost Cabin Member fauna. He concurred with the conclusions of Granger, indicating that most fossils were recovered from a 40 ft (12 m) interval of strata where a "maroon shale layer" at both Sullivan Ranch and Buck

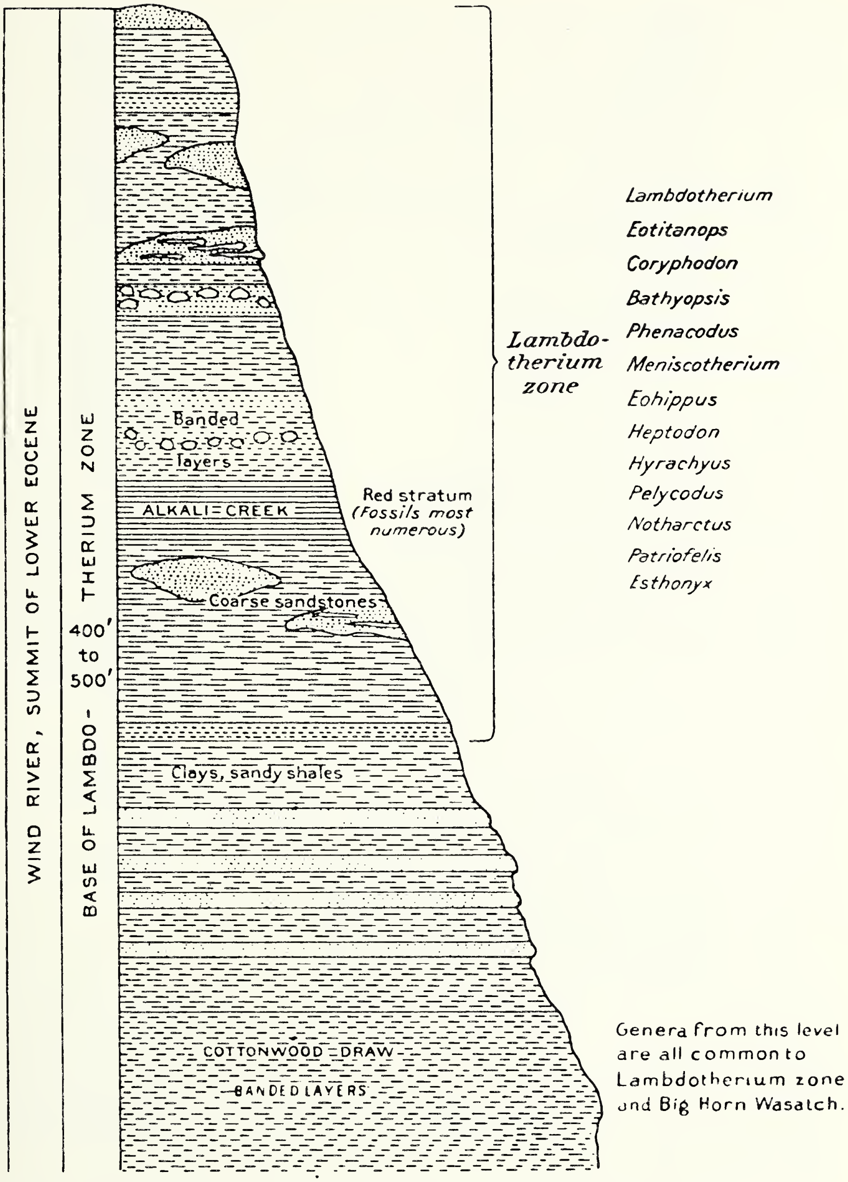

Fig. 14.—Granger's (1910, fig. 2) interpretation of the biostratigraphy of the Wind River Formation. Both of the zones proposed by Osborn (1909) were included in Granger's "*Lambdotherium* zone."

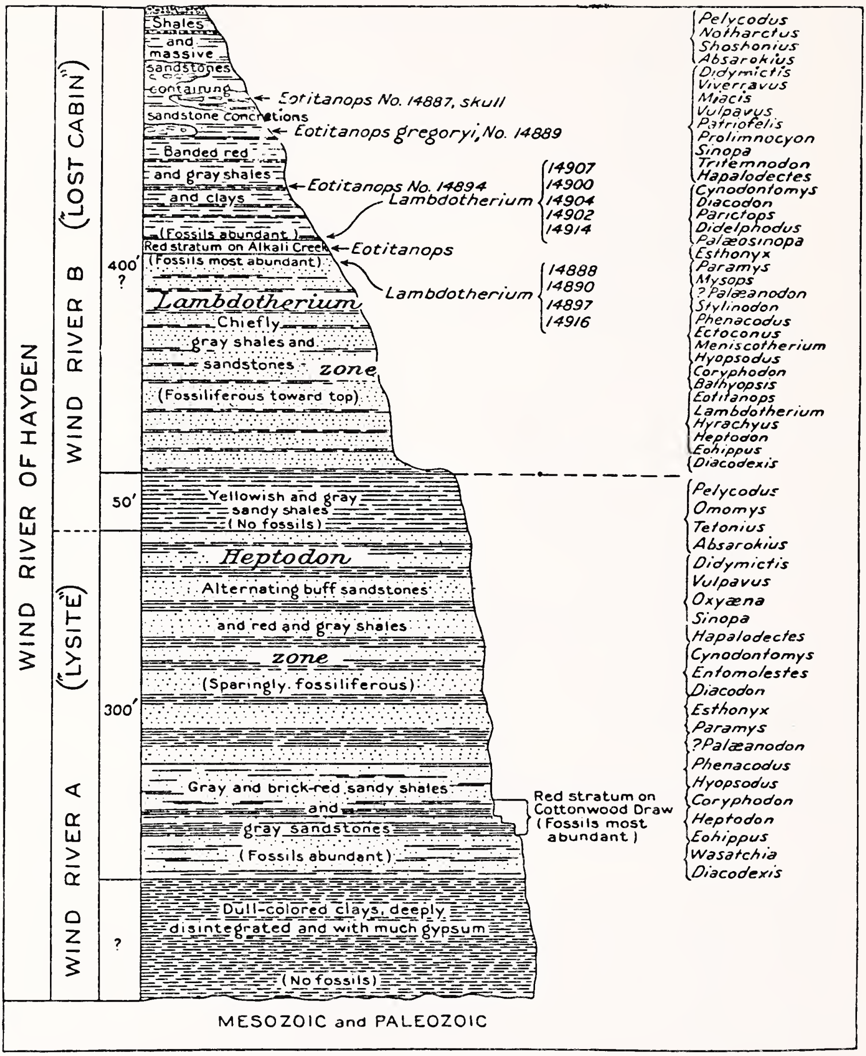

Fig. 15.—Osborn's (1929, fig. 48) modified interpretation of the biostratigraphy of the Wind River Formation. The overlapping ranges of *Palaeosyops* (=*Eotitanops*) *borealis* and *Lambdotherium popoagicum* were apparently based on Granger's (1910) correlation of dark red stratum.

Spring produced the most abundant fossils. More recently, Korth (1982) has followed previous workers but suggests that the Lost Cabin Member localities occur in a much thicker interval than Guthrie believed. Korth (1982) indicated that Buck Spring and Guthrie's Locality 4 were similar in stratigraphic position and placed Davis Ranch (Guthrie's Locality 1) at 90 to 100 m above Buck Spring, and Wolton (Guthrie's Locality 2) some 125 to 250 m above Davis Ranch. These interpretations were based on elevation and bed attitudes without considering geologic structure between these widely separate localities.

The relations of the Davis Ranch (Locality 1) and Wolton (Locality 2) localities suggested by Korth are probably in error. A fault may be present between these two localities along the Alkali Creek valley. Biostratigraphic evidence suggests that the Wolton locality is older than Davis Ranch and thus lies lower in the Lost Cabin Member.

One final note is of some historical importance. The specific localities of the type specimens from the Wind River Formation collected in the nineteenth century are unknown (Cope, 1880, 1881, 1884). Wortman (1892) was not specific in indicating the location of many of the fossils he collected. In fact, some type specimens first reported from the Wind River Basin are now known to have been collected in the Bighorn Basin (Gazin, 1953). Now that it is known that Bridgerian age sediments are preserved in the Wind River Formation (Tourtelot and Thompson, 1948; Stucky, 1984*b*), there is some question as to whether the original specimens collected prior to 1900 are truly of Lostcabinian subage. Reevaluation of many of the type specimens in systematic revisions should take this into account and ignore any *a priori* assumption that they are typical late Wasatchian Age mammals.

Biostratigraphic Zones

The biostratigraphic distribution of mammalian taxa in the Red Creek and Deadman Butte stratigraphic sections forms the primary data for the biostratigraphic zones recognized here in the upper part of the Wind River Formation (Table 3). Faunal lists from other stratigraphic sections and previously reported localities provide additional support to the recognition of these zones (Table 4). The positions of fossiliferous horizons are shown in Fig. 4 and described in Stucky (1984*a*). The systematics of the mammalian fauna and a list of lower vertebrate taxa in UCM collections are provided by Stucky (1982:103–226) and, in part, revised by Krishtalka and Stucky (1983*a,* 1983*b*) and Stucky and Krishtalka (1982, 1983). The biostratigraphic zones are proposed *only* for the documented localities in the upper part of the Wind River Formation in the northeastern Wind River Basin. Future field studies and systematic revisions may indicate that these zones can be extended elsewhere and modified accordingly.

Lambdotherium Range Zone (=*Lambdotherium* zone)

Reference sections.—Red Creek, Deadman Butte and Buck Spring stratigraphic sections (Stucky, 1984*a*). See Granger (1910), Osborn

Table 3.—*Faunal lists for major fossiliferous horizons in the Red Creek and Deadman Butte stratigraphic sections. Faunal lists are ordered from oldest to youngest (left to right) in each stratigraphic section. Positions of UCM Locs. 80065, 80083 and 81010 are inferred from lithostratigraphic and structural data. Numbers indicate the number of specimens for each species. Single vertical lines indicate divisions between* Lambdotherium *Range Zone and* Palaeosyops borealis *Assemblage Zone within each stratigraphic section of the Wind River Formation.*

	Red Creek section							Deadman Butte section					
Taxon	80083	79045	79039	80061	79040	80065	80064	81008	81009	80089	80062	80090	81010
Ectyopodus sp. cf. *E. childei*								1			2		
Peratherium marsupium				1	3						4		
Peratherium comstocki											2		
Peratherium innominatum				9	4			2			4		
Peradectes chesteri				1							1		
Amrintodelphys blacki				1									
Didelphodus sp. cf. *D. altidens*				3							2		1
Palaeictops multicuspis											4		
Palaeictops sp. cf. *P. bridgeri*					1								1
Leptictidae sp. indet.											2		
Palaeosinopa didelphoides											1		
Pantolestes longicaudus					1								
Apatemys sp. cf. *A. bellulus*				2	1								
Apatemys sp. A											2		
Proteutheria, sp. indet.											1		
Scenopagus edenensis				1	3								
Scenopagus sp. cf. *S. edenensis*											4		
S. priscus				2									1
cf. *Scenopagus* sp.											2		
Macrocranion nitens								1			1		
Adapisoricidae, probably new				2							1		
Centetodon bembicophagus				3							1		
Centetodon, sp. indet.				2							7		

Table 3.—*Continued.*

Taxon	Red Creek section							Deadman Butte section					
	80083	79045	79039	80061	79040	80065	80064	81008	81009	80089	80062	80090	81010
Nyctitherium sp. cf. *N. serotinum*				4							2		
Icaronycteris?, n. sp.					1								
Ageina tobeini								1					
Microsyops sp. cf. *M. scottianus*	1			8	14	1		3			20		4
M. lundeliusi													1
Uintasorex sp. cf. *U. parvulus*				4				1			20		
Alveojunctus sp.											1		
cf. *Ignacius* sp.											8		
Phenacolemur sp.		1											1
cf. *Anemorhysis*											1		
Absarokius sp. cf. *A. noctivagus*											3		
A. witteri	1					1							
Aycrossia lovei					1								
Loveina zephryi								3	1				
Shoshonius cooperi					3						22		
Washakius sp.													1
Huerfanius sp.				1									
Omomyidae, sp. indet.											1		
Notharctus nunienus											1		
Notharctus sp. cf. *N. venticolus*	1	3						1			5		
Notharctus sp. cf. *N. robinsoni*				2	7	1							
Copelemur consortutus											2		
cf. *Copelemur* sp.													1
cf. *Smilodectes* sp.					1								
cf. Taeniodonta, sp. indet.											1		
Esthonyx acutidens									1	2	1		
Trogosus sp.					1								

Table 3.—*Continued.*

Taxon	Red Creek section							Deadman Butte section					
	80083	79045	79039	80061	79040	80065	80064	81008	81009	80089	80062	80090	81010
Oxyaenidae, sp. undet.									1				
Prolimnocyon antiquus					1								
cf. *Prototomus* sp.						1							
Hyaenodontidae, sp. indet.					1								
cf. Creodonta, sp. indet.								2					
Viverravus lutosus					1			1					
Viverravus sp. cf. *V. gracilis*											2		1
Viverravinae, gen. et sp. nov.								1					
Miacis sp. cf. *M. exiguus*				1									1
Miacis sp. cf. *M. latidens*					1						1		
Miacis sp., cf. *M. parvivorus*					1								
cf. *Uintacyon* sp.											1		
Vulpavus canavus					1			1			3		
cf. *Vassocyon* sp.				1	1								
Coryphodon sp.	2		2		1	1		1			1	1	
cf. *Bathyopsis* sp.			1		2								
Mesonychidae, sp. indet.					1	1							
Thryptacodon loisi	1												
Hyopsodus wortmani					9			1		1	10		
H. paulus			1	2		2	1	3			13		7
Hyopsodus sp. cf. *H. minusculus*						1							
H. walcottianus											1		
Hyopsodus, sp. indet.													1
Phenacodus vortmani								2			1		
P. primaevus					2			1			4		
Hyracotherium craspedotum		3						4			10		
H. vasacciense	1	2	1				1	1	1	1	15		1

Table 3.—*Continued.*

Taxon	Red Creek section							Deadman Butte section					
	80083	79045	79039	80061	79040	80065	80064	81008	81009	80089	80062	80090	81010
Orohippus sp.		2		1	5								
Lambdotherium popoagicum		3	2					3	1	1	13		
Palaeosyops borealis					4	1						1	1
Heptodon ventorum			1			1					1		
Heptodon n. sp. near *H. ventorum*					1								
Heptodon? *posticus*		1	1								1		
Helaletes nanus					1								
Hyrachyus sp. cf. *H. eximius*					3								
Diacodexis sp. A											4		
D. olseni								1			5		3
Bunophorus sinclairi								1			1		
Bunophorus sp. A					1	1					2		
Antiacodon pygmaeus					3								
Paramys copei				6	10			1		1	16		1
Paramys excavatus											1		
Acritoparamys francesi				2							6		
?*Thisbemys* sp.					1								
Microparamys sp.											4		
Mattimys kalicola					1						4		
Knightomys depressus	1			4	5			1			12		
K. huerfanensis				1	3						3		
K. senior				4	1								
Pauromys sp.				6							11		
Sciuravus sp.													1
Ischyromyidae sp. indet.				1	1			4			2		
Palaeanodonta sp. A				1		1							
Total species	7	7	7	28	39	12	2	25	5	5	59	2	17

Table 4.—*Provisional mammalian faunal lists for Guthrie's Localities and UCM Loc. 80063 in the Lost Cabin Member of the Wind River Formation.*

Taxon	Arminto UCM Loc. 80063	Guthrie Locality 3 Buck Spring[1]	Guthrie Locality 2 Wolton[2]	Guthrie Locality 4[3]	Locality 1 Davis Ranch[4]
Peratherium marsupium					+
P. comstocki				+	+
P. innominatum				+	+
Armintodelphys blacki		+			
A. dawsoni					+
Didelphodus sp. cf. *D. altidens*		+		+	+
Palaeictops multicuspis		+			+
Palaeictops sp.		+			+
Palaeosinopa didelphoides		+	+	+	+
P. veterrima		+			
Apatemys sp. cf. *A. bellulus*			+		+
cf. *Plagioctenodon* sp.		+			
Scenopagus sp.				+	+
Microsyops sp. cf. *M. scottianus*	+	+	+	+	+
M. lundeliusi					+
Microsyops sp.		+			
Uintasorex sp. cf. *U. parvulus*				+	+
Phenacolemur sp.					+
Loveina zephryi				?	
Shoshonius cooperi		+	+	+	+
Absarokius noctivagus				+	+
A. witteri		+		+	
Notharctus sp. cf. *N. venticolus*		+			
Notharctus sp. cf. *N. robinsoni*				+	+
Notharctus sp. A		+			
Copelemur consortutus					+
Copelemur sp. near *C. feretutus*					+
Esthonyx acutidens	+	+	+	+	+
Trogosus sp.					+
Oxyaenidae sp. indet.				+	+
Prolimnocyon antiquus		+	+		+
cf. *Prototomus*		+			
Tritemnodon strenua					+
Hyaenodontidae sp. indet.					+
Limnocyon sp.					+
Creodonta sp. indet.					+
Didymictis altidens		+	+	+	+
Viverravus lutosus		+			+
Viverravus sp. cf. *V. gracilis*			+	+	+
Miacis sp. cf. *M. exiguus*		+		+	+
Miacis sp. cf. *M. latidens*		+			+
Miacis sp. cf. *M. parvivorus*		+			+
cf. *Oodectes* sp.					+
cf. *Uintacyon* sp.		+	+		+

Table 4.—*Continued.*

Taxon	Arminto UCM Loc. 80063	Guthrie Locality 3 Buck Spring[1]	Guthrie Locality 2 Wolton[2]	Guthrie Locality 4[3]	Locality 1 Davis Ranch[4]
Vulpavus canavus		+	+		+
cf. *Vassocyon* sp.		+	+		
Coryphodon sp.	+	+	+		
Bathyopsis fissidens		+	+		+
Mesonychidae sp. indet.					+
Thryptacodon loisi		+	+		+
Hyopsodus wortmani		+			+
H. paulus	+	+	+	+	+
Hyopsodus sp. cf. *H. minusculus*		cf.	cf.	+	+
Hyopsodus sp. indet.					+
H. walcottianus		+			
Phenacodus vortmani		+		+	+
P. primaevus		+	+	+	+
Ectocion superstes					+
Hyracotherium craspedotum		+	+	+	+
H. vasacciense	+	+	+		+
Orohippus sp.	+			+	+
Lambdotherium popoagicum	+	+	+	+	
Palaeosyops borealis (including *P. gregoryi*)		+			+
Heptodon ventorum		+		+	+
Heptodon n. sp. near *H. ventorum*					+
H. posticus		+	+	+	+
Helaletes sp. cf. *H. nanus*				+	
Selenaletes scopaeus					+
Hyrachyus sp. cf. *H. eximius*		+			+
Diacodexis olseni		+	+	?	+
Diacodexis sp.			+		
Diacodexis sp. A					+
Bunophorus sinclairi (=*B. gazini*)		+	+	+	+
Bunophorus sp. A					+
Antiacodon vanvaleni					+
Helohyus sp. cf. *H. plicodon*					+
Paramys copei	+	+	+	+	+
P. excavatus		+		+	+
Acritoparamys francesi				+	+
Mattimys kalicola				+	+
Knightomys huerfanensis					+
K. depressus				+	+
K. senior					+
Palaeanodonta sp. A					+
Palaeanodonta sp. B					+
Tubulodon taylori					+

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[1] Based on AMNH, CM and UCM collections. Several fossiliferous horizons are represented. As far as known the specimens of *Lambdotherium* were recovered from lower horizons at Buck Spring whereas specimens of *Palaeosyops* and *Hyrachyus* were recovered

(1929), Tourtelot (1948), and Keefer (1965*a*) for more information on the stratigraphy of the Buck Spring area.

Key localities.—UCM Locs. 79039 and 79045 in the Red Creek stratigraphic section; UCM Locs. 80062, 80089 and 81008 in the Deadman Butte stratigraphic section; UCM Loc. 80063 located north and east of Arminto; Buck Spring "dark red stratum" (Guthrie's Locality 3, UCM Loc. 81029, not including upper horizons); Wolton locality (Guthrie's Locality 2).

Lower boundary.—Lowest occurrence of *Lambdotherium popoagicum*; presently recognized at Unit 8 (MS-1, UCM Loc. 79045), Red Creek stratigraphic section, approximately 60 ft (18 m) above Wind River Formation contact on Mesozoic strata. Lowest occurrence in the Deadman Butte stratigraphic section is at MS-18 and 19, Unit 1A (UCM Loc. 81008). Although a number of specimens of *Lambdotherium* are known from Buck Spring, only those from UCM Loc. 81029 have a known stratigraphic position.

Upper boundary.—Directly below lowest occurrence of *Palaeosyops borealis*; presently recognized at the 140 ft (43 m) level (UCM 80090; MS-18 and 19, U-18) in Deadman Butte stratigraphic section, which is 60 ft (18 m) (UCM Loc. 80089) above last known occurrence of *Lambdotherium popoagicum.* Osborn's (1929) observations suggest that *P. borealis* (as *P. gregoryi* see Wallace, 1980; Bown, 1982) occurs at a level 100 ft (30 m) above "dark red stratum" of Granger (1910) in the Buck Spring area. Lowest occurrence of *P. borealis* in Red Creek stratigraphic section is at unit 61 (UCM Loc. 79040) approximately 200 ft (61 m) above last documented occurrence of *L. popoagicum.*

Taxa restricted to this zone.—*Loveina zephryi*; Viverravidae?, gen. et sp. nov.; *Hyopsodus walcottianus*; *Lambdotherium popoagicum.*

Apparent first local appearances.—*Armintodelphys* spp.; *Scenopagus* spp.; *Nyctitherium* sp. cf. *N. serotinum*; *Alveojunctus* sp.; *Uintasorex*

←

from upper horizons (Osborn, 1929; Dawson, oral communication, 1982). All other taxa occur in lithosympatry with *Lambdotherium.*

[2] Based on AMNH and CM collections.

[3] Based on CM collections.

[4] Based on AMNH, CM, PU and UCM collections. Most specimens were recovered from a single fossiliferous horizon, the "dark red stratum" (Granger, 1910) or the "maroon shale" layer (Guthrie, 1971). A number of fossiliferous horizons are preserved at this locality; however, all are within the *Palaeosyops borealis* Assemblage Zone of the Wind River Formation. The specimen of *Trogosus* was recovered from UCM Loc. 81028 and that of *Helohyus* from UCM Loc. 79043, which are horizons distinct from the "dark red stratum" (UCM Loc. 79042; CM Loc. 34; Guthrie's Locality 1). Faunal list includes all occurrences of fossil vertebrates from fossiliferous horizons shown in stratigraphic columns of Fig. 4, Measured sections 11, 12, 10, 9, 1979, and 8. See Stucky (1984*a*) for descriptions of measured sections and fossiliferous horizons.

sp. cf. *U. parvulus*; *Shoshonius cooperi*; *Absarokius witteri*; *Esthonyx acutidens*; *Orohippus* sp.; *Pauromys* sp. and taxa restricted to this zone.

Commonly occurring taxa.—*Palaeosinopa* spp.; *Microsyops* sp. cf. *M. scottianus*; *Uintasorex* sp. cf. *U. parvulus*; *Notharctus* sp. cf. *N. venticolus*; *Viverravus* spp.; *Didymictis altidens*; *Miacis* spp.; *Vulpavus canavus*; *Esthonyx acutidens*; *Hyopsodus paulus*; *H. wortmani*; *Phenacodus* spp.; *Hyracotherium* spp.; *Lambdotherium popoagicum*; *Heptodon ventorum*; *Diacodexis* spp.; *Bunophorus sinclairi*; *Paramys* spp.; *Knightomys* spp.

Apparent extinctions.—*Loveina zephryi*; *Hyopsodus walcottianus*; *Lambdotherium popoagicum*; *Meniscotherium* sp.

Zone recognition.—*Lambdotherium popoagicum* is usually one of the first taxa recovered by surface prospecting from a fossiliferous horizon in this zone. This taxon and associated *Coryphodon* sp., *Paleosinopa* spp., *Esthonyx acutidens, Hyopsodus paulus, Hyracotherium craspedotum, Heptodon ventorum, Diacodexis* spp. and *Bunophorus* are usually diagnostic. The absence of taxa that first appear in the *Palaeosyops borealis* zone is also useful in fossiliferous horizons that have large samples.

Comments.—Maximum thickness of the *Lambdotherium* zone is approximately 140 ft (43 m, base not exposed) in the Deadman Butte section and 300 ft (90 m) in the Red Creek stratigraphic section, including an unfossiliferous sequence above the last known occurrence of *Lambdotherium* and below the first known occurrence of *Palaeosyops borealis, Trogosus, Hyrachyus* and *Antiacodon.* Lithology plays no role in the recognition of this biostratigraphic unit.

To the best of my knowledge, Locality 48FR76 (White, 1952) is the only Wind River Formation locality where *Lambdotherium* and *Palaeosyops* may occur within the same fossiliferous horizon. White (p. 204) indicates the fossils from this locality came from "a small area of banded red and greenish clays with local concretionary zones." Thus White does *not* provide sufficient data to assess this possible lithosympatric occurrence of the two genera. My observations of the specimens of these two genera from this locality indicate that fossil preservation is nearly identical, thus suggesting that they may have come from the same fossiliferous horizon. If this is true, 48FR76 would be within the *Palaeosyops borealis* assemblage zone by definition. They may, however, have come from different horizons.

White's (1952) Localities 48FR75 and 48FR78 occur in the *Lambdotherium* zone because of the presence of *Lambdotherium.* White also reports *Hyopsodus powellianus* (=*H. walcottianus*) from 48FR75. 48FR80 may also be within the *Lambdotherium* zone because of the presence of *Meniscotherium.* A skull and lower jaws of *Meniscotherium* are known from exposures on the divide between Poison and Alkali creeks near Moneta (PU 14875). This genus has also been found in the Muddy Creek area (Granger, 1910). Its absence in the Red Creek–Deadman Butte area is of paleobiogeographic and stratigraphic interest, especially because *Meniscotherium* is so common in localities in the Green River Basin which preserve *Lambdotherium* (Gazin, 1952, 1962; West, 1973*a*). Most localities in the Wind River Formation reported by Keefer (1965) are also in the *Lambdotherium* zone. Olsen (in Sinclair and Granger, 1911) recovered a fauna with *Lambdotherium* and no *Palaeosyops, Hyrachyus* or *Trogosus* from the Beaver Divide area in the southern part of the Wind River Basin.

Guthrie (1967) and Korth (1982) have reported *Lambdotherium* from the Lysite Member of the Wind River Formation. The *Lambdotherium* specimen (ACM 2620) reported by Guthrie (1967) was collected in 1951 by L. and D. Kelley. According to a retyped field label (1951, Field label no. L31), the specimen was collected "about 3 miles along road that is first fork from Lysite P.O. going west towards Copper Mountain. At level of erosion plain at base of butte in red and white." This would place the locality south of Dolis Hill, in an area where the Lysite and Lost Cabin Members of the Wind River Formation are in fault contact in Sec. 35, T.39N., R.91W. Without precise stratigraphic data, the report of this specimen from the Lysite Member is questionable. The two teeth identified as *Lambdotherium* by Korth (1982) are M_3 talonid fragments of an equid, probably of *Xenicohippus* (see discussion of *Lambdotherium popoagicum* in Stucky, 1982).

Guthrie (1971) reports *Homogalax* from the Lost Cabin Member. Of the two specimens figured, CM 22389 is an upper molar of *Hyracotherium craspedotum* (prominent metaconule and paraconule; bunodonty), and CM 22390 is a composite specimen of two lower molars of *H. craspedotum* and *H. vasaccience* (hypolophid not complete, twinned metaconid). Froelich and Reser (1981) have also questioned the occurrence of *Homogalax* in the Lost Cabin Member. Systematic revision of tapiroids from the Wind River Formation should clarify the stratigraphic occurrence of *Homogalax* in the Wind River Basin.

Guthrie's (1971) Locality 4 is of some interest. I (Stucky, 1982) erroneously believed that *Lambdotherium* was not known from this locality. Several specimens of *Lambdotherium* are now known. Also known are specimens of *Helaletes* and *Notharctus* sp. cf. *N. robinsoni* which do not occur at other fossiliferous horizons in the *Lambdotherium* zone. If Guthrie's Localities 3 (Buck Spring) and 4 are indeed lithostratigraphic equivalents, as both Guthrie (1971) and Korth (1982) have suggested, detailed stratigraphic studies may more clearly define the boundary between the *Lambdotherium* and *Palaeosyops borealis* zones in these exposures.

Korth (1982) reported that Guthrie's (1971) Locality 2 (Wolton) was between 125 m and 250 m stratigraphically above Locality 1 (Davis Ranch). He based this interpretation on present elevation and attitudes of strata at these two localities. The fauna from Locality 2 suggests these exposures are in the *Lambdotherium* zone, whereas Locality 1 is used to define the *Palaeosyops borealis* assemblage zone (see Table 4). Structural data suggests that Locality 2 may be stratigraphically lower than Locality 1.

UCM Loc. 80083, which does not contain *Lambdotherium,* could not be placed directly in the Red Creek stratigraphic section because of its geographic position on the west side of Red Creek; repetitions of strata were not recognized on the opposite sides of Red Creek. The locality appears to be, stratigraphically, the lowest fossiliferous horizon in the Red Creek area. Until the fauna from this locality is better known, it is tentatively included in the *Lambdotherium* zone.

Palaeosyops borealis Assemblage Zone (=*Palaeosyops borealis* zone)

Reference sections.—Red Creek, Deadman Butte, Buck Spring, Rainbow Butte and Davis Ranch stratigraphic sections. See Osborn (1929) for record of *Palaeosyops gregoryi* (? = *P. borealis,* see Wallace, 1980; Bown, 1982) in the Buck Spring type area.

Key localities.—UCM Locs. 79040 and 80061 in the Red Creek stratigraphic section; UCM Locs. 80090 and 81010 in the Deadman Butte stratigraphic sections (placement of UCM Loc. 81010 inferred from structural and lithostratigraphic data); Davis Ranch localities (Locality 1 of Guthrie, 1971; Sullivan Ranch locality 1 on CM specimen labels; 5 mi north and west of Arminto on PU specimen labels; UCM Locs. 79041, 79042, 79043, 81016–81028, 81048); Rainbow Butte (UCM Loc. 80065); horizon 100 ft above dark red stratum at Buck Spring (Osborn, 1929).

Lower boundary.—Lowest occurrence of *Palaeosyops borealis* (including *P. gregoryi*), *Trogosus* sp., *Microsyops lundeliusi, Antiacodon* and/or possibly *Hyrachyus* sp. cf. *H. eximius.* Presently recognized at 100 ft (30 m) above "dark red stratum" at the Buck Spring locality in the type area of the Lost Cabin Member (Osborn, 1929). In the Red Creek section, *P. borealis, Trogosus* sp. and *Hyrachyus* sp. cf. *H. eximius* first occur lithosympatrically at unit 61 (MS-1, UCM Loc. 79040), approximately 200 ft (60 m) above last occurrence of *L. popoagicum.* Unit 56 (UCM Loc. 80061) is the lowest fossiliferous horizon in the Red Creek section that is included in this zone. In the Deadman Butte stratigraphic section, *P. borealis* first occurs at unit 18 (MS-18 and 19), 61 ft (29 m) above last occurrence of *Lambdotherium.*

Upper boundary.—Not preserved; upper strata in the Red Creek, Deadman Butte, Buck Spring, Rainbow Butte and Davis Ranch stratigraphic sections are either poorly exposed or covered by vegetation and/or Quaternary gravel. Based on data of Tourtelot and Thompson (1948) and Wallace (1980) the boundary could probably be placed at the first occurrence of *P. huerfanensis.* Other potentially useful taxa which do not occur, so far as known, in the Wind River Formation in the northeastern Wind River Basin but have restricted biostratigraphic ranges in southwestern Wyoming and elsewhere include *Omomys carteri, Anaptomorphus* spp., *Bathyopsis middleswarti, Sciuravus nitidus,* and *Tillomys.* Additionally, the extinction of more typically Wasatchian genera could be used. Such genera would include those indicated below in the apparent extinctions.

Taxa restricted to this zone.—Ectocion superstes; *Microsyops lundeliusi* (s.s.); *Palaeosyops borealis*; *Selenaletes scopaeus*; *Huerfanius.*

Apparent first local appearances.—Palaeictops sp., cf. *P. bridgeri*; *Pantolestes* sp., cf. *P. longicaudus*; *Washakius* sp.; *Notharctus* sp. cf. *N. robinsoni*; cf. *Smilodectes* sp.; "*Copelemur*" *consortutus*; *Trogosus* sp.; *Hyopsodus* sp., cf. *H. minisculus*; *Hyopsodus* sp. A; *Helaletes nanus*; *Hyrachyus* sp. cf. *H. eximius*; *Antiacodon* spp.; *Helohyus* sp. cf. *H. plicodon*; *Homacodon* sp.; *Pristichampsus* sp.

Commonly occurring taxa.—Peratherium spp.; *Scenopagus* spp.; *Uintasorex* sp. cf. *U. parvulus*; *Microsyops* sp. cf. *M. scottianus*; *Shoshonius cooperi*; *Notharctus* sp. cf. *N. robinsoni*; "*Copelemur*" *consortutus*; *Esthonyx acutidens*; *Hyopsodus* spp.; *Phenacodus primaevus*; *Hyracotherium vasaccience*; *Palaeosyops borealis*; *Heptodon ventorum*; *Selenaletes scopaeus*; *Hyrachyus* sp. cf. *H. eximius*; *Diacodexis* spp.; *Bunophorus sinclairi*; *Antiacodon* spp.; *Paramys* spp.; *Knightomys* spp.; *Pauromys* sp.

Apparent extinctions.—Palaeosinopa spp.; *Absarokius* spp.; *Hyopsodus wortmani*; *Phenacodus vortmani*; *Ectocion superstes*; *Thryptacodon loisi*; *Esthonyx acutidens*; *Selenaletes scopaeus*; *Bunophorus* spp.; *Diacodexis* spp.; *Coryphodon* sp. (Extinction events are extremely difficult to verify and as such must be only generally identified. Data from outside the biostratigraphic sequence has been incorporated with the understanding that local populations varied in the time of last occurrence, see Stucky, 1984*b*).

Zone recognition.—Large mammals usually recovered in the first surface collection from a fossiliferous horizon in this zone include *P. borealis, Trogosus* sp. and *Hyrachyus* sp., cf. *H. eximius. Antiacodon* is also common. These taxa plus any taxa listed under first local appearances, and, in all well documented cases, the lack of *Lambdotherium popoagicum* are also diagnostic.

Comments.—Hyrachyus appears not to be present in the *Lambdotherium* zone of the Wind River Formation. Dawson (CM, oral communication, 1982) found associated isolated teeth of *Hyrachyus* in the upper levels of the Buck Spring area. *Hyrachyus* is present at

UCM Locs. 81048 and 79040 and is relatively common in the dark red stratum at Davis Ranch (Locality 1 of Guthrie). These localities also preserve *Palaeosyops borealis.*

White's (1952) localities 48FR65 and 48FR79 contain *Palaeosyops borealis* in their assemblages and are thus referrable to the *Palaeosyops borealis* zone. The type of *Microsyops lundeliusi* was also recovered from 48FR65.

Tourtelot and Thompson (1948) report *Eotitanops* (=*P. borealis*) from the lower part of the Wind River Formation in the Boysen Reservoir area. *Heptodon*? (=*Helaletes nanus,* personal observations) and *Coryphodon* were also recovered. Above these occurrences, *P. huerfanensis* (see Wallace, 1980) and *Hyrachyus* are reported. Gazin (1953) also reports an unusually large skull of *Esthonyx acutidens* from this area. These occurrences suggest the potential for defining a biostratigraphic zone above the *Palaeosyops borealis* zone in the Wind River Formation, which would be defined on the basis of stage of evolution of *Palaeosyops* rather than the first appearance of exotic taxa.

Fossiliferous horizons at the Davis Ranch locality (all included by Guthrie (1971) in his Locality 1) represent the most extensive collection of fossil vertebrates from any area of exposure within the *Palaeosyops borealis* zone and the Wind River Formation. Literally thousands of specimens of approximately 75 mammalian species are represented. Lower vertebrates are also abundant but have not as yet been studied in detail. Most mammal species are represented by at least ten specimens, and some are represented by as many as a hundred. Fortunately, most fossils come from a single fossiliferous horizon, the "maroon shale" or "dark red stratum" (Granger, 1910; Guthrie, 1971). Preservational characteristics of fossils from this locality can be used to determine the general level from which undocumented fossils were recovered in this area (see descriptions of UCM Locs. 79041, 79042 and 81023 in Stucky, 1984*a*).

The lithostratigraphic relations of Badwater Locality 17 (see Black, 1969; West and Atkins, 1970) are uncertain. West and Atkins (1970) suggest that this locality is younger than the typical Lost Cabin fauna. Although the typical Wasatchian species *Phenacodus primaevus* is well represented, specimens of *Antiacodon* and *Sciuravus* suggest that this fauna is Bridgerian in age. The lack of *Hyrachyus, Palaeosyops* or *Trogosus* is puzzling, but could well be related to small sample size and/or taphonomic factors.

Homacodon sp. has recently been recovered from the *Palaeosyops borealis* zone in the Boysen Reservoir area (Krishtalka and Stucky, in preparation).

Many of the species recorded in the *Palaeosyops borealis* zone of the Wind River Formation are represented by only one or two specimens from a fossiliferous horizon. However, these occurrences in this zone and their absence in the *Lambdotherium* zone appear significant; many of the taxa which first appear within the *Palaeosyops borealis* zone are also characteristic of faunas which have been described as either transitional between the Wasatchian and Bridgerian (upper Huerfano Formation fauna of Robinson, 1966; Cathedral Bluffs Tongue fauna of Morris, 1954; Gazin, 1962; and West, 1973) or early Bridgerian (lower Bridger Formation fauna of McGrew and Sullivan, 1970; West, 1973; Gazin, 1976; Aycross Formation fauna of Bown, 1982).

The differences in biostratigraphic occurrences of *Lambdotherium* and the taxa which make their first appearance in the *Palaeosyops borealis* zone are not due to environmental or ecological differences, as indicated by the following criteria: 1) Non-overlapping ranges in three separate stratigraphic sections in the Wind River Formation as well as non-overlap in the Huerfano Formation and elsewhere (Stucky, 1984*b*); 2) The occurrence of these taxa in rocks with similar depositional environments; and 3) The close geographic proximity (less than one mile apart in each case) of the localities in all three stratigraphic sections from which the species were recovered. Indirectly, most large, herbivorous ungulates usually have gregarious habits and large home ranges that encompass a number of differing ecological settings as well as depositional environments.

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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 6. STRATIGRAPHIC SECTIONS AND LOCALITY DESCRIPTIONS, UPPER PART OF THE WIND RIVER FORMATION

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Abstract

Measured sections and fossiliferous horizons in the Red Creek Facies and Lost Cabin Member of the Wind River Formation, northeastern Wind River Basin are described. These data supplement lithostratigraphic and biostratigraphic conclusions of Stucky (1984).

Introduction

This report provides the primary data from stratigraphic sections and fossiliferous horizons from the Red Creek Facies and Lost Cabin Member of the Wind River Formation in the Red Creek-Deadman Butte and Buck Spring (type area of the Lost Cabin Member, see Stucky, 1984) areas in the Northeastern Wind River Basin. Narrative descriptions and correlations of the measured sections are in Stucky (1984).

Measured Sections

A vertebrate fossiliferous horizon is marked by an asterisk to the left of the unit number. Locality numbers are in parentheses following the unit description. Thicknesses of units are in feet and meters (in parentheses). Hand samples for many units are in the locality collections of the Museum, University of Colorado (UCM). Locations for the transects of the measured sections are shown in Fig. 3 of Stucky (1984) and generalized stratigraphic columns of the measured sections are correlated in Fig. 4 of the same paper.

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Abbreviations used in the text are: AMNH, American Museum of Natural History (New York); CM, Carnegie Museum of Natural History (Pittsburgh); PU, Princeton University (Princeton); UCM, Museum, University of Colorado (Boulder); loc., locality; MS, measured section; U, unit.

RED CREEK STRATIGRAPHIC SECTION

Measured Section 1. Red Creek stratigraphic section, section of Wind River Formation and Middle (?) Eocene sequence. Measured at Wind River Formation contact on Mowry Shale, Sec. 17, T.38N., R.87W. to SE ¼ Sec. 25, T.38N., R.88W. General east–west strike; dip 4–6 degrees south.

Quaternary alluvium:

92. Gravel, poorly sorted, cobble to boulder, clast supported 3.0 (0.9)

Unconformity
Middle (?) Eocene Volcaniclastic Sequence:

*91. Paraconglomerate, brown, massive, poorly sorted, matrix supported; very fine to coarse grained matrix; pebble to cobble size clasts, well rounded volcaniclastics (basalts) and claystone balls; some minor lentiles of mudstones and carbonaceous shales; silicified wood logs; fossil vertebrates rare, some well rounded bone fragments, randomly distributed in unit; unit faulted to south against Wind River Formation (UCM Loc. 80064-C) 80.0 (24.4)
90. Carbonaceous shale, moderate yellowish brown (10 YR 5/4), tabular, thinly laminated parallel to bedding plane; leaf impressions, sharp lower contact 4.5 (1.4)
*89. Mudstone, pale olive green (10 Y 6/2), tabular, sharp lower contact, more than 95% clay with subangular quartz; calcite and gypsum crystals, spheroidal barite crystal clusters; aquatic fossil vertebrates (UCM Loc. 80064-A) 7.0 (2.1)

Wind River Formation, Lost Cabin Member:

Upper Gray Sequence:

88. Paraconglomerate, dusky yellow (5 Y 6/4), massive, matrix medium to coarse quartz and rock fragments, micaceous; quartzite pebbles, matrix supported; top of unit well sorted medium to coarse rock fragments, micaceous; calcareous cannonball concretions; top of unit with iron oxide cement 39.5 (12.0)
87. Mudstone, light greenish gray (5 GY 8/1), silty, poorly exposed 18.0 (5.5)

86. Mudstone, light greenish gray (5 GY 8/1), silty, poorly exposed 31.0 (9.5)
85. Sandstone, yellow gray (5 YR 4/1), crossbedded; fine to medium subrounded quartz and rock fragments; conglomeratic at base; calcareous cannonball concretions; carbonaceous shale lentiles with leaf impressions; fossil logs in place at 10.0 ft (3.0 m) above base (UCM Loc. 80102) 82.0 (25.0)
84. Mudstone, yellowish gray (5 Y 7/2), silty 15.0 (4.6)
83. Mudstone, pale red-gray mottled, silty; weathers red 12.0 (3.7)
*82. Mudstone, greenish gray (5 GY 6/1), micaceous, well rounded quartz grains; coprolites and turtle shell fragments, lepisosteid scales (UCM Loc. 80103) 7.0 (2.1)
81. Sandstone, greenish brown, fine to coarse grained, pebble conglomerate in part 4.0 (1.2)
80. Mudstone and sandstone, poorly exposed 18.0 (5.5)
79. Mudstone, mottled pale red-gray, silty; some fine to medium quartz sand 4.0 (1.2)
78. Mudstone, pale olive (10 Y 6/2), sand and silt increases towards top of unit 7.0 (2.1)
77. Sandstone, light gray (N-7), very fine, muddy 11.0 (3.4)
76. Mudstone and sandstone, greenish gray (5 GY 6/1), micaceous (10% of volume), pedotubules and calcareous glaebules 10.0 (3.0)
75. Claystone, greenish gray, calcareous; sharp lower contact 2.0 (0.6)
74. Mudstone, gray, laminated; sharp contact below 7.0 (2.1)
73. Claystone, very light gray (N-8) to medium light gray (N-6), alternating laminations; mud volcano structures, excellent marker bed, tabular unit, sharp contact below 3.0 (0.9)
72. Mudstone, light greenish gray (5 GY 8/1), silty; some very fine grained quartz sand; becomes coarser towards top of unit; sharp lower contact 8.0 (2.4)
71. Sandstone, light gray, micaceous, calcareous, poorly sorted, muddy, graded and laminated bedding; angular to subangular fine to coarse grains; intraformational mudstone and calcareous glaebule pebbles and abundant biotite crystals at base; sharp lower contact 8.5 (2.6)
70. Mudstone, light gray (N-7), silty, micaceous; becomes coarser grained toward top of unit; sharp contact with lower unit 3.0 (0.9)
69. Mudstone, greenish gray (5 GY 6/1), silty, micaceous, laminated, some angular claystone clasts at base; sharp contact with lower unit 3.0 (0.9)

68. Mudstone, greenish gray (5 GY 6/1), silty; some rhizoliths 2.0 (0.6)
67. Mudstone, medium gray 2.0 (0.6)
66. Mudstone, light gray; poorly exposed 37.0 (11.3)
65. Mudstone, green, silty 2.0 (0.6)

Variegated Sequence:

64. Mudstone, red-green mottled 2.0 (0.6)
63. Sandstone, greenish gray (5 GY 7/1), very fine grained, micaceous 11.0 (3.4)
62. Mudstone, grayish yellow-green (5 GY 7/2), silty, bioturbated; non-preferentially cemented pedotubules, noncarbonized leaf and small invertebrate impressions 5.0 (1.5)
*61. Mudstone, red-green mottled; sandy to silty, calcareous pedotubules and glaebules, non-preferentially cemented pedotubules, coprolites, eggshell fragments, silicified plant (very rare), abundant turtle and crocodile remains, mammals common; lower part of unit is a green silty mudstone which grades to red-green mottled mudstone, to brick red-gray mottled mudstone with abundant calcareous glaebules at top (Someday locality, UCM Loc. 79040) 8.0 (2.4)
60. Sandstone, yellowish gray, fine to medium grained, subangular rock fragments, well sorted, crossbedded; conglomeratic at base; clasts of Precambrian quartzites and schists, Flathead Formation sandstones and conglomerates and Paleozoic limestones and dolomites; shoestring channel geometry, channeled into lower units 9.0 (2.7)
59. Mudstone, grayish red (5 R 4/2)-green mottled, sandy, calcareous; large light gray calcareous glaebules 6.0 (1.8)
58. Claystone, light greenish gray (5 GY 8/1), abundant calcareous glaebules (25% of volume); small burrows 3.5 (1.1)
57. Mudstone, light greenish gray (5 G 8/1), sandy 3.5 (1.1)
56. Mudstone, grayish yellow-green (5 GY 7/2), silty, calcareous in part; some fine sand; calcareous glaebules distributed in horizontal planes, calcareous pedotubules; abundant microvertebrates consisting of relatively complete elements (Lightning Butte, UCM Loc. 80061) 5.5 (1.7)
55. Mudstone, light greenish gray (5 GY 8/1), highly calcareous; some very fine grained sand; calcareous glaebules 3.0 (0.9)
54. (Number inadvertently omitted)
53. Sandstone, grayish yellow-green (5 GY 7/2), fine grained, micaceous, well sorted rock fragments; highly calcareous 2.5 (0.8)

52. Sandstone, grayish yellow-green (5 GY 6/2), fine to medium grained, muddy, tabular geometry 2.0 (0.6)
51. Mudstone, light greenish gray (5 G 8/1), sandy 5.0 (1.5)
50. Sandstone, yellowish gray (5 Y 8/1), medium to coarse grained, calcareous; preferentially cemented, ironstone concretions, calcite crystals; channeled into lower units 4.0 (1.2)
49. Mudstone, gray; calcareous glaebules 10.0 (3.0)
48. Sandstone, yellowish gray (5 Y 7/2), crossbedded, micaceous, calcareous; fine to medium grained; lower 0.5 ft (0.2 m) resistant; ironstone concretions 6.0 (1.8)
47. Claystone and mudstone, light greenish gray (5 GY 8/1), laminated bedding, slightly calcareous 11.0 (3.4)
46. Mudstone, red-green mottled, silty; laterally loses red color shifting to gray; calcareous glaebules 3.0 (0.9)
45. Sandstone, yellowish gray (5 Y 7/2), medium grained, subangular, well sorted, calcareous, coarsens upward into pebble conglomerate, channeled into lower units 7.0 (2.1)
44. Mudstone, light greenish gray (5 GY 8/1), sandy, micaceous, calcareous 4.0 (1.2)
*43. Mudstone, red-green mottled; coprolites 3.0 (0.9)
42. Sandstone, yellowish gray (5 Y 7/2), very fine to medium grained, poorly sorted, calcareous, resistant 5.0 (1.5)
41. Sandstone, light green (5 GY 6/1), very fine to fine grained, muddy; some dark yellowish orange streaks (10 YR 6/6) 11.0 (3.4)
40. Mudstone, greenish gray (5 GY 6/1), sandy, numerous calcareous glaebules 6.0 (1.8)
*39. Sandstone, yellowish gray (5 Y 7/2), fine to coarse grained, angular to subangular grains, poorly sorted, micaceous, calcareous, crossbedded; coarsens upward; moderate reddish brown (10 R 4/6), ironstone concretions; channeled into lower units; rare lower vertebrates (UCM Loc. 80087) ... 4.0 (1.2)
38. Mudstone, greenish gray (5 GY 7/1), sandy; calcareous glaebules 2.5 (0.8)
37. Mudstone, pale olive (10 Y 5/2), sandy 2.0 (0.6)
36. Mudstone, pale red-greenish gray, mottled 1.0 (0.3)
35. Mudstone, light olive gray (5 Y 7/1), sandy; calcareous glaebules 5.0 (1.5)
34. Sandstone, yellowish gray (5 Y 8/1), very fine grained, friable, calcareous 6.0 (1.8)
33. Mudstone, red-brown-yellow, mottled, sandy 1.0 (0.3)
32. Sandstone, dusky yellow (5 Y 6/4), fine to medium grained rock fragments, angular to subangular grains, bioturbated, some pedotubules 10.0 (3.0)

31.	Mudstone, dusky yellow-green (5 GY 4/2), sandy; coarse angular sand grains, very little silt, predominantly clay	5.0 (1.5)
30.	Sandstone, light olive gray (5 Y 6/1), coarse to fine grained, subangular to rounded rock fragments, poorly sorted, crossbedded, calcareous; resistant ridge forming; reddish brown (10 R 4/6)-yellow mottled at base	6.0 (1.8)

Wind River Formation, Red Creek Facies:

29.	Mudstone, purplish red	2.0 (0.6)
28.	Mudstone, green; calcareous glaebules	4.0 (1.2)
27.	Mudstone, red-green mottled; calcareous glaebules	4.0 (1.2)
26.	Mudstone, green	3.0 (0.6)
25.	Sandstone, yellowish gray	4.0 (1.2)
24.	Mudstone, light gray	4.0 (1.2)
23.	Mudstone, medium gray	1.0 (0.3)
22.	Mudstone, gray; light brown mottling, gypsum crystals	3.0 (0.9)
21.	Sandstone, greenish gray (5 GY 6/1) with yellowish brown (10 YR 6/4) streaks; very fine grained; calcareous	2.5 (0.8)
20.	Sandstone, dusky yellow (5 Y 6/4), fine grained, well sorted, subangular rock fragments, micaceous; intraformational claystone clasts at base	2.5 (0.8)
19.	Mudstone, greenish gray with yellow streaking; carbonaceous; bioturbated; numerous gypsum crystals; fossil wood encrusted with gypsum	3.5 (1.1)
18.	Mudstone, pale olive (10 Y 6/2), sandy; numerous gypsum crystals	4.0 (1.2)
*17.	Mudstone, grayish yellow green (5 GY 7/2), silty, fissile, some gypsum crystals; fossil wood and small bone fragments (no locality number)	2.0 (0.6)
*16.	Mudstone, grayish yellow green, calcareous glaebules, turtle shell fragments (no locality number)	3.0 (0.9)
15.	Claystone, medium gray, laminated; excellent marker bed; well preserved seed impressions locally	1.0 (0.3)
*14.	Claystone, grayish yellow green (5 GY 7/2), calcareous pedotubules and glaebules; coprolites; eggshells; partially articulated skeletal material of *Allognathosuchus* and *Crocodylus,* associated limbs of *Coryphodon* sp., microvertebrates and turtles common in spots (UCM Loc. 79039)	3.0 (0.9)
*13.	Mudstone, yellowish gray (5 Y 8/1), silty (no locality number)	4.0 (1.2)
12.	Mudstone, light gray-light greenish yellow mottled, sandy; calcareous glaebules, some pebbles	2.0 (0.6)

*11. Sandstone, yellowish gray (5 Y 8/1), laminated bedding, calcareous; rip up clasts at base; black bone fragments; sharp lower contact (no locality number) 3.0 (0.9)

*10. Claystone, greenish gray (5 GY 7/1), black bone fragments (no locality number) 0.5 (0.2)

9. Mudstone, yellowish gray (5 Y 7/1), some very fine sand, carbon streaked in part; high clay content 2.0 (0.6)

*8. Sandstone, light gray, fine to coarse grained; some interbedded conglomerates with Mesozoic clasts (sandstones, conglomerates, porcelainite and limestone), vertebrate fossils at top of unit (UCM Loc. 79045) 31.0 (9.5)

7. Vegetation covered 15.0 (4.6)

6. Conglomerate, pale olive (10 Y 6/2), intraformational, micaceous, angular, fine to medium grained quartz sand matrix, muddy, laminated bedding, laterally becomes fine grained sandstone, dusky yellow (10 Y 6/2) and greenish gray (5 GY 6/1) claystone clasts at base, channeled into lower unit 4.0 (1.2)

5. Mudstone, yellowish gray (5 Y 7/2), sandy, sharp lower contact 2.0 (0.6)

4. Sandstone, yellowish gray (5 Y 9/1), very fine to coarse grained, well rounded to angular grains, muddy; interbedded conglomerates composed of well rounded Mesozoic rock fragments, matrix of conglomerates primarily well rounded and well sorted quartz grains 8.0 (2.4)

3. Mudstone, moderate red (5 R 4/6)-pinkish red (5 YR 5/1) mottled, sandy, bioturbated, non-preferentially cemented burrows; laterally contacts Mowry Shale where large angular blocks of porcelainite are incorporated into unit 2.0 (0.6)

2. Mudstone, gray 0.5 (0.2)

1. Sandstone, gray; unconformable on Mowry Shale 6.0 (1.8)

Unconformity
Mowry Shale

Measured Section 2. West of Red Creek. Partial section of Wind River Formation. Sec. 7, T.38N., R.87W.

Wind River Formation:

9. Sandstone, yellowish gray (5 Y 7/2), fine grained, poorly sorted, calcareous, occasional red mottling and glaebules 10.0 (3.0)

8. Mudstone, greenish gray (5 GY 6/1), silty, calcareous; grades upward into red-green and green-purple mottled mudstone 9.0 (2.7)

7. Mudstone, pale red (10 R 6/2), some sand and silt, calcareous; some mottling 7.0 (2.1)
6. Sandstone, mottled green-red, fine grained; some calcareous glaebules 3.0 (0.9)
5. Mudstone, grayish yellow (5 GY 6/2); some sandy lentiles with angular to subangular coarse quartz grains; some calcareous glaebules 25.0 (7.6)
4. Sandstone, mottled green-red, very fine to fine grained; red mottles increase at top; calcareous glaebules at top 2.0 (0.6)
3. Sandstone, light greenish gray (5 GY 8/1), very fine grained, calcareous; highly calcareous glaebules 8.0 (2.4)
2. Conglomerate, greenish gray, cobble clasts primarily derived from Mesozoic; matrix is fine to coarse grained sand ... 5.0 (1.5)
1. Mudstone, reddish brown (10 R 5/6) and gray (5 GY 6/1) mottled; noncalcareous glaebules, sharp lower contact 12.0 (3.6)

Unconformity
Chugwater group

RAINBOW BUTTE STRATIGRAPHIC SECTION

Measured Section 3. Rainbow Butte stratigraphic section. Partial section of the Lost Cabin Member of the Wind River Formation. Rainbow Butte, Hill 6335, Sec. 19, T.38N., R.87W.; dip 6 degrees South, strike N. mag 82 degrees W., 25 June 1980.

Quaternary:

25. Gravel, poorly sorted, clast supported, cobble 2.0 (0.6)

Wind River Formation, Lost Cabin Member:

Variegated Sequence:

24. Mudstone, red-green mottled; highly weathered 2.2 (0.7)
23. Mudstone, green, calcareous; highly weathered 1.0 (0.3)
22. Mudstone, red-green mottled; highly weathered 6.5 (2.0)
21. Sandstone, gray (5 GY 7/1), fine to medium grained, micaceous, muddy, friable; preferentially cemented zones 9.0 (2.7)
20. Mudstone, gray (lower part) to mottled red-gray (upper part), silty; calcareous glaebules and vertically oriented pedotubules; sharp undulatory lower contact 2.0 (0.6)
19. Mudstone, mottled red-gray (5 GY 6/1), silty; calcareous glaebules 3.5 (1.1)
18. Mudstone, gray (5 GY 6/1), calcareous, sandy 4.0 (1.2)
*17. Mudstone, grayish yellow green (5 GY 7/2), sandy; contains

rounded intraformational claystone pebbles at base (UCM Loc. 80065-17) 3.5 (1.1)

16. Mudstone, yellowish green (5 GY 6/2), micaceous, sandy 3.0 (0.9)

*15. Sandstone, greenish gray, fine grained, micaceous, muddy (UCM Loc. 80065-15) 2.5 (0.8)

*14. Sandstone, greenish gray, fine grained; intraformational mudstone clasts; calcareous glaebules formed in two layers, one at base and one 1.0 ft (0.3 m) above base; fossils restricted to glaebule horizons (UCM Loc. 80065-14) 4.5 (1.4)

13. Mudstone, grayish yellow green (5 GY 6/2), silty; calcareous glaebules and noncalcareous pedotubules 1.5 (0.5)

12. Sandstone, greenish gray (5 GY 6/1), fine grained, calcareous; glaebules oriented in horizontal plane 6.0 (1.8)

*11. Mudstone, gray; spheroidal calcareous glaebules and calcareous pedotubules (UCM Loc. 80065-11) 2.0 (0.6)

*10. Mudstone, mottled red-green, calcareous; color mottles shift from green-red at bottom to red-gray to orange-gray at top; calcareous glaebules at top and base of unit (UCM Loc. 80065-10) 2.5 (0.8)

9. Sandstone, yellow-green (5 GY 6/2), subangular fine to very coarse grained, poorly sorted, slightly calcareous; calcareous glaebules 2.5 (0.8)

*8. Mudstone, mottled brick red-pale yellowish green (5 GY 6/1), sandy, bioturbated; calcareous glaebules; green mottles occur in thin non-preferentially cemented pedotubules (UCM Loc. 80065-8) 2.0 (0.6)

7. Mudstone, greenish gray, micaceous, silty; glaebules; mica decreases in grain size from bottom to top from coarse to fine; sharp lower contact 5.5 (1.7)

*6. Sandstone, greenish gray, medium to coarse grained, poorly sorted, calcareous; subrounded pebble conglomerate at base, well rounded bone fragments; top forms resistant ledge (UCM Loc. 80065-6) 3.0 (0.9)

*5. Mudstone, brick red below to mottled red-green above, calcareous, bioturbated; yellowish brown glaebules and pedotubules (UCM Loc. 80065-5) 3.0 (0.9)

*4. Claystone, greenish gray-light brownish gray (5 YR 6/1) mottled, micaceous; non-preferentially cemented pedotubules (UCM Loc. 80065-4) 5.0 (1.5)

3. Mudstone, grayish green (10 GY 5/2), micaceous, silty, bioturbated; noncalcareous pedotubules 2.5 (0.8)

*2. Mudstone, green-yellow-red mottled, silty, bioturbated (UCM Loc. 80065-2) 3.0 (0.9)

*1.	Mudstone, grayish green (10 GY 5/2), silty; calcareous chocolate brown to orange-brown pedotubules oriented perpendicular to bedding plane; glaebule concentration (25–40% total volume) at top of bed; conglomeratic lense at 3.0 ft (0.9 m) above base of unit, clasts up to 1.0 cm in diameter (UCM Loc. 80065-1); basal contact not exposed	5.0 (1.5)

Base not exposed.

DAVIS RANCH STRATIGRAPHIC SECTIONS

Measured Section 1979. Davis Ranch (Sullivan Ranch Locality or Guthrie's (1971) Locality 1). Partial section of Wind River Formation, Lost Cabin Member. Sec. 6, T.37N., R.87W.

Wind River Formation, Lost Cabin Member:

12.	Mudstone, gray and sandstone, gray	10.0+ (3.0)
11.	Sandstone, tan to light brown, fine to very fine grained, calcareous, biotite flakes present	26.9 (8.2)
*10.	Mudstone, bluish gray, sandy, calcareous; pedotubules and glaebules (UCM Loc. 79041)	44.7 (13.6)
*9.	Sandstone, buff to tan, calcareous, fine to medium, subangular, arkosic (no locality number)	7.7 (2.3)
8.	Ash, off-white, calcareous, resistant	2.3 (0.7)
*7.	Mudstone, gray, some medium to fine sand (no locality number)	12.8 (3.9)
6.	Mudstone, yellowish gray, noncalcareous, occasional calcareous sandstone lenses, micaceous, fine grained, occasional glaebules	7.0 (2.1)
*5.	Mudstone, gray, sandy (UCM Loc. 79043)	12.8 (3.9)
*4.	Mudstone, mottled red, grades laterally into Unit 5 (UCM Loc. 79043)	3.7 (1.1)
3.	Mudstone, purple	2.3 (0.7)
*2.	Mudstone, mottled red, micaceous, calcareous (UCM Loc. 79042)	10.5 (3.2)
1.	Mudstone, mottled red-gray, glaebules	4.0 (1.2)

Base not exposed.

Measured Section 8. West Davis Ranch. Partial section of Lost Cabin Member of Wind River Formation. Center Sec. 36, T.38N., R.88W.

Wind River Formation, Lost Cabin Member:

15.	Sandstone, gray, crossbedded	25.0+ (7.6)
14.	Mudstone, gray	12.0 (3.6)
*13.	Mudstone, red, predominantly clay with some silt, calcar-	

eous, not laterally persistent (equivalent to Measured Section 1979, Unit 2 to Unit 4, UCM Loc. 79042) 21.5 (6.6)

12. Mudstone, green, calcareous glaebules at base 17.0 (5.8)

*11. Mudstone, mottled red-gray, calcareous, tabular (UCM Loc. 81021) 1.5 (0.5)

*10. Mudstone, green, micaceous; turtle shell fragments 3.0 ft (0.9 m) above base; lenticular (UCM Loc. 81020) 12.5 (3.8)

9. Mudstone, gray, calcareous 11.5 (3.5)

8. Mudstone, purple with white top; tabular, excellent marker bed 4.0 (1.2)

7. Mudstone, alternating red and gray silt and very fine sand layers, calcareous, micaceous 6.0 (1.8)

6. Sandstone, green, subrounded to angular medium grained, well sorted, calcareous; quartz arenite, some biotite and feldspar; preferentially cemented 2.0 (0.6)

*5. Mudstone, mottled purple-green; tabular, calcareous glaebules and pedotubules; associated partial skeletons of primate and crocodile, fossil vertebrates abundant (UCM Loc. 81019) 3.5 (1.1)

*4. Mudstone, mottled dark gray-light gray, calcareous; some quartz and biotite grains; calcareous lense-shaped glaebules and pedotubules; laterally grades to sandstone; associated skeletal remains of ?varanid and *Palaeosyops* (UCM Loc. 81018) 10.5 (3.2)

3. Mudstone, mottled gray-red, calcareous; alternating mottled red and gray horizons with distinct lower contacts; laterally grades into sandstone where red coloration is less apparent 3.0 (0.9)

*2. Mudstone, red, tabular; biotite at base; some pedotubules; grades laterally into sandstone (UCM Loc. 81017) . . . 1.5 (0.5)

1. Mudstone, mottled brown-yellow-green, silty with some subangular sand and biotite; laminated in part; iron oxide nodules; carbonaceous in part; sharp upper contact 6.5 (2.0)

Base not exposed.

Measured Section 9. Davis Ranch. Partial section of Lost Cabin Member of Wind River Formation. NW ¼ NW ¼ Sec. 6, T.37N., R.87W.

Wind River Formation, Lost Cabin Member:

10. Conglomerate, pale yellow-brown (10 YR 6/2), intraformational; calcareous at base; matrix with alternating claystone and silty mudstone laminations 2.5 (0.8)

9. Mudstone, mottled gray-red, sandy, slightly calcareous 3.5 (1.1)

*8. Mudstone, red, calcareous glaebules; laterally grades into apron-channel sandstone (UCM Loc. 79043) 2.5 (0.8)

7. Mudstone, mottled; color changes from mottled yellow-red at base to mottled red-green to mottled green-red at top; calcareous glaebules at base 10.0 (3.0)

*6. Mudstone, dark reddish brown (10 R 3/4), micaceous, silty; abundant calcareous glaebules and pedotubules; some carbonaceous material; abundant fossil vertebrates, including some articulated remains; bone *in situ* surrounded by layer of green colored mudstone approximately 2 to 5 mm thick (UCM Loc. 79042) 14.0 (4.3)

*5. Claystone, mottled red-green, vertebrate fossils at top of unit (UCM Loc. 81025) 2.5 (0.8)

*4. Mudstone, mottled red to red-gray; red mudstone is non-calcareous whereas gray mudstone is calcareous; glaebules at top of unit (UCM Loc. 81024) 4.0 (1.2)

*3. Mudstone, gray, laterally changing to mottled gray-red; fossils weathering out at 3 ft (0.9 m) and 7 ft (2.1 m) above base; ?creodont skull and jaws (CM collections) (UCM Loc. 81023) 7.0 (2.1)

2. Sandstone, gray, fine grained, tabular, laminated bedding 0.5 (0.2)

*1B. Mudstone, gray, calcareous; mottled red horizons at 3 and 4.5 ft above base of unit; fossils at 4.0 ft (1.2 m) above base and at base of unit; sharp contact with lower unit (UCM Loc. 81022, ant hill collection) 6.5 (2.0)

*1A. Mudstone, gray, calcareous glaebules at 1.5 ft (0.4 m) above base; fossils at 2.0 ft (0.6 m) above base (UCM Loc. 80101) 3.0 (0.9)

Base not exposed.

Section 10. Davis Ranch. Partial section of Lost Cabin Member of the Wind River Formation. Measured in NW ¼ NW ¼ Sec. 6, T.37N., R.87W.

Wind River Formation, Lost Cabin Member:

14. Mudstones and sandstones, alternating .... 10.0+ (3.0)

13. Sandstone, gray, conglomeratic at base; apron-channel geometry; conglomerate contains intraformational glaebules and probable Precambrian clasts, calcareous canonball concretions 17.5 (5.3)

*12. Mudstones and sandstones, alternating; fossil fragments 1 ft (0.3 m) above base (no locality number) 24.0 (7.3)
*11. Mudstone, gray, contains numerous calcareous glaebules and pedotubules, well preserved mammalian fossils (UCM Loc. 79041) 4.0 (1.2)
*10. Sandstones and mudstones, alternating; fossil fragments at 2.0 ft (0.6 m) above base (no locality number) 30.0 (9.2)
9. Ash, weathers white, resistant, laterally extensive, good horizon marker 2.0 (0.6)
*8. Sandstone, greenish gray, medium to coarse grained, multistoried, apron-channel geometry; highly calcareous glaebules at top, some gypsum crystals (UCM Loc. 81027, ant hill collection) 19.5 (5.9)
*7B. Mudstone, gray, resistant; forms low rounded knolls; associated skeletal elements of single individuals (UCM Loc. 81026) 4.5 (1.4)
7A. Sandstone, greenish gray, channeled 1.0 (0.3)
*6. Mudstone, alternating red and gray tabular units, some red-gray mottling, silty and sandy; calcareous glaebules, associated skeletal elements of single individuals; laterally equivalent to apron-channel sandstone which cuts into lower unit (UCM Loc. 81043) 4.5 (1.4)
5. Sandstone, gray, fine grained, predominantly quartz, calcareous; red mottled at top 3.5 (1.0)
4. Mudstone, mottled red-grayish green; lower 2.0 ft (0.6 m) mottled purple-green; middle 1.0 ft (0.3 m) mottled brown-yellow with iron oxide glaebules; upper 2.5 ft (0.8 m) mottled green-red (same bed as Measured Section 9, Unit 7) 5.5 (1.7)
*3. Mudstone, brick-red, calcareous; greenish gray calcareous glaebules and pedotubules common in upper part, fossiliferous throughout (UCM Loc. 79042) 12.5 (3.8)
2. Mudstone, mottled red-gray 5.0 (1.5)
*1. Mudstone, gray, silty; upper 3.0 ft (0.9 m) contains more sand; fossils and calcareous glaebules in lower 4.0 ft (1.2 m) (UCM Loc. 81023) 7.0 (2.1)

Base not exposed.

Measured Section 11. Davis Ranch East. Partial section of Wind River Formation. NW ¼ NE ¼ Sec. 6, T.37N., R.87W.

Wind River Formation, Lost Cabin Member:

12. Claystone, dark gray 2.0 (0.6)
*11. Mudstone, gray, turtle shell fragments (no locality number) 3.0 (0.9)

10. Claystone, gray, fissile; sharp lower contact 1.0 (0.3)
*9. Sandstone, greenish gray, medium to coarse grained, micaceous; sharp lower contact; turtle shell and crocodile fragments (no locality number; correlates with Measured Section 12, Unit 4) 1.0 (0.3)
8. Claystone, dark gray, calcareous, fissile; upper 4.0 ft (1.2 m) silty mudstone 6.0 (1.8)
7. Mudstone, dark gray 2.5 (0.8)
6. Mudstone, light yellowish brown, calcareous, sandy; forms semi-resistant ridge; sharp lower contact 1.0 (0.3)
5. Mudstone, dark gray, sandy 4.5 (1.4)
4. Mudstone, light yellowish brown, sandy 3.0 (0.9)
*3. Mudstone, gray, silty, intraformational claystone pebbles at base, sharp lower contact; mammalian skeletal fragments (no locality number) 9.5 (2.9)
2. Sandstone, yellowish brown, medium grained, predominantly quartz sand, calcareous; calcareous pedotubules in upper part; grades upward into mudstone 6.5 (2.0)
*1. Mudstone, gray, sandy; noncalcareous at base becoming more calcareous toward top; calcareous glaebules at 5 ft (1.5 m) above base with dark brown interior (UCM Loc. 81028) 11.5 (3.5)

Base not exposed.

Measured Section 12. Davis Ranch East. Partial section of Lost Cabin Member of Wind River Formation. SE ¼ NE ¼ NE ¼ Sec. 6, T.37N., R.87W.

Wind River Formation, Lost Cabin Member:

10. Mudstone, gray 10.5 (3.2)
9. Sandstone, gray, medium to coarse grained, poorly sorted, calcareous, apparent gradational contact with upper unit 1.0 (0.3)
8. Mudstone, gray 9.5 (2.9)
*7. Mudstone, red, lower part calcareous glaebules and pedotubules, upper part orange-red-yellow-green mottling; highly weathered (UCM Loc. 80100, unit equivalent to Measured Section 9, Units 6 and 7) 14.0 (4.2)
6. Mudstone, gray, highly weathered (equivalent to Measured Section 9, Units 1 to 5) 21.0 (6.3)
*5. Mudstone and sandstone, gray; unit shifts from sandstone at base to mudstone to claystone to mudstone at top; calcareous glaebules and turtle shell and crocodile fragments (no locality number) 7.0 (2.1)

4. Sandstone, grayish green, medium to coarse grained, micaceous, calcareous (correlates with Measured Section 11, Unit 9) 0.5 (0.2)
3. Mudstone, gray, silty 1.5 (0.5)
2. Sandstone, light yellowish brown, fine to medium grained, noncalcareous 3.0 (0.9)
1. Mudstone, gray, silty 7.0 (2.1)

Base not exposed.

BUCK SPRING STRATIGRAPHIC SECTION

Measured Section 13. Buck Spring stratigraphic section, probable type area of the Lost Cabin Member of the Wind River Formation. Partial section of Lost Cabin Member measured in SW ¼ Sec. 15, T.38N., R.89W. Beds nearly horizontal, slight dip to south.

Wind River Formation, Lost Cabin Member:

17. Sandstone, yellowish brown, apron-channel geometry 10.0 (3.0)
16. Mudstone, greenish gray 9.0 (2.7)
15. Mudstone, mottled red-gray 5.0 (1.5)
14. Mudstone, greenish gray 9.0 (2.7)
*13. Mudstone, mottled red-green; calcareous glaebules and pedotubules; mottling occurs as thin striae (?rhizoliths); associated skeletal elements of mammal individuals (UCM Loc. 81033) 5.0 (1.5)
12. Mudstone, greenish gray 4.5 (1.4)
*11. Mudstone, alternating grayish red (5 R 4/2) and greenish gray (5 G 7/1) bands, thinly laminated, silty, very little sand; color bands vary from several centimeters to approximately .3 m thick; numerous calcareous glaebules, some calcareous pedotubules; some articulated skeletal remains of mammals (UCM Loc. 81032) 10.5 (3.2)
*10. Mudstone, same lithology as Unit 11, with well-defined red horizon at top (UCM Loc. 81031) 4.0 (1.2)
*9. Sandstone, green, fine to very coarse grained, calcareous; apron-channel geometry; abraided and unabraided bone fragments (UCM Loc. 81030) 3.0 (0.9)
*8. Mudstone, grayish red (10 R 4/2) with very pale green, anastomizing striae (10 G 8/3) (?rhizoliths); fossils extremely abundant; calcareous glaebules at base. Same unit as Granger's (1910) dark red stratum and Unit 2, Measured Section 9 of Tourtelot (in Keefer, 1965) (UCM Loc. 81029) 12.0 (3.6)

7. Sandstone, yellow-brown, fine to medium grained; grades from well sorted medium grained sandstone at base to poorly sorted mudstone at top 8.5 (2.6)
6. Mudstone, gray 6.5 (2.0)
5. Sandstone, gray, fine to medium grained, poorly sorted, micaceous, crossbedded 3.5 (1.0)
4. Mudstone, purple mottled, calcareous glaebules throughout, septarian concretions 3.0 (0.9)
*3. Sandstone and mudstone, yellow-brown; calcareous pedotubules; turtle and crocodilian fragments at top (no locality number) 9.0 (2.7)
2. Mudstone, gray, silty 4.5 (1.3)
1. Sandstone, yellowish green, micaceous; preferentially cemented 6.5 (2.0)

Base not exposed.

DEADMAN BUTTE STRATIGRAPHIC SECTIONS

Measured Section 16. Deadman Butte Area. Partial section of Red Creek Facies of Wind River Formation. NE ¼ NE ¼ NE ¼ Sec. 33, T.38N., R.87W.

Wind River Formation:

4. Sandstone, yellow-brown, medium grained, calcareous; dark brown iron oxide stain at base .... 1.0+ (0.3)
*3. Shale, carbonaceous, very dark brown, turtle shell fragments (no locality number) 4.0 (1.2)
2. Mudstone, gray with yellow-orange mottling; silty 11.0 (3.3)
1B. Vegetation cover, poorly exposed 30.0 (9.1)
*1A. Mudstone, light gray, sandy; black bone fragments (no locality number) 10.0 (3.0)

Base not exposed.

Measured Section 17. *Palaeosyops* jaw locality, Deadman Butte Area. Partial section of Lost Cabin Member of Wind River Formation. SW ¼ SW ¼ SW ¼ Sec. 27, T.38N., R.87W.

Wind River Formation, Lost Cabin Member:

Upper Gray Sequence (?):

5. Mudstone, gray 9.0 (2.7)
4. Sandstone, dusky yellow (5 Y 6/4) with dark yellowish orange striae (10 YR 6/6); fine grained, well sorted, tabular 2.0 (0.6)
*3. Mudstone, grayish olive (10 Y 4/2), silty; upper part predom-

inantly clay; calcareous glaebules at 1.0 ft (0.3 m) above base (UCM Loc. 81011) 14.0 (4.2)
2. Sandstone, dusky yellow (10 Y 6/4) to pale olive (5 Y 6/2); very fine grained, calcareous 3.5 (1.1)
*1. Mudstone, light grayish green (5 G 7/1), silty, some fine sand; small calcareous pellet-shaped glaebules; calcareous rhizoliths and intraformational burrows; popcorn weathering, weathers bluish gray in outcrop; associated *Palaeosyops borealis* skeletal elements, abundant mammal fossils; calcified wood fragments and carbonized and noncarbonized plant impressions (UCM Loc. 81010) 16.5 (5.0)

Base not exposed.

Measured Section 17a. *Palaeosyops* jaw locality, Deadman Butte Area. Partial section of Lost Cabin Member of Wind River Formation. SW ¼ SW ¼ SW ¼ Sec. 27, T.38N., R.87W.

Wind River Formation, Lost Cabin Member:

9. Mudstone, gray, silty; silt increases in unit up to 15 ft (4.5 m) above base; at 15.0 ft (4.5 m) sediments are dark gray claystone as in Unit 5 . . . . 24.0 (7.2)
8. Sandstone, yellowish gray to dusky yellow, fine grained, calcareous; semi-resistant; upper part contains more medium to coarse sand grains and is micaceous 2.0 (0.6)
*7. Mudstone, gray, calcareous; invertebrate and vertebrate fossil fragments at 2.0 ft (0.6 m) above base (UCM Loc. 81011) 22.0 (6.6)
6. Sandstone, pale olive (10 Y 6/2), fine grained, calcareous, vertically weathering 3.0 (0.9)
5. Claystone, gray 1.0 (0.3)
4. Mudstone, gray, silty; calcareous glaebules 4.0 (1.2)
3. Sandstone, gray, crossbedded 3.5 (1.0)
*2. Mudstone, gray, bluish cast from distance, calcareous glaebules (UCM Loc. 81010) 20.5 (6.2)
1. Sandstone, light olive gray (5 Y 5/2), fine to medium grained, angular to subangular quartz grains 4.0 (1.2)

Base not exposed.

Measured Sections 18 and 19. Deadman Butte Area. Partial section of Red Creek Facies and Lost Cabin Member of Wind River Formation. W ½ Sec. 22, T.38N., R.87W. Dip to 10 degrees South, N. mag 60 degrees East, 22 June 1981.

Wind River Formation, Lost Cabin Member:

Variegated Sequence:

19. Sandstone, light yellowish gray, medium to coarse subangular quartz, feldspar and lithic fragments, calcareous, crossbedded; iron oxide concretions; apron-channel geometry; channeled into underlying units 30.0 (9.0)
*18. Claystone, dark bluish gray; associated skeletal elements of *Coryphodon* and crocodile (UCM Loc. 80090) 2.0 (0.6)
17. Shale, carbonaceous, dark grey 1.0 (0.3)
*16. Mudstone, mottled red-gray, calcareous (UCM Loc. 80088) 8.0 (2.4)
15. Sandstone, light olive to white, fine grained, calcareous; orange mottles at top of unit; calcareous glaebules and pedotubules 5.0 (1.5)
14. Sandstone, mottled red-yellow-gray, fine grained, poorly sorted; gypsum crystals litter surface; weathers brick red 9.0 (2.7)

Wind River Formation, Red Creek Facies:

13. Mudstone, alternating yellowish gray and gray bands; gypsum crystals litter surface 35.0 (10.7)
12. Mudstone, dark gray 0.5 (0.2)
11. Sandstone, light olive green, medium grained, quartz arenite 1.0 (0.3)
10. Mudstone, dark gray 1.5 (0.5)
*9. Sandstone, yellowish gray, very fine to fine, well rounded to subrounded quartz grains, calcareous, poorly sorted; calcareous glaebules and pedotubules; fossiliferous at top of unit (UCM Loc. 80089, probable correlate of UCM Loc. 80062) 3.5 (1.1)
8. Mudstone, greenish gray, sandy 3.0 (0.9)
7. Sandstone, light olive, very fine to fine grained; some pebble conglomerate lenses 3.5 (1.1)
6. Mudstone, dark olive gray, silty 6.5 (2.0)

Offset

5. Sandstone, grayish yellow green (5 GY 7/2), very fine to fine rounded quartz grains; perferentially cemented; lenticular conglomerates with chert and porcelainite pebble clasts; calcareous rhizoliths, reticulate glaebule-pedotubule masses; pedotubules in vertical position and in horizontal zones 25.0 (7.6)

4. Claystone, olive gray (5 Y 4/1); intraformational mudstone clasts from Unit 3 at base 1.0 (0.3)
3. Mudstone, greenish gray to pale olive, silty, micaceous; sharp lower contact 6.5 (2.0)
2. Mudstone, pale olive, some quartz sand grains which are all well rounded 2.5 (0.8)
*1B. Mudstone, yellowish gray to pale olive, sandy, micaceous; sand decreases toward top of bed, fossil vertebrates in lower 3.0 ft (0.9 m) (UCM Loc. 81009) 19.0 (5.7)
*1A. Sandstone, gray, poorly sorted; calcareous rhizoliths, pedotubules and glaebules in upper part; conglomeratic lenses of chert and porcelainite with some mammal bone fragments; numerous isolated bone and teeth fragments (UCM Loc. 81008) .... 5.0+ (1.5)

Base not exposed.

Measured Section 20. Deadman Butte Area. Partial section of Red Creek Facies and Lost Cabin Member of the Wind River Formation. E ½ Sec. 22, T.38N., R.87W.

Wind River Formation, Lost Cabin Member:

Variegated Sequence:

11. Sandstone, yellow-brown; highly weathered (equivalent to Measured Sections 18 and 19, Unit 19) .... 10.0+ (3.0)
10. Mudstone, red, highly weathered 1.0 (0.3)
9. Sandstone, yellow-brown, highly weathered 4.0 (1.2)
8. Mudstone, red, highly weathered 3.5 (1.1)
7. Sandstone, light gray, highly weathered 3.5 (1.1)
6. Mudstone, light brown, sandy; gypsum crystals litter surface 4.0 (1.2)
5. Shale, carbonaceous 3.0 (0.9)

Wind River Formation, Red Creek Facies:

4. Mudstone, dark gray to yellowish brown, gypsum crystals litter surface 10.0 (3.0)
3. Mudstone, light gray 12.5 (3.8)
*2. Mudstone, yellowish olive, some quartz sand grains; numerous fossil vertebrates randomly distributed within unit; fossiliferous at 5 to 15 ft (1.5 to 4.6 m); laterally shifts to sandstone with conglomeratic lenses of Mesozoic clasts (UCM Loc. 80062) 21.5 (6.5)
*1. Conglomerate, clay ball, carbonaceous, dark gray to black;

thinly laminated; gypsum crystals, turtle shell fragments somewhat abundant (no locality number) 1.0 (0.3)

Base not exposed.

Measured Section 21. West of Rainbow Butte and Red Creek. Partial section of Wind River Formation. SW ¼ Sec. 22, T.38N., R.88W.

Wind River Formation:

9. Sandstones and conglomerates, yellowish green, crossbedded; channeled into lower units; Precambrian and Flathead clasts in conglomerates 9.0 (2.7)
*8. Mudstones, gray, sandy, calcareous, calcareous glaebules and vertical pedotubules, small bone fragments (UCM Loc. 81040) 20.0 (6.1)
7. Sandstone and sandy mudstones, gray to yellow-brown, alternating, matrix supported conglomerate with probable Paleozoic and Precambrian cobbles; lower contact iron stained 21.0 (6.4)
6. Mudstone, gray; calcareous glaebules 1.0 (3.0)
5. Sandstone, reddish brown, matrix supported conglomerate at top with dolomite, limestone and sandstone clasts of probable Paleozoic origin and Precambrian clasts, channeled into lower unit 16.0 (4.9)
4. Mudstone, greenish gray; calcareous glaebules; unit purple mottled at top 7.0 (2.1)
3. Sandstone, yellowish gray, multistoried, small scale crossbedding; pebble conglomerate lenses; conglomerate clasts derived from Paleozoic and Precambrian strata; becomes coarser at top 13.0 (3.9)
2. Mudstone, gray 8.0 (2.4)
1. Carbonaceous shale, chocolate brown 2.0 (0.6)

FOSSILIFEROUS HORIZONS

Each fossiliferous horizon from which mammalian fossils were recovered is listed in numerical order according to the UCM locality number. The location of a fossiliferous horizon is given as the measured section (MS) number, unit (U) position within that measured section and legal location. Stucky (1984) provides the position of each fossiliferous horizon within a measured section (Fig. 4) and a list of mammalian taxa recovered from the horizons (Tables 3 and 4).

UCM Loc. 79039: "Unit 13" Blue Croc Bed.

Location.—MS-1, U-14; Sec. 17–20, T.38N., R.87W.

Horizon description.—Bioturbated, gray claystone with calcareous glaebules and pedotubules.

Material preserved.—Articulated and scattered skeletal elements of single individuals, turtle shell fragments, isolated teeth, coprolites, burrows.

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect, excavation.

Comments.—Locality is exposed for one km. In several places associated bones of single crocodile and *Coryphodon* individuals can be found, some, in part, articulated. Some elements show concoidal depressions suggestive of carnivore activity. *In situ* bones are black with no mineralogical surface coating. Crocodiles and turtles are most abundant.

UCM Loc. 79040: Someday locality.

Location.—MS-1, U-61; SE ¼, Sec. 19, T.38N., R.87W.

Horizon description.—Bioturbated, mottled red-gray mudstone, with calcareous glaebules and pedotubules occurring at specific horizons; intraformational burrows and some rhizoliths present.

Material preserved.—Disarticulated and scattered partial skeletons of *Hyrachyus,* numerous isolated turtle and crocodile elements, one complete shell of trionychid, isolated limb elements and teeth of mammals and lower vertebrates common, eggshells, some coprolites with gar scales and lizard scutes, small meniscate burrows, rare silicified plant materials.

Paleoenvironment.—Overbank/paleosol; abundant aquatic and semiaquatic vertebrate materials suggest near permanent body of water.

Methods.—Surface prospect, screen wash, excavation.

Comments.—Taphonomic data collected during excavation indicate random orientation for long bones. Many bone fragments are vertical. Burrows are filled with intraformational sediment and oriented vertically as are many rhizoliths. *In situ* bones are black in color with no mineralogical surface coating. Elements are exceptionally well preserved and some show concoidal depressions indicating carnivore activity. Crocodiles and turtles are extremely common. Isolated teeth are the most common mammalian element.

UCM Loc. 79041: Sullivan Ranch Unit 10, AMNH Davis Ranch locality, in part.

Location.—MS-1979, U-10; top of hill 6164, NW ¼, Sec. 6, T.37N., R.87W.

Horizon description.—Gray mudstone with calcareous glaebules and pedotubules.

Material preserved.—Primarily mammalian remains. Some associated skeletal elements of single individuals (snake, large and small mammal). *Knightomys* partial skeleton, including partial skull and both lower jaws with articulated vertebrae and hind limb elements. Few turtle or crocodile remains.

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect.

Comments.—Jaw materials of mammals are very well preserved. The bone is white with chocolate brown colored teeth. Bones may have a calcareous glaebule covering. Very few isolated teeth are found. Associated skeleton of *Knightomys* may be from a coprolite, owl pellet or mummified carcass. Some materials in AMNH from "Davis Ranch" come from this fossiliferous horizon and can be distinguished from other fossils at this locality by their preservation.

UCM Loc. 79042: UCM Sullivan Ranch Bed 2; AMNH Davis Ranch locality; PU 5 mi N and E of Arminto; CM 8–15′ red bed, Guthrie's Locality 1, Sullivan Ranch.

Location.—MS-1979, U-2; Sec. 6, T.37N., R.87W.

Horizon description.—Bright prominent brick red mudstone. Mottled red-brown-yellow at top, lateral to large, shoestring channel sandstone, abundant calcareous glaebules and pedotubules.

Material preserved.—Some associated mammal and lower vertebrate skeletal materials of single individuals. Well preserved mammal jaws abundant; eggshell, gastropod casts and silicified wood in small amounts. Articulated specimens of burrowing vertebrates (snakes, amphisbaenids).

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect, quadrant sampling.

Comments.—This fossiliferous horizon is the most fossiliferous of any horizon in the Lost Cabin Member; easily several thousand specimens known. Most mammals represented by at least 10 specimens. Jaws are fragmentary and reddish or orange-white in color, with teeth that have black, very dark brown or translucent gray enamel and white dentine. Teeth are often covered with calcareous glaebule mass which often infills alveoli or covers areas where the enamel has been spalled off, that was lost prior to burial. Some remains show subaerial weathering. Abundant collections from this horizon in AMNH, CM and PU. Fossil materials can be easily recognized by their color.

UCM Loc. 79043: Sullivan Ranch Bed 4.

Location.—MS-1979, U-4; Sec. 6, T.37N., R.87W.

Horizon description.—Mottled red-gray mudstone, semi-resistant with calcareous glaebules; lateral to small shoestring channel sandstone.

Material preserved.—Primarily jaw and skull fragments of mammals and relatively complete turtle shells. Some associated bird bones. Isolated teeth somewhat common.

Paleoenvironment.—Overbank/paleosol; lateral to shoestring channel.

Methods.—Surface prospect.

Comments.—This fossiliferous horizon is difficult to distinguish without careful scrutiny from UCM Loc. 79042. Some associated bones of single mammal individuals and well preserved turtles were found, including a crushed skull of *Heptodon ventorum* with a dentary showing predepositional weathering. Jaw elements have gray or black, never white, bone and brown to black teeth. A calcareous glaebule mineral covering on fossils is common. The unit can be traced directly into a shoestring channel sandstone that is channeled into the fossiliferous horizon of UCM Loc. 79042. Fossil vertebrates are rare in the channel but become more common laterally in finer grained sediments.

UCM Loc. 79045: Jane's locality.

Location.—MS-1, U-8; Sec. 17, 20, T.38N., R.87W.

Horizon description.—Top of fine to medium quartz sandstone.

Material preserved.—Isolated teeth of mammals and lower vertebrates, one dentary of an anguid, some limb elements and turtle shell fragments.

Paleoenvironment.—?Braidplain.

Methods.—Surface prospect.

UCM Loc. 80061: Lightning Butte locality.

Location.—MS-1, U-56; SW ¼, Sec. 19, T.38N., R.87W.

Horizon description.—Bioturbated gray mudstone with calcareous glaebules and pedotubules.

Material preserved.—Isolated teeth, jaws and limb elements of mammals; abundant amphibian bones (primarily anuran), snake vertebrae and anguid scutes. Rare turtle, crocodile, and fish elements.

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect, screen wash.

Comments.—This fossiliferous horizon preserves an unusual assemblage of species, many of which are known only from this horizon. Rare mammals include *Armintodelphus blacki,* Adapisoricidae, probably new, and *Huerfanius* sp. The largest mammal recovered is *Orohippus* sp. Abundant anuran fossils include most all skeletal elements of several species. This fossiliferous horizon undoubtedly preserves an assemblage of unique ecology. Bones are natural color and most teeth are translucent gray or light brown in color. This fossiliferous horizon has the potential for yielding well preserved material when excavated.

UCM Loc. 80062: Deadman Butte locality.

Location.—MS-20, U-2 (lower part); E ½, Sec. 22, T.38N., R.87W.

Horizon description.—Very fine grained, poorly sorted quartz arenite and mudstone. Most sand particles are very well rounded.

Material preserved.—Abundant isolated mammalian teeth and bone fragments ranging from *Lambdotherium* to *Pauromys* size. Turtle shell fragments and lizard remains common. Crocodilian elements rare and from very small individuals.

Paleoenvironment.—Braidplain.

Methods.—Surface prospect, screen wash.

Comments.—Isolated mammalian teeth are extremely abundant, representing approximately 60 mammalian species. Only four jaw fragments containing teeth are known, all of which are identified as *Shoshonius cooperi.* Amphibian, lizard and turtle remains are common, whereas crocodile materials are rare and represented by small individuals. Pedogenic structures are not known from this locality. Fossils are randomly distributed within this fossiliferous horizon (see Stucky and Krishtalka, 1982).

UCM Loc. 80063: Kevin's locality.

Location.—SE ¼, NW ¼, T.37N., R.87W.

Horizon description.—Light colored sandstone.

Material preserved.—Abundant turtle and crocodile, some large mammals. Small mammals rare.

Paleoenvironment.—Fluvial system, presumably a stream channel.

Methods.—Surface prospect.

Comments.—Many bone and teeth elements have been abraided by stream transport. Jaw remains often show post-depositional distortion.

UCM Loc. 80064A–C: Sally's Catfish locality.

Location.—MS-1, U-89–91; Sec. 30, T.38N., R.87W.

Horizon description.—Three fossiliferous horizons are recognized, only two of which preserve fossil vertebrates. UCM Loc. 80064-A is the lowermost horizon and is a claystone which is tabular and laterally extensive. UCM Loc. 80064-B is a carbonaceous shale that is conformable on UCM 80064-A. UCM 80064-C is a volcaniclastic paraconglomerate.

Material preserved.—UCM Loc. 80064-A preserves aquatic vertebrates. UCM Loc. 80064-B preserves plant remains and UCM Loc. 80064-C preserves rare teeth and limb fragments of mammals and turtle shell fragments.

Paleoenvironment.—80064-A is a probable lacustrine unit, 80064-B is probably paludal and 80064-C probably represents a mudflow deposit.

Methods.—Surface prospect, screen wash.

Comments.—Catfish spines and small fish bones are extremely abundant in 80064-A. Fossils are randomly distributed within the unit.

UCM Loc. 80065: Rainbow Butte locality.

Location.—MS-3, U-1, 2, 4, 5, 6, 8, 10, 11, 14, 15, 17; NE ¼, NW ¼, Sec. 19, T.38N., R.87W.

Horizon description.—Fossils recovered from eleven different horizons. See Measured Section 3.

Material preserved.—Primarily fossil vertebrates but also including some eggshell fragments and invertebrates.

Paleoenvironment.—Most fossiliferous horizons are overbank/paleosol deposits, although some fossils occur in conglomerates and sandstones (Units 6 and 15) and are probably stream transported.

Methods.—Surface prospect.

Comments.—The Rainbow Butte locality preserves eleven distinct fossiliferous horizons in a vertical section of 90 ft (27 m). Associated partial skeletons of a mesonychid, snake and crocodilian were collected. In Unit 7 an unusual abundance of amphibian remains of several individuals was recovered in a very small area. These amphibian bones may represent a predator accumulation.

UCM Loc. 80083: West Red Creek locality.

Location.—NE ¼, NW ¼, Sec. 18, T.38N., R.87W.

Horizon description.—Gray claystone.

Material preserved.—Primarily isolated teeth and bones of mammals, turtles and crocodiles. Well preserved coprolites.

Paleoenvironment.—Overbank deposit.

Methods.—Surface prospect, screen wash.

Comments.—This locality is probably the lowest, stratigraphically, in the Red Creek-Deadman Butte area. Although the fauna is not diverse, the lack of *Lambdotherium* and any exotic taxa known from the *Palaeosyops borealis* zone suggests this locality may be Lysitean in age. Several limb elements of *Coryphodon* sp. may be from the same individual.

UCM Loc. 80088.

Location.—MS-18 and 19, U-16; Sec. 22, T.38N., R.87W.

Horizon description.—Mottled red-gray mudstone.

Material Preserved.—Rare fossil mammals and turtle shell fragments.

Paleoenvironment.—Paleosol?

Methods.—Surface prospect.

UCM Loc. 80089.

Location.—MS-18 and 19, U-9; Sec. 22, T.38N., R.87W.
Horizon description.—Yellowish gray sandstone.
Material preserved.—Isolated teeth and bones of mammals.
Paleoenvironment.—Braidplain or paleosol.
Methods.—Surface prospect.
Comments.—Highest occurrence of *Lambdotherium* in Deadman Butte sections. Probably correlates with UCM Loc. 80062.

UCM Loc. 80090.

Location.—MS-18 and 19, U-18; Sec. 22, T.38N., R.87W.
Horizon description.—Dark bluish-gray claystone.
Material preserved.—Large vertebrates, including associated partial skeleton of *Coryphodon* sp. and a crocodile.
Paleoenvironment.—Unknown.
Comments.—Lowest occurrence of *Palaeosyops borealis.*

UCM Loc. 80092.

Location.—Sec. 27, T.38N., R.88W.
Horizon description.—Red mottled mudstone at base of exposure.
Material preserved.—Isolated teeth and bones. One badly damaged partial skeleton of *Coryphodon* seen but not collected.
Paleoenvironment.—Overbank/paleosol.
Methods.—Surface prospect.

UCM Loc. 81008: *Viverravus* locality.

Location.—MS-18 and 19, U-1A; Sec. 22, T.38N., R.87W.
Horizon description.—Gray sandstone with rhizoliths and burrows at top.
Material preserved.—Mostly isolated teeth and bone fragments of mammals, but some well preserved jaw materials. Few turtle or crocodile specimens.
Paleoenvironment.—Braidplain.
Methods.—Surface prospect, screen wash (Tylor 35).
Comments.—Lowest locality in Deadman Butte sections. Teeth of the same individual of *Phenacodus primaevus* found *in situ.* Only traces of the jaw bone remained, suggesting diagenetic dissolution of some bone material. *In situ* teeth and bone are randomly distributed in this fossiliferous horizon (See Stucky and Krishtalka, 1982).

UCM Loc. 81009.

Location.—MS-18 and 19, U-1B; Sec. 22, T.38N., R.87W.
Horizon description.—Gray mudstone.

Material preserved.—Isolated mammal teeth found as surface lag.
Paleoenvironment.—Overbank.
Methods.—Surface prospect.

UCM Loc. 81010: *Palaeosyops* jaw locality.

Location.—MS-17a, U-2; SW ¼, Sec. 27, T.38N., R.87W.
Horizon description.—Gray mudstone with calcareous glaebules.
Material preserved.—Well preserved mammal jaw remains. Associated *Palaeosyops borealis* bones. Several hundred mammal and lizard bones, one turtle shell fragment. Calcareous fossil wood.
Paleoenvironment.—Overbank/paleosol.
Methods.—Surface prospect.
Comments.—Species known only from this locality in the Wind River Formation include *Washakius* n. sp., *Sciuravus* n. sp., and cf. *Copelemur* sp. Probably the youngest fossiliferous horizon with abundant mammal remains in the northeastern exposures of the Wind River Formation.

UCM Loc. 81017.

Location.—MS-8, U-2; Sec. 36, T.38N., R.87W.
Horizon description.—Red mudstone.
Material preserved.—Single astragalus of *Palaeosyops borealis.*

UCM Loc. 81018.

Location.—MS-8, U-4; Sec. 36, T.38N., R.88W.
Horizon description.—Mottled gray mudstone.
Material preserved.—Partial skeletons of varanid (UCM collections) and *Palaeosyops borealis* (very fragmentary, CM collections).

UCM Loc. 81019: Kevin's *Notharctus* Bed.

Location.—MS-8, U-5; Sec. 36, T.38N., R.88W.
Horizon description.—Mottled red mudstone with calcareous pedotubules and glaebules.
Material preserved.—Associated skeletal elements of a crocodile and primate. Fairly abundant mammalian remains.

UCM Loc. 81022.

Location.—MS-9, U-1B; Sec. 6, T.38N., R.87W.
Horizon description.—Ant hill collection; gray mudstone.
Material preserved.—Isolated elements of vertebrates.
Paleoenvironment.—Unknown.
Methods.—Surface prospect, screen wash (Tylor 12).
Comments.—Some bone elements found *in situ* lateral to ant hill.

UCM Loc. 81023.

Location.—MS-9, U-3; Sec. 6, T.37N., R.87W.

Horizon description.—Gray mudstone.

Material preserved.—Isolated bones of mammals. One oxyaenid skull and lower jaws *in situ* (CM collections).

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect, excavation.

Comments.—All teeth observed have very dark brown enamel and dentine.

UCM Loc. 81026.

Location.—MS-10, U-7; Sec. 6, T.37N., R.87W.

Horizon description.—Gray mudstone.

Material preserved.—Rare isolated bones. One partial skeleton of a carnivorous mammal (CM collections).

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect.

UCM Loc. 81027.

Location.—MS-10, U-8; Sec. 6, T.37N., R.87W.

Horizon description.—Ant hill in sandstone.

Material preserved.—Isolated teeth and bones of vertebrates.

Paleoenvironment.—Fluvial system?

Methods.—Surface prospect, screen wash (Tylor 12).

UCM Loc. 81028.

Location.—MS-11, U-1; Sec. 6, T.37N., R.87W.

Horizon description.—Gray mudstone.

Material preserved.—One isolated tooth of *Trogosus* sp.

UCM Loc. 81029: Buck Spring "dark red stratum" (Granger, 1910).

Location.—MS-13, U-8, Sec. 15, T.38N., R.89W.

Horizon description.—Mottled purple mudstone with calcareous glaebules.

Material preserved.—Extremely abundant turtle and crocodile remains and isolated teeth and bones of mammals. Very few jaw remains. No associated skeletal elements of single individuals known.

Paleoenvironment.—Overbank/paleosol?

Methods.—Surface prospect.

Comments.—This is the "dark red stratum" of Granger (1910) and "maroon shale" horizon of Guthrie (1971). Fairly abundant remains of *Lambdotherium* are known from this horizon. No specimens of *Palaeosyops* or *Hyrachyus* are known. Teeth are always black in color.

Very few jaw remains are known, all of which show post-depositional distortion.

UCM Loc. 81030.

Location.—MS-13, U-9; Sec. 15, T.38N., R.89W.

Horizon description.—Green apron-channel sandstone.

Material preserved.—One lower jaw of *Phenacodus primaevus* and turtle shell fragments.

Paleoenvironment.—Stream channel deposit.

Methods.—Surface prospect.

UCM Loc. 81031.

Location.—MS-13, U-10; Sec. 15, T.38N., R.89W.

Horizon description.—Red and gray banded mudstone.

Material preserved.—Fragmentary skull and lower jaw of *Notharctus* sp., cf. *N. venticolus* and jaws of mammals. Limb elements extremely rare.

Paleoenvironment.—Unknown, but probably overbank deposit.

Methods.—Surface prospect.

UCM Loc. 81032.

Location.—MS-13, U-11; Sec. 15, T.38N., R.89W.

Horizon description.—Red and gray banded mudstone.

Material preserved.—Fragmentary skeleton of *Palaeictops multicuspis.*

Paleoenvironment.—Unknown, but probably overbank deposit.

Methods.—Surface prospect.

UCM Loc. 81033.

Location.—MS-13, U-14; Sec. 15, T.38N., R.89W.

Horizon description.—Mottled red mudstone with calcareous glaebules and pedotubules.

Material preserved.—Numerous mammal postcrania. Associated pair of lower jaws of *Coryphodon* sp. Teeth and jaws are rare.

Paleoenvironment.—Overbank/paleosol.

Methods.—Surface prospect, excavation.

Comments.—The abundant postcrania but rare jaw remains are a paradox.

UCM Loc. 81034.

Location.—NE ¼, Sec. 17, T.38N., R.89W.

Horizon description.—Mottled red mudstone with calcareous glaebules.

Material preserved.—Isolated bones and teeth of vertebrates.
Paleoenvironment.—Overbank/paleosol.
Methods.—Surface prospect.

UCM Loc. 81035.

Location.—NE ¼, Sec. 15, T.38N., R.89W.
Horizon description.—Mottled red mudstone with calcareous glaebules.
Material preserved.—Isolated bones, jaws and teeth of vertebrates.
Paleoenvironment.—Overbank/paleosol.
Methods.—Surface prospect.

UCM Loc. 81040: Croc Skull locality.

Location.—MS-21, U-8; Sec. 22, T.38N., R.88W.
Horizon description.—Gray mudstone.
Material preserved.—Isolated teeth and bones of vertebrates. One fragmentary skull of a small crocodile.
Paleoenvironment.—Unknown.
Methods.—Surface prospect.
Comments.—Paleozoic clasts are common in conglomerates both above and below this horizon, suggesting that the sequence of strata in this area may be referrable to the Lysite Member of the Wind River Formation. No age assignment can be made on the basis of the fossil assemblage.

UCM Loc. 81047.

Location.—SW ¼, Sec. 31, T.38N., R.87W.
Horizon description.—Gray mudstone.
Material preserved.—Isolated teeth and bones of vertebrates.
Paleoenvironment.—Overbank.
Methods.—Surface prospect.
Comments.—Correlates with UCM Loc. 81022 to 81023.

UCM Loc. 81048.

Location.—NW ¼, Sec. 12, T.37N., R.88W.
Horizon description.—Gray mudstone with calcareous glaebules and pedotubules.
Material preserved.—Associated skeletal elements of *Hyrachyus* sp., cf. *H. eximius,* teeth of *Palaeosyops borealis* and *Paramys.*
Paleoenvironment.—Overbank/paleosol.
Methods.—Surface prospect.
Comments.—Correlates with UCM Loc. 79041.

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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. IX. BATS OF THE GENUS *TONATIA* (MAMMALIA: CHIROPTERA) IN SURINAME

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Abstract

Five species of *Tonatia* (*bidens, brasilense, carrikeri, schulzi,* and *silvicola*) are known to occur in Suriname. *Tonatia bidens* and *silvicola* are the largest in overall size (forearm length over 50 mm and greatest length of skull over 27.0 mm). However, *T. bidens* has a broader postorbital region (5.0 mm or more) and narrower mastoid region (less than 13.0 mm). The lower incisors of *T. bidens* are also noticeably broader than those of *T. silvicola.* These two species were found throughout most of the forested areas of Suriname. *T. bidens* displayed no secondary sexual variation in nine measurements tested, whereas female *T. silvicola* were significantly larger than the males in four of these measurements.

Tonatia brasilense can be distinguished from all other species in Suriname by its smaller size (forearm length less than 40 mm, greatest length of skull less than 21.0 mm). This species was often taken in association with secondary vegetation, or restricted forest, in savannah regions.

The two medium-sized species—*carrikeri* and *schulzi*—can be distinguished because the underparts of *carrikeri* are entirely white except on the chin and sides of the abdomen and in *schulzi* the dorsal surfaces of most membranes are covered with unique small wart-like granulations. Although the samples of these two species are small, it appears that specimens of *T. carrikeri* are slightly larger than specimens of *T. schulzi.* Both species were taken in dense lowland rainforest characterized by tall trees. The geographic distribution of *T. schulzi* is confined to the undisturbed forests of four nature preserves in central Suriname.

Submitted 21 October 1983.

INTRODUCTION

Six species (*T. bidens, T. brasiliense, T. carrickeri, T. evotis, T. schulzi,* and *T. silvicola*) presently are recognized in the bat genus *Tonatia* Gray (Davis and Carter, 1978; Koopman, 1982). Recently, there has been considerable controversy about the taxonomic status of four nominal, small-sized species of the genus—*brasiliense, nicarguae, minuta,* and *venezualae*—but most recent authors have treated these taxa as conspecific under the senior synonym *T. brasiliense* (Gardner, 1976; Handley, 1976; Koopman, 1978, 1982; Jones and Carter, 1979). Five of the six recognized species are known to occur in South America (Koopman, 1982); the sixth species, *T. evotis* (Davis and Carter, 1978), is confined to southern Mexico and northern Central America.

Suriname is the only geopolitical unit in which all five South American species of *Tonatia* are currently known to occur (Husson, 1978; Genoways and Williams, 1979, 1980). We have taken the opportunity to study material obtained during our field research to derive a better understanding of the morphological and ecological relationships of the species within this rather poorly known genus.

METHODS AND MATERIALS

Specimens were taken with nets and preserved as skin and skull or fluid preparation. Field weights were taken with Pisola scales, which are accurate to 0.1 g. Reproductive condition of the skin and skull specimens was determined by gross dissection in the field, whereas fluid preserved specimens were dissected in the laboratory.

Measurements of forearm and cranial dimensions were taken with dial calipers accurate to 0.1 mm. Only adult specimens (phalangeal epiphyses completely fused) were measured in this study. Our measurements were taken as follows:

Length of forearm.—Taken from the posteriormost projection of the elbow (olecranon process) to the anteriormost projection of the wrist joint with the wing in a flexed position.

Greatest length of skull.—Distance from the posteriormost projection of the cranium to the anterior edge of the upper incisors.

Condylobasal length.—Distance from the posteriormost projection of the exoccipal condyles to the anteriormost projection of the premaxillae.

Zygomatic breadth.—Greatest distance across the zygomatic arches at right angles to the longitudinal axis of cranium.

Postorbital breadth.—Least distance across the postorbital constriction at right angles to the longitudinal axis of cranium.

Mastoid breadth.—Greatest distance across the mastoid processes at right angles to the longitudinal axis of cranium.

Breadth of braincase.—Greatest distance across the braincase at right angles to the longitudinal axis of cranium.

Length of maxillary toothrow.—Distance from posterior lip of alveolus of M^3 to the anterior lip of alveolus of C^1.

Breadth across upper molars.—Greatest distance across upper molars at right angles to the longitudinal axis of cranium; measured at the lateralmost projections of the labial edges of the upper molars.

Univariate analyses of the foregoing measurements were undertaken with the UNIVAR program. This program yields standard statistics (mean, range, standard deviations, standard error of the mean, variances, and coefficient of variation), and employs a single-classification analysis of variance (F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sum of Squares Simultaneous Test Procedure (SS-STP) developed by Gabriel (1964) was used to determine maximally nonsignificant subsets. The UNIVAR program was run on a DEC-10 computer at the University of Pittsburgh and used only with samples of three or more specimens.

The information available on the species of *Tonatia* in Suriname was summarized. This information includes variation within species, distribution in the country, differences among species, karyology, and natural history. A dichotomous key and a listing of collecting localities were constructed for purposes of future reference for work in Suriname and adjacent areas. Unless otherwise indicated, specimens listed for each account are maintained at the Section of Mammals, Carnegie Museum of Natural History.

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GENERIC ACCOUNT

Tonatia Gray, 1827

1827. *Tonatia* Gray, *in* Griffith, The animal kingdom . . . by Baron Cuvier . . . 5:71.

Type species.—*Vampyrum bidens* Spix.

Diagnosis.—A genus of long-eared bats with well-developed noseleaf and short tail, most closely resembling some members of the genus *Micronycteris*. Lower incisors reduced to two giving a dental formula of i 2/1, c 1/1, p 2/3, m 3/3 = 32. Members of the genus *Mimon* have only two lower incisors as well, but have only two lower premolars. First upper premolar broader than long; middle lower premolar much reduced and crowded between the anterior and posterior teeth (see also Goodwin, 1942).

Key to Species of Tonatia *in Suriname*

1. Length of forearm over 50 mm; greatest length of skull 27.0 mm or more 2
1′. Length of forearm less than 50 mm; greatest length of skull less than 27.0 mm 3

2\. Postorbital breadth 5.0 mm or more; mastoid breadth less than 13.0 mm (Fig. 2); lower incisors broad (Fig. 3); ears smaller (range 30–32); tragus small and simple (Fig. 4); ears not connected by a low band across the forehead; 2N = 16, FN = 20 .... *T. bidens*

2′. Postorbital breadth less than 5.0 mm; mastoid breadth 13.0 mm or more (Fig. 2); lower incisors slender (Fig. 3); ears larger (range 33–40); tragus long, with three small tooth-like projections near base of outer border (Fig. 4); small connecting band present behind each ear, these two bands meeting near middle of forehead; 2N = 34, FN = 60 .... *T. silvicola*

3\. Forearm less than 40 mm; greatest length of skull less than 21 mm (Fig. 2); 2N = 30, FN = 56 .... *T. brasiliense*

3′. Forearm more than 40 mm; greatest length of skull more than 21 mm 4

4\. Forearm over 45 mm; greatest length of skull over 24 mm (Fig. 2); hair of underparts entirely white except on chin and sides of abdomen; lacking small wart-like granulations; 2N = 26, FN = 46 .... *T. carrikeri*

4′. Forearm less than 45 mm; greatest length of skull less than 24.0 mm (Fig. 2); hair of underparts drab to grayish olive but with white bases; small wart-like granulations on dorsal surfaces of forearms, digits, and hind legs and on ears and noseleaf; 2N = 28, FN = 36 .... *T. schulzi*

SPECIES ACCOUNTS

Tonatia bidens bidens (Spix, 1823)

Specimens examined (31).—BROKOPONDO: Brownsberg, 1 (RMNH); Brownsberg Nature Park, 3 km S, 20 km W Afobakka, 1; Brownsberg Nature Park, 8 km S, 2 km W Brownsberg, 5; 1½ km W Rudi Kappelvliegveld, 2; 3 km SW Rudi Kappelvliegveld, 3. MAROWIJNE: Oelemarie, 2; Perica, 1. NICKERIE: Avanavero, 1; Grassalco, 4; Kabalebo, 1; Sipaliwini airstrip, 1. PARA: Zanderij, 1. SARAMACCA: Bigi Poika, 1; Bitagron (=Witagron), 1; Lower Geyskes Creek, Tafelberg, 1; SE side of Arrowhead Basin, Augustus Creek, Tafelberg, 1; Voltzberg, 4.

Remarks.—Although this species was not recorded from Suriname by Husson (1962, 1978), Spix's round-eared bat appears to be fairly common in Suriname (Genoways and Williams, 1979; Williams and Genoways, 1980). The species occurs throughout much of the country appearing to be excluded only from the coastal swamps and highly disturbed areas of human agriculture and occupation (Fig. 1). The report by Jentink (1887) of this species from Suriname was shown by Husson (1978) to be based upon a specimen of *Mimon bennettii.*

Generally *Tonatia bidens* is ubiquitous to any kind of forest situation—undisturbed or disturbed. It has been taken at localities such as Perica, Avanavero, Kabalebo, Zanderij, Bigi Poika, and Bitagron, where dominant coastal savannah-type vegetation is closely associated with forests. It has also been collected in undisturbed lowland rainforest at localities such as Brownsberg Nature Park, Rudi Kappelvliegveld, Oelemarie, and Voltzberg. Two specimens were collected in montane rainforest on Tafelberg, and a single specimen was obtained in forests bordering the Brazilian savannah at Sipalwini.

Spix's round-eared bat has been reported as being taken in associ-

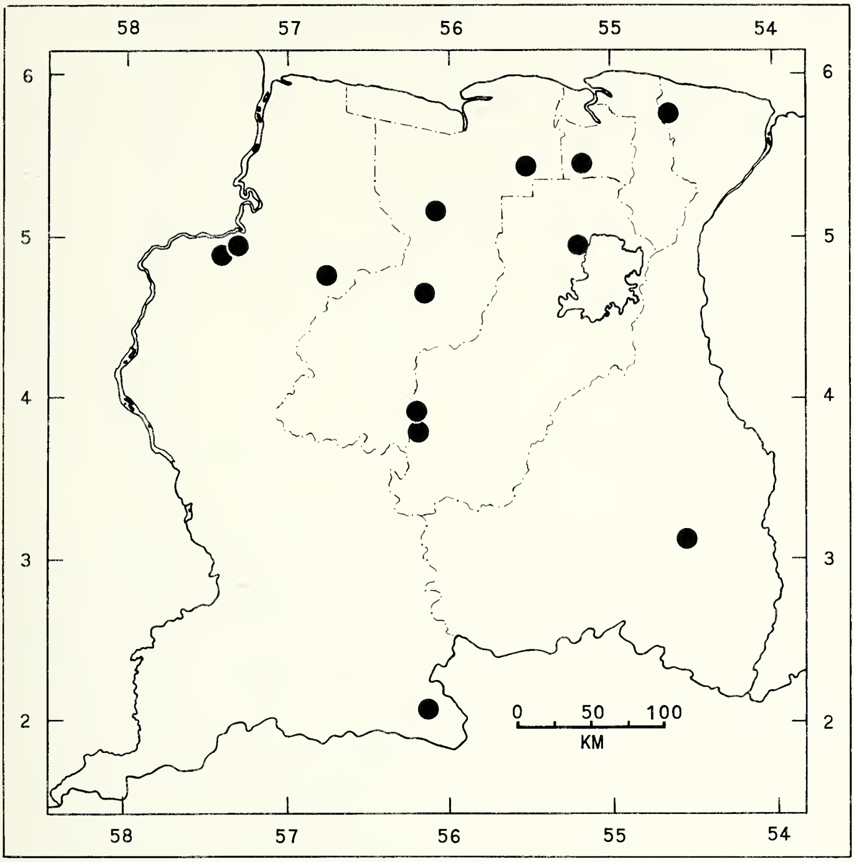

Fig. 1.—Geographic distribution of *Tonatia bidens* in Suriname.

ation with 40 other species of bats in Suriname (Table 1). Among these species are those with widespread distributions such as *Pteronotus parnellii, Lonchophylla thomasi, Carollia perspicillata,* and *Rhinophylla pumilio.* However, the more interesting associations are with the large number of phyllostomines, which undoubtedly reflects the forest dwelling habits of members of this subfamily. Other species having a relatively high association with *Tonatia bidens* are *Saccopteryx bilineata, Anoura caudifer, Sturnira lilium, Uroderma bilobatum, Vampyressa bidens,* and *Vampyrops helleri.*

One subadult male, as indicated by open phalangeal epiphyses, was taken in Brownsberg Nature Park on 7 July 1977. Testes lengths of

Table 1.—*Species of bats taken in association with specimens of* Tonatia *in Suriname. The numbers in each column represent numbers of localities.*

Species of bats	*T. bidens*	*T. brasiliense*	*T. carrikeri*	*T. schulzi*	*T. silvicola*
No. of localities for which data are available	14	4	3	4	10
Saccopteryx bilineata	4	1	2	1	2
Saccopteryx canescens	0	1	0	0	0
Saccopteryx leptura	1	1	0	3	3
Cormura brevirostris	0	0	1	0	1
Peronymus leucopterus	0	0	0	0	1
Centronycteris maximiliani	0	0	0	0	1
Pteronotus parnellii	10	1	2	3	6
Pteronotus personata	1	0	0	0	0
Chrotopterus auritus	1	0	0	2	1
Micronycteris hirsuta	0	0	1	0	0
Micronycteris megalotis	3	1	0	2	0
Micronycteris minuta	1	1	2	0	3
Micronycteris nicefori	1	1	0	1	1
Micronycteris sylvestris	0	0	0	0	1
Tonatia bidens	—	0	1	1	3
Tonatia brasiliense	0	—	1	0	1
Tonatia carrikeri	1	1	—	0	1
Tonatia schulzi	1	0	0	—	1
Tonatia silvicola	3	1	1	1	—
Mimon crenulatum	0	0	0	1	0
Phyllostomus discolor	1	0	1	0	2
Phyllostomus elongatus	5	2	3	4	7
Phyllostomus hastatus	3	2	3	2	2
Phyllostomus latifolius	2	0	0	1	1
Trachops cirrhosus	3	0	0	0	3
Phylloderma stenops	3	1	2	1	2
Anoura caudifer	4	1	0	1	1
Anoura geoffroyi	1	0	0	0	1
Lionycteris spurrelli	1	0	0	0	0
Lonchophylla thomasi	7	1	2	3	5
Glossophaga soricina	2	2	0	0	1
Carollia brevicauda	2	1	1	0	0
Carollia perspicillata	11	4	2	3	6
Rhinophylla pumilio	9	3	3	3	6
Sturnira lilium	4	4	2	0	2
Sturnira tildae	3	1	1	1	1
Ametrida centurio	1	0	0	0	0
Artibeus concolor	0	1	0	0	0
Artibeus (large species)	13	4	3	3	7
Artibeus (small species)	7	3	1	0	2
Uroderma bilobatum	3	2	1	1	2
Chiroderma trinitatum	1	0	1	0	2
Vampyressa bidens	3	0	0	0	1
Vampyressa brocki	0	1	0	0	0
Vampyrops brachycephalus	0	1	0	0	0

Table 1.—*Continued.*

Species of bats	*T. bidens*	*T. brasiliense*	*T. carrikeri*	*T. schulzi*	*T. silvicola*
Vampyrops helleri	4	2	2	1	3
Vampyrodes caraccioli	0	0	0	0	1
Mesophylla macconnelli	1	1	1	0	0
Desmodus rotundus	1	0	2	0	1
Thyroptera discifera	0	0	0	0	1
Thyroptera tricolor	1	2	1	0	0
Natalus tumidirostris	0	1	1	0	0
Myotis nigricans	1	1	2	1	1
Eptesicus brasiliensis	2	2	1	1	1
Eptesicus sp.	1	0	0	0	1
Molossus ater	0	0	1	0	0
Molossus molossus	0	0	1	0	0
Promops centralis	0	0	0	0	1
Total species (57)	40	32	31	23	41

adult males (date of capture in parentheses) are as follows: 8 (28 May 1980); 7 (14 July 1977); 11 (28 August 1979); 10 (7 September 1979); 10 (8 September 1979); 10 (21 September 1979); 4, 4, 8, 8 (23 September 1979); 10, 11 (1 October 1979); 10 (3 October 1979); 8 (4 October 1979); 8 (5 November 1981); 8 (18 November 1981); 7 (24 November 1981); 7 (29 November 1981).

A female carrying a single fetus that measured 30 mm in crown–rump length was taken on 7 September 1979 at Grassalco. This was the only pregnant individual taken during the current study, but lactating females were captured on 25 May 1980 at Avanavero and 2 November 1981 on the southeastern side of Arrowhead Basin on Tafelberg. Adult females that evinced no gross indication of reproduction were taken on the following dates: 28 August 1979 (2); 7 September 1979; 3 October 1979; 24 October 1981. Although these data are sketchy, they tend to support Wilson's (1979) hypothesis that *T. bidens* is a binodal, polyestrous species.

The mean weight of nine males was 24.3 (22–27) and of five females was 23.3 (22–25). The pregnant female weighed 30 g.

The sample of *T. bidens* was submitted to statistical analysis to determine the presence and amount of secondary sexual and individual variation present in this species (Table 2). No significant (0.05 level) secondary sexual variation was found in any of the nine measurements tested. In four measurements (length of forearm, greatest length of skull, condylobasal length, and breadth across upper molars), males averaged slightly larger than females, whereas, in three measurements (postorbital constriction, breadth of braincase, and mastoid breadth), the fe-

Table 2.—*Forearm and cranial measurements of two species of* Tonatia *from Suriname. Analyses of variance were performed to determine the presence of significant (.05 level) differences between sexes within each species and between the two species.*

Species	Sex	N	Mean (range) ± 2 SE	CV	Significant difference	
					Between sexes	Between species ♂♂/♀♀
			Length of forearm			
T. bidens	♂	8	55.5 (54.5–56.7) ± 0.47	1.2	ns	
	♀	8	55.3 (52.7–56.9) ± 1.04	2.7		*/ns
T. silvicola	♂	11	56.9 (54.9–59.3) ± 0.94	2.7	ns	
	♀	11	56.1 (52.1–58.1) ± 1.11	3.3		
			Greatest length of skull			
T. bidens	♂	8	27.8 (27.5–28.0) ± 0.15	0.8	ns	
	♀	8	27.5 (27.0–28.2) ± 0.26	1.3		*/*
T. silvicola	♂	11	28.9 (27.4–29.8) ± 0.45	2.6	*	
	♀	11	28.2 (27.3–29.5) ± 0.40	2.3		
			Condylobasal length			
T. bidens	♂	8	23.3 (23.1–23.6) ± 0.16	1.0	ns	
	♀	8	23.2 (22.5–23.8) ± 0.31	1.9		*/ns
T. silvicola	♂	11	23.8 (22.7–24.7) ± 0.34	2.3	*	
	♀	11	23.1 (22.2–23.9) ± 0.34	2.5		
			Zygomatic breadth			
T. bidens	♂	8	13.7 (13.3–14.0) ± 0.17	1.8	ns	
	♀	8	13.7 (13.3–14.2) ± 0.20	2.1		ns/ns
T. silvicola	♂	11	14.0 (13.3–14.7) ± 0.24	2.8	*	
	♀	11	13.5 (13.1–14.0) ± 0.18	2.2		
			Postorbital constriction			
T. bidens	♂	8	5.3 (5.1–5.6) ± 0.13	3.4	ns	
	♀	8	5.4 (5.2–5.5) ± 0.08	2.2		*/*
T. silvicola	♂	11	4.1 (3.8–4.4) ± 0.11	4.5	ns	
	♀	11	4.1 (3.9–4.4) ± 0.11	4.2		
			Breadth of braincase			
T. bidens	♂	8	10.3 (10.0–10.5) ± 0.12	1.6	ns	
	♀	8	10.4 (10.0–11.0) ± 0.21	2.9		*/*
T. silvicola	♂	11	10.7 (10.3–11.1) ± 0.16	2.4	ns	
	♀	11	10.6 (10.2–11.0) ± 0.13	2.1		
			Mastoid breadth			
T. bidens	♂	8	12.4 (11.8–12.7) ± 0.21	2.4	ns	
	♀	8	12.5 (12.4–12.9) ± 0.14	1.6		*/*
T. silvicola	♂	11	14.1 (13.2–14.8) ± 0.30	3.5	*	
	♀	11	13.7 (13.3–14.0) ± 0.17	2.0		
			Length of maxillary toothrow			
T. bidens	♂	8	9.3 (9.0–9.6) ± 0.13	2.0	ns	
	♀	8	9.3 (9.0–9.6) ± 0.18	2.8		*/*

Table 2.—*Continued.*

Species	Sex	N	Mean (range) ± 2 SE	CV	Significant difference Between sexes	 Between species ♂♂/♀♀
T. silvicola	♂	11	9.7 (9.1–10.1) ± 0.16	2.7	ns	
	♀	11	9.5 (9.2–9.8) ± 0.13	2.2		
			Breadth across upper molars (M–M)			
T. bidens	♂	8	8.5 (8.1–8.8) ± 0.16	2.7	ns	
	♀	8	8.4 (8.0–8.7) ± 0.19	3.1		*/*
T. silvicola	♂	11	9.1 (8.3–9.6) ± 0.21	3.8	ns	
	♀	11	8.9 (8.4–9.4) ± 0.17	3.2		

males averaged slightly larger than males. The mean value was the same for males and females in zygomatic breadth and length of maxillary toothrow. The lack of secondary sexual variation in *T. bidens* is in contrast to the situation found in *T. silvicola* (see the account for this species), in which males were significantly larger than females in four measurements.

The amount of individual variation in the sample of *Tonatia bidens* was consistently lower than that in the sample of *T. silvicola.* Only in breadth of braincase and length of maxillary toothrow of females did the coefficient of variation of *T. bidens* exceed that of *T. silvicola.* The values of *T. bidens* were within the range values given by Taddei (1975) for other species of phyllostomines in Brazil. Only in postorbital breadth and mastoid breadth did individual variation of males exceed that of females. Postorbital constriction exhibited the largest amount of individual variation in males and breadth across upper molars exhibited the most in females.

Tonatia bidens is easily separated from other members of the genus living in Suriname, except *T. silvicola,* by its much larger size (Tables 2–3). On the average, *T. bidens* is smaller than *T. silvicola* for most measurements (Fig. 2). This is particularly true for mastoid breadth where there is no overlap in the range of measurements for the two species (11.8 to 12.9 for *T. bidens* as compared to 13.2 to 14.8 for *T. silvicola*). In contrast to the other measurements, *T. bidens* is much broader in postorbital constriction than is *T. silvicola*; in fact, in the Suriname material there is no overlap between the species in this measurement (5.1 to 5.6 for *T. bidens* as compared to 3.8 to 4.4 for *T. silvicola*). One of the best field characters for separating these two species is the noticeably broader lower incisors possessed by *T. bidens* (Fig. 3). Externally, the tragus is small and simple in *T. bidens,* but long

Table 3.—*Forearm and cranial measurements of three species of* Tonatia *from Suriname.*

Specimen	Sex	Forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Breadth of braincase	Mastoid breadth	Length of maxillary toothrow	Breadth across molars
Tonatia brasiliense										
CM 52777	Male	35.5	19.6	16.6	9.2	3.0	7.9	8.8	6.6	6.1
CM 76775	Male	35.5	20.2	16.6	9.1	3.2	8.0	9.0	7.0	6.3
CM 63667	Female	34.5	19.5	16.3	9.3	3.0	7.8	8.9	6.7	6.4
Tonatia carrikeri										
CM 68400	Female	46.7	26.0	20.5	11.6	3.7	9.8	12.0	8.7	7.7
CM 63668	Female	45.8	25.0	20.3	11.2	3.8	9.7	12.2	8.1	7.6
Tonatia schulzi										
CM 63686	Male	43.3	23.3	18.9	11.0	3.5	9.2	11.8	7.5	7.2
CM 63687	Male	42.0	23.0	19.0	11.1	3.5	9.3	11.6	7.4	7.3
CM 68409	Male	44.0	23.4	18.9	11.3	3.8	9.6	12.1	7.8	7.3
RMNH 26111	Male	—	23.8	19.8	11.0	3.7	9.5	12.0	7.7	7.0

with three small tooth-like projections near the outer border of the base in *T. silvicola* (Fig. 4). The ears are larger in *T. silvicola* and behind each ear small connecting bands meet near the middle of the forehead; these are absent in *T. bidens.*

Only one living mainland subspecies, *T. bidens bidens,* is currently recognized in this species (Jones and Carter, 1976). The only other recognized subspecies is known as a fossil from Jamaica. We have followed this arrangement, but believe that a thorough analysis of geographic variation is needed for this species.

The karyotype of *T. bidens* based upon material from Suriname is 2N = 16, FN = 20. The X-chromosome is metacentric and the Y-chromosome is acrocentric (Honeycutt et al., 1980).

Tonatia brasiliense (Peters, 1866)

Specimens examined (6).—Brokopondo: Brownsberg, 1 (RMNH); Brownsberg Nature Park, 7 km S, 18.5 km W Afobakka, 1. Commewijne: Nieuwe Grond Plantation, 1. Marowijne: 3 km SW Albina, 1. Nickerie: Sipaliwini airstrip, 1; Wageningen, 1 (RMNH).

This small species of *Tonatia* is known from four localities in northern Suriname and one in extreme southern Suriname (Genoways and Williams, 1979; Williams and Genoways, 1980; Fig. 4). This species was not recorded from Suriname by Husson (1978), although now there are specimens in the Rijksmuseum van Natuurlijke Historie. The species can probably be expected throughout the country in appropriate habitats, but nowhere have we found it to be abundant.

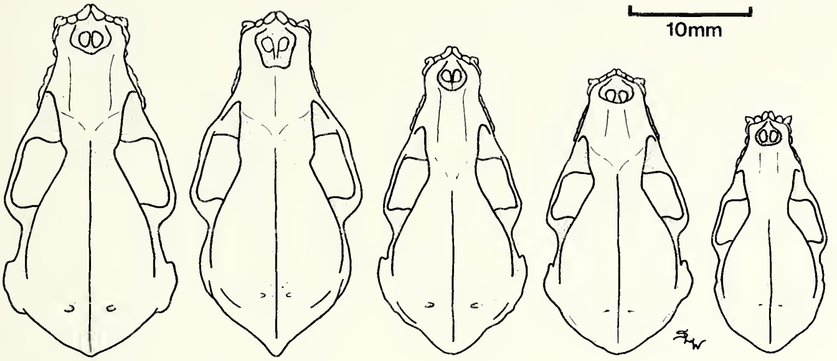

Fig. 2.—Dorsal view of the crania of five species of *Tonatia* from Suriname. From left to right, *T. silvicola* (CM 52779), *T. bidens* (CM 52776), *T. carrikeri* (CM 63668), *T. schulzi* (CM 63687), and *T. brasiliense* (CM 52777).

Unlike other species of *Tonatia,* the localities were *T. brasiliense* has been captured are often associated with secondary vegetation, or restricted forest, in savannah regions. Many of these areas, such as Afobakka, Nieuwe Grond Plantation, Albina, and Wageningen, lie along the coastal savannah and have been subjected to a variety of local ecological disturbances by man (for example, road construction, gardening, mining, and deforestation). The habitat at Brownsberg may be considered atypical for the species; however, this area does border the coastal savannah. Sipaliwini is the only locality not associated with the coastal savannah; instead it has affinities with the Brazilian savannah to the south.

In the relatively few places where this species was taken, it was captured in association with a high number of other species of bats in Suriname (Table 1). Looking beyond the widespread species, a significant association is found for this species with others preferring more open habitats, such as *Glossophaga soricina, Artibeus concolor, Uroderma bilobatum, Vampyrops helleri, Thyroptera tricolor,* and *Eptesicus brasiliensis.* This was predictable based upon the habitat preferences of *T. brasiliense.*

The only adult female obtained during our studies carried a single fetus that measured 18 mm in crown–rump length when taken on 13 September 1979 at Nieuwe Grond Plantation. The pregnant female weighed 10 g. Three adult males had testes measurements as follows: 4 (9 July 1977); 4 (20 October 1981); 5 (16 November 1981).

As mentioned in the Introduction, there has been disagreement about the taxonomy of the small-sized members of the genus *Tonatia.*

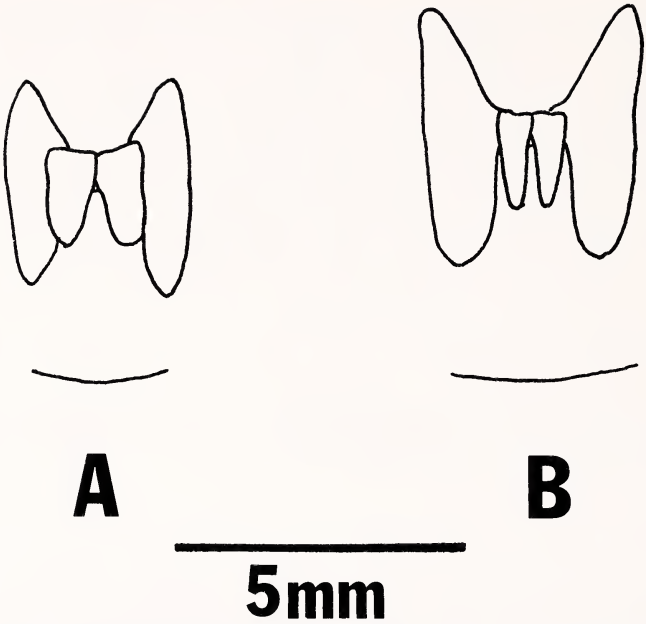

Fig. 3.—Lower incisors of *Tonatia bidens* (A) and *T. silvicola* (B).

The names *brasiliense* (Peters, 1866; type locality: Baia, Brazil), *venezuelae* (Robinson and Lyon, 1901; type locality: Macuto, Venezuela), *minuta* Goodwin, 1942 (type locality: Boca del Curaray, Peru), and *nicaraguae* Goodwin, 1942 (type locality: Kanawa Creek, near Cukra, Nicaragua) are available for bats in this group. Many recent authors (Gardner, 1976; Handley, 1976; Koopman, 1978, 1982; Jones and Carter, 1979) have treated these taxa as a single species under the name *Tonatia brasiliense,* which is the senior synonym. Our examination of material in the National Museum of Natural History and American Museum of Natural History and comparison of this material with our Suriname specimens revealed no consistent morphological character separates these taxa. However, it must be pointed out that Baker (1979) has retained the names *brasiliense, minuta,* and *venezuelae* in reporting karyological information. Possibly, future chromosomal or genic studies will lead to a better understanding of the relationships of these taxa. However, for the present, we are following other authors in recognizing a single small-sized species of *Tonatia.* We have not used a subspecific designation because there is not sufficient material available at this time to do an adequate analysis of geographic variation.

Tonatia brasiliense is easily separated from all other species of the

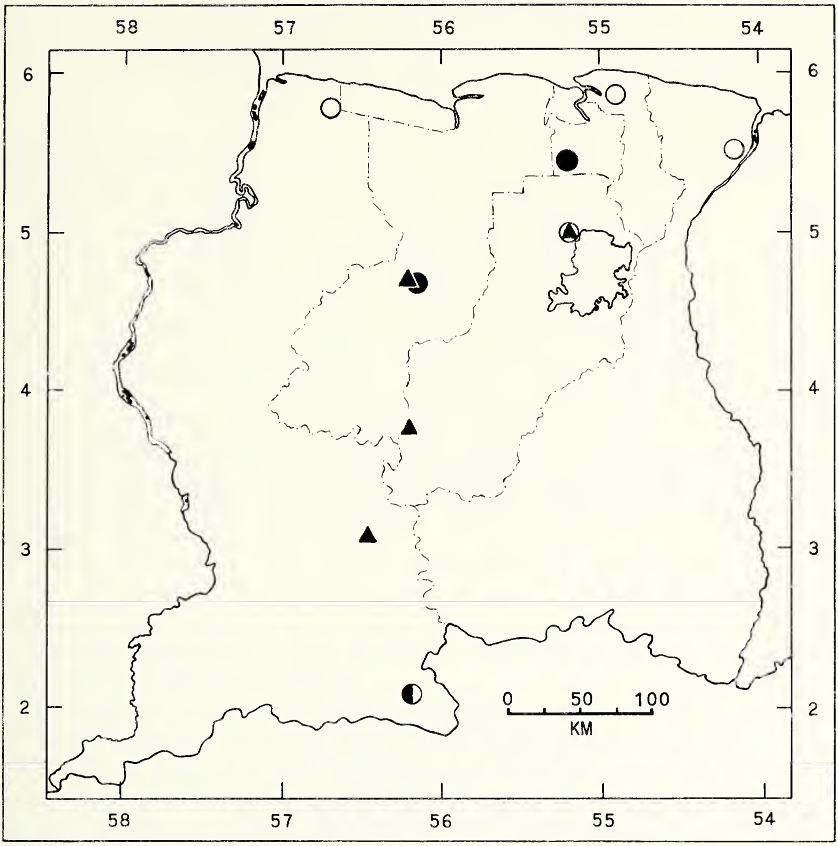

Fig. 4.—Geographic distribution in Suriname of *Tonatia brasiliense* (open circles), *T. carrikeri* (closed circles), and *T. schulzi* (closed triangles). Combined symbols indicate that two species were taken at the same locality.

genus in Suriname by its much smaller size (forearm less than 40.0 and greatest length of skull less than 21.0) in all external and cranial measurements (Tables 2–3; Fig. 2). This species is much more likely to be confused with some members of the genus *Micronycteris*. However, generic characters such as two lower incisors as opposed to four and the size and shape of the first upper and middle lower premolars, will set this species apart from any member of the genus *Micronycteris*.

The karyotype of *T. brasiliense* based upon a female specimen from Suriname is 2N = 30 and the FN is probably 56. The sex chromosomes were not determined (Honeycutt et al., 1980).

Tonatia carrikeri (J. A. Allen, 1910)

Specimens examined (3).—NICKERIE: Sipaliwini airstrip, 1. PARA: Zanderij, 1. SARAMACCA: Voltzberg, 1.

Additional record (Husson, 1978).—Suriname: no specific locality.

The three specimens of *T. carrikeri* that we took during our work were from three widely separated sites (Williams and Genoways, 1980; Genoways et al. 1981) that are arranged in an almost straight north-south line through central Suriname (Fig. 4). This species is very rare in collections and its exact distribution and ecological requirements are not fully understood. The localities in Suriname currently form the northeastern boundary of the known geographic distribution of the species (Koopman, 1982). We suspect that the specimen of *T. carrikeri* reported previously from Suriname by Husson (1978) may represent the species *T. schulzi.* Husson even allocated the specimen to *T. carrikeri* "with some reserve" because of its small size and because most of the color of its pelage had been lost because of the action of the preservative. The size of the specimen and the description of the tragus seem to fit *T. schulzi* best (Fig. 5). It would not be surprising that the small granulations on the membranes typical of *T. schulzi* would be missed in a specimen that has been in preservative for about 100 years.

Specimens of *Tonatia carrikeri* taken in Suriname were typically associated with dense lowland rainforest with a moderate understory. At Sipaliwini and Voltzberg, the forest was characterized by very tall trees (about 50 to 60 m in height) and occasional, standing dead trees. These areas were undisturbed, whereas the area near Zanderij had been subjected to controlled forest management. The collecting sites at Zanderij and Sipaliwini bordered extensive savannahs. Specimens of *T. carrikeri* were taken in Suriname in association with 31 other species of bats (Table 1). In addition to association with common, widespread species, *T. carrikeri* also was associated frequently with several other species of phyllostomines, such as *Micronycteris minuta, M. hirsuta* (both taken near Zaderij), *Phyllostomus elongatus, P. hastatus,* and *Phylloderma stenops.* Of the stenodermines, it was taken most often with *Sturnira lilium* and *Vampyrops helleri.* Perhaps the most interesting association is with *Desmodus rotundus,* a rare species in Suriname, which also was taken at two of the three localities where we obtained *T. carrikeri.*

Among the three specimens from Suriname that we examined, two are adult females and one is an adult male. One of the females was lactating when captured on 18 May 1980 (Zanderij); the other female revealed no gross evidence of reproductive activity when netted on 28 August 1979 (Voltzberg). This latter specimen weighed 18 g. The male

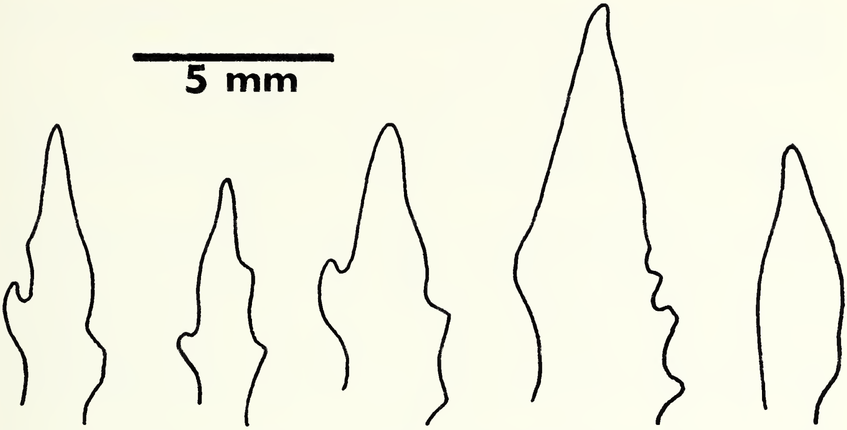

Fig. 5—Tragus of five species of *Tonatia* from Suriname. From left to right, *T. schulzi* (CM 63687), *T. brasiliense* (CM 63667), *T. carrikeri* (CM 63668), *T. silvicola* (CM 63674), and *T. bidens* (CM 63659). The left side of each illustration represents the inner margin of the tragus.

had testes measuring 7 mm in length when taken on 16 November 1981 at the Sipaliwini airstrip.

Tonatia carrikeri is a medium-sized species of *Tonatia*. It is easily distinguished from all other species in the genus, except *T. schulzi*, by size alone. It is much smaller than *T. bidens* and *T. silvicola* and much larger than *T. brasiliense* (Tables 2–3; Fig. 2). Based on available material it appears that *T. carrikeri* is slightly larger than *T. schulzi*; however, more material of both species will be necessary to confirm this observation. Externally the two species are easily separated as pointed out by Genoways and Williams (1980). In *carrikeri*, the underparts are pure white except on the chin and sides of the abdomen, whereas in *schulzi* the underparts are uniformly drab gray, although the bases of the hairs are white. The small wart-like granulations found on the dorsal surfaces of the membranes in *schulzi* are lacking in *carrikeri*.

Currently, *Tonatia carrikeri* is regarded as monotypic. The measurements of two females taken during our survey are listed in Table 3. These measurements match closely with those of specimens of *T. carrikeri* from Venezuela, Bolivia, and Peru (Gardner, 1976; Goodwin, 1953; Swanepoel and Genoways, 1979).

The karyotype of *T. carrikeri* based upon a female specimen from

Suriname is 2N = 26, FN = 46. The sex chromosomes have not been determined (Baker et al., 1981).

Tonatia schulzi Genoways and Williams, 1980

Specimens examined (5).—BROKOPONDO: Brownsberg, 1 (RMNH); 1 km N Rudi Kappelvliegveld, 1; 3 km SW Rudi Kappelvliegveld, 1. NICKERIE: Kayserberg airstrip, 1. SARAMACCA: Raleigh Falls, 1.

Schulz's round-eared bat was recently described (Genoways and Williams, 1980) based upon material from Suriname, and all of the known specimens are from localities in the central part of that country (Genoways and Williams, 1980; Genoways et al., 1981; Fig. 4). Four specimens were taken during our work in Suriname; however, a fifth specimen, from Brownsberg, was found in the collections of the Rijksmuseum van Natuurlijke Historie. It was labeled as *Tonatia carrikeri,* but it is not the specimen reported by Husson (1978) and discussed in the account of *carrikeri* herein. To our knowledge, the specimen from Brownsberg (RMNH 26111) has not appeared previously anywhere in the literature.

The habitats where *Tonatia schulzi* has been obtained are characterized by dense, undisturbed, lowland rainforest where the understory often provided moderate groundcover. In such areas the local influence of man on the habitat either has been limited or nonexistent (all known localities for this species are within designated nature preserves of Suriname). Secondary vegetation was not observed at any collecting site. At 3 km SW Rudi Kappelvliegveld and at Kayserberg the species was taken in mist nets set on hillsides where tall dakama forest dominated. Specimens of *T. schulzi* were taken in association with only 23 other species of bats during our work in Suriname. The list of associated species is far less than for any other species of *Tonatia* (Table 1). Excluding the obviously widespread species, interesting associations are found with *Phyllostomus elongatus* (which was taken at all four localities), *Saccopteryx leptura* (taken from three of the four localities), and *Chrotopterus auritus, Micronycteris megalotis,* and *Phyllostomus hastatus* (taken at two of the four localities).

All known specimens of Schulz's round-eared bat are males. All specimens have the phalangeal epiphyses closed, but the pelage of the specimen from 1 km N Rudi Kappelvleigveld is darker and finer, which may indicate that it is a young animal just completing closure of the epiphyses. This specimen weighed 15 g (30 September 1979), and the other specimen from nearby weighed 16 g (1 October 1979). The testes of the specimen from Kayserberg measured 5 mm in length on 6 May 1980, and those of the specimen from Raleigh Falls measured 7 on 10 May 1980.

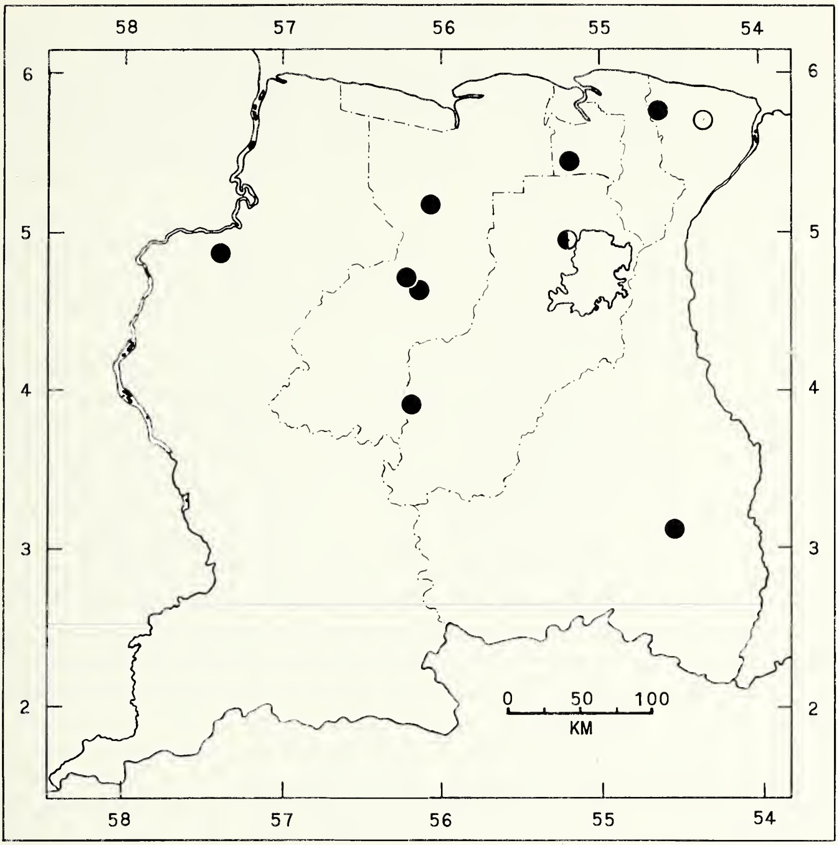

Fig. 6.—Geographic distribution of *Tonatia silvicola* in Suriname. Closed circles indicate specimens examined; open circles indicate localities based upon the literature.

Tonatia schulzi is a medium-sized member of the genus, which may be confused only with *T. carrikeri* based on size alone (Tables 2–3; Fig. 2). Characters for separating these species are discussed in the account of *carrikeri* and by Genoways and Williams (1980). The unique character exhibited by this species is the presence of small wart-like granulations on the dorsal surfaces of the forearms, digits, and hind legs and on the ears and noseleaf. This character is found in no other member of the genus or any other phyllostomid bat.

The karyotype of *T. schulzi* based upon material from Suriname is 2N = 28, FN = 36. The X-chromosome and Y-chromosome are acrocentric (Honeycutt et al., 1980; Baker et al., 1981).

Tonatia silvicola laephotis Thomas, 1910

Specimens examined (48).—BROKOPONDO: Brownsberg Nature Park, 7 km S, 18.5 km W Afobakka, 1; Brownsberg Nature Park, 8 km S, 2 km W Brownsweg, 14. MAROWIJNE: 10 km N, 24 km W Moengo, 1; between Moengotapoe and the Wiawia Bank, 2 (RMNH); Oelemarie, 4. NICKERIE: Kabalebo, 1. PARA: Zanderij, 2. SARAMACCA: Bitagron (=Witagron), 1; Lower Geyskes Creek, Tafelberg, 1; Raleigh Falls, 15; Voltzberg, 6.

Additional records (Husson, 1978).—BROKOPONDO: Brownsberg near the west bank of Brokopondo Lake; no specific locality.

D'Orbigny's round-eared bat is known from 12 localities scattered throughout all but southern Suriname (Fig. 6). However, we see no reason why *T. silvicola* should not occur in southern Suriname at such places as Kayserberg or Sipaliwini.

The habitat of *T. silvicola* is essentially the same as *T. bidens* and includes a wide variety of forest situations. The savannah forests are represented with localities such as Moengo, Zanderij, Bitagron, and Kabalebo. Localities such as Brownsberg Nature Park, Oelemarie, Raleigh Falls, and Voltzberg represent the lowland rainforest habitats. This species has also been taken in montane rainforest on Tafelberg. Although *T. silvicola* occurs in many forest situations, the higher concentrations (based on netting-success rate) of individuals in lowland rainforest localities suggests that such habitats are most suitable for high population densities. During work in Suriname, *T. silvicola* was taken in association with 41 other species of bats (Table 1). The pattern of species association for *T. silvicola* follows very closely the pattern for *T. bidens.*

Testes lengths of adult male *T. silvicola* from Suriname were as follows (date of capture in parentheses): 9 (12 May 1980); 10, 12 (14 May 1980); 8 (8 July 1977); 10 (6 August 1977); 8, 10 (28 August 1979); 10 (20 September 1979); 10, 12, 13, 13, 13 (21 September 1979); 13 (23 September 1979); 12 (24 September 1979); 8 (26 September 1979); 11 (29 November 1981). Two males taken at Raleigh Falls on 14 May 1980 were subadults based on unfused phalangeal epiphyses (length of forearm, 49.7, 51.4). A female carrying a single fetus that measured 25 mm in crown–rump length was taken on 28 August 1979 at Voltzberg. Lactating individuals were captured on 14 May 1970 at Raleigh Falls and 21 and 22 September 1979 in the Brownsberg Nature Park. Females that exhibited no gross reproductive activity were netted on the following dates: 14 May 1980; 19 May 1980; 28 May 1980; 4 September 1979; 21 September 1979 (2); 24 September 1979. Although these data certainly are not definitive, they do suggest a reproductive pattern similar to that of *T. bidens.* However, Wilson (1979) found no evidence of more than one young being produced per year with births occurring during the early half of the rainy season.

The mean weight of 13 adult males was 33.4 (27–38); of eight females, 28.4 (24–36). The pregnant female weighed 32 g.

Our analysis of secondary sexual variation in the material from Suriname (Table 2) agrees closely with the results of a similar analysis of material from Panama conducted by Davis and Carter (1978). Male *T. silvicola* from Suriname are significantly larger than females in four measurements (greatest length of skull, condylobasal length, zygomatic breadth, and mastoid breadth) of the nine that were studied. Males averaged larger than females in all remaining measurements except postorbital constriction in which the mean was the same for both sexes. Males from Suriname were significantly larger in mastoid breadth than females, whereas there was no significant secondary sexual variation in cranial breadth in the Panamanian sample. We found no significant difference between males and females in length of maxillary toothrow, whereas the material studied by Davis and Carter (1978) revealed significant differences between the sexes.

The amount of individual variation exhibited by the Surinamese material (Table 2) is low. Postorbital constriction was the most highly variable measurement studied for both males and females. Condylobasal length showed the lowest amount of individual variation in males and mastoid breadth displayed the lowest amount for females.

Davis and Carter (1978) did not include material of *T. s. laephotis* in their review of the *Tonatia silvicola* complex. Examining their tables reveals that the Suriname material has on the average longer forearms and broader skulls than other populations of the species. The maxillary toothrow in *laephotis* may be proportionally shorter than in other populations. The material assignable to *laephotis* appears to be closer in size to specimens from Central America described by Davis and Carter (1978) as *T. s. centralis* than other named taxa. An assessment of the exact status of *T. s. laephotis* will await an analysis of geographic variation of the species that includes this material.

A comparison of *T. silvicola* and *T. bidens* in Suriname is given in the account of the latter species. Davis and Carter (1978) gave reasons for the spellings of *silvicola* and *laephotis* used in our paper.

The karyotype of *T. silvicola* based upon material from Suriname is 2N = 34, FN = 60. The X-chromosome is submetacentric and the Y-chromosome is acrocentric (Honeycutt et al., 1980).

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THE WASATCHIAN-BRIDGERIAN LAND MAMMAL AGE BOUNDARY (EARLY TO MIDDLE EOCENE) IN WESTERN NORTH AMERICA

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Abstract

Mammalian faunas from western North America of late Wasatchian through early Bridgerian age (late early Eocene to early middle Eocene) are reviewed. Faunas of late Wasatchian age (Lostcabinian) are characterized by the presense of *Lambdotherium.* It is suggested that the Wasatchian-Bridgerian boundary be placed at the first occurrence in the fossil record of *Palaeosyops* (including *Eotitanops*), *Hyrachyus, Trogosus, Helaletes, Omomys, Helohyus, Pantolestes, Homacodon, Washakius,* and/or *Smilodectes.* Most all of these genera overlap in biostratigraphic occurrence with taxa typical of the Wasatchian, including *Coryphodon, Esthonyx, Palaeosinopa, Didymictis, Hapalodectes, Bunophorus, Diacodexis, Phenacodus, Hyracotherium, Heptodon,* and *Shoshonius,* all of which last appear in either Gardnerbuttean faunas or Bridger A, B or C. The Gardnerbuttean is recognized as earliest Bridgerian; marked faunal turnover occurred during this time interval.

Introduction

North American Land Mammal Ages were originally defined for continental strata by Wood et al. in 1941 (see Tedford, 1970, and Rose, 1981, for the history of these ages since 1941). They proposed 18 provincial time terms which divided the Cenozoic record of mammalian faunas from rock units scattered throughout western North America. This new terminology served to clarify correlations within North America without a direct reliance on terms defined outside of this continent.

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The Wasatchian and Bridgerian Land Mammal Ages (middle and late Eocene, respectively) were based on the mammalian faunas of the Wasatch and Bridger formations of southwestern Wyoming. Since the original definitions of these ages, additional discoveries and revisions of fossil mammal faunas have been made. Several of these faunas are intermediate in age and composition between the Wasatchian and Bridgerian—Cathedral Bluffs Tongue of the Wasatch Formation (Wyoming) fauna (Morris, 1954; Gazin, 1962; West, 1973*a*; West and Dawson, 1973); New Fork Tongue of the Wasatch Formation (Wyoming) fauna (Gazin, 1952, 1962; West, 1973*a*); upper Wind River Formation (Wyoming) fauna (Stucky, 1982, 1984; Krishtalka and Stucky, 1983*a*; Guthrie, 1971); and upper Huerfano Formation (Colorado) fauna (Robinson, 1966). More typical late Wasatchian faunas—LaBarge and Dad (Wyoming) local faunas (Gazin, 1952, 1962); upper Willwood Formation (Wyoming) fauna (Schankler, 1980); lower Huerfano Formation (Colorado) fauna (Robinson, 1966); and upper Debeque Formation (Colorado) fauna (Kihm, 1984)—and more typical Bridgerian faunas—lower Bridger Formation (Wyoming) faunas (McGrew and Sullivan, 1970; West, 1973*a*; Gazin, 1976); Powder Wash (Utah) local fauna (Krishtalka and Stucky, 1984); and Aycross Formation (Wyoming) fauna (McKenna, 1980*a*; Eaton, 1980, 1982; Bown, 1982)—have also been described. The Almagre and Largo faunas from the San Jose Formation of northwestern New Mexico, previously thought by some to be late Wasatchian (Lostcabinian) in age (for example, Gingerich and Simons, 1977; Gingerich and Gunnell, 1979) have been shown to be of middle Wasatchian age (Late Graybullian or Lysitean; Lucas et al., 1981; Schoch, 1981). The occurrence of *Anacodon* and *Apheliscus* in the Lysite Member and San Jose Formation adds support to their correlation (Table 1; see Stucky and Krishtalka, 1983).

Classically, the Wasatchian has been divided into early, middle, and late units—the Graybullian, Lysitean, and Lostcabinian, respectively (see Bown and Schankler, 1982). Gingerich (1983) has recently shown that the Sandcouleean is valid and the earliest subage of the Wasatchian. This faunal unit was formerly considered to be part of the "early" Graybullian. The Graybullian is based on the lower Willwood Formation fauna of the Bighorn Basin (in part), and the Lysitean and Lostcabinian are based on the Lysite and Lost Cabin member faunas of the Wind River Formation of the Wind River Basin. Robinson (1966) defined the term Gardnerbuttean for the upper Huerfano Formation fauna, which he regarded as latest Wasatchian, intermediate between the Lost Cabin Member and Bridger Formation faunas as they were understood in 1966. Savage (1977) has recently suggested that the Wasatchian "stage" could be recognized worldwide. He also defined the *Lambdotherium* concurrent range zone as a recognizable unit throughout western North America. Bown (1979*a*) and Schankler (1980) have, in part, abandoned the classic (Graybullian, Lysitean, and Lostcabinian) subdivisions of the Wasatchian in the Willwood Formation, substituting detailed biostratigraphic data. Gingerich and Simons (1977) have used species of notharctid primates as basis for subdivision of the Wasatchian.

Matthew (1909) divided the Bridger Formation into five lithologic units—Bridger A, B, C, D, and E. The mammal genera from Bridger A were not discussed by Matthew. Wood (1934) described the Twin Buttes member of the Bridger Formation for Bridger A and B and the Black's Fork member for Bridger C and D. Both Bradley (1964) and Robinson (1966) have suggested that these members are useful as faunal terms (Twinbuttean and Blacksforkian, see Robinson, 1966). McGrew and Sullivan (1970) were the first to report a relatively diverse mammalian fauna from Bridger A. Gazin (1976) has referred to Matthew's Bridger A and B as lower Bridger, and Bridger C and D as upper Bridger. Bridger E is not very fossiliferous (Gazin, 1976).

Stucky (1982, 1984) recently revised the biostratigraphic interpretations of fossil mammals in the upper part of the Wind River Formation, recognizing a lower *Lambdotherium* Range Zone and an upper *Palaeosypos borealis* Assemblage Zone. Previous interpretations (Granger, 1910; Osborn, 1929; Guthrie, 1971; but see Osborn, 1907, 1909) indicated that the fauna from the upper part of the Wind River Formation was all of the same age and came from either the same horizon or a narrow interval of strata within the Lost Cabin Member. The fauna from the *Lambdotherium* zone of Stucky (1984) was used to characterize the Lostcabinian Land Mammal Subage, and that from the *Palaeosyops borealis* zone was considered to be most similar to the Gardnerbuttean fauna from the upper Huerfano Formation described by Robinson (1966). This paper is a direct result of that work and is intended to clarify the relationships of the faunas of late Wasatchian and early Bridgerian age known from throughout North America.

Despite the increase in knowledge of the late Wasatchian and early Bridgerian faunas, the boundary between these land mammal ages is not clearly defined (see West et al., in press, manuscript 1982). The recognition of the *Lambdotherium* Range Zone and the *Palaeosyops borealis* Assemblage Zone in the upper part of the Wind River Formation (Stucky, 1984) suggests several alternatives for placing this boundary. Mammalian faunas from rocks that are homotaxic with these zones are discussed below. Comparisons of these faunas are made primarily at the generic level, because of the variable taxonomic agreement at the specific level among paleontologists. The genus seems to be the most intersubjective taxonomic rank (Savage, 1977). Genera that either are common throughout the late Wasatchian and early Bridgerian or are poorly studied or represented are not generally used or discussed. A heavy reliance is placed on the larger and more common mammals, specifically the perissodactyls, tillodonts, and artiodactyls, with a lesser reliance on the condylarths and primates. This is because these five groups of mammals have classically been used as biostratigraphic indicators, and they are usually among the first taxa recovered and identified from a fossiliferous horizon. Several groups of Sauria also appear to be useful in determining biostratigraphic age through the Wasatchian and Bridgerian (Stucky, in preparation). Table 1 lists the mammalian genera from the better represented faunas of medial Wasatchian through Bridgerian age. New records or revised identifications documented in the footnotes to Table 1 are based on either systematic reviews that have been published since the original description of the faunas or firsthand study of the specimens. The geographic position of these faunas is shown in Fig. 1.

Abbreviations used in the text are: ACM, Pratt Museum, Amherst College (Amherst); AMNH, American Museum of Natural History (New York); CM, Carnegie Museum of Natural History (Pittsburgh); DMNH, Denver Museum of Natural History (Denver); KU, Natural History Museum, University of Kansas (Lawrence); FM, Field Museum of Natural History (Chicago); JHU, Johns Hopkins University (Baltimore); LACM, Los Angeles County Museum (Los Angeles); PU, Princeton University (Princeton); UCM, Museum, University of Colorado (Boulder); UM, Museum of Paleontology, University of Michigan (Ann Arbor); USGS, United States Geological Survey (Denver); USNM, United States National Museum (Washington); UW, Geological Museum University of Wyoming (Laramie); YPM, Yale Peabody Museum (New Haven); Loc., Locality.

WIND RIVER BASIN, WYOMING

Recent biostratigraphic and systematic studies of the fauna from the upper part of the Wind River Formation (Krishtalka and Stucky, 1983*a*; Stucky and Krishtalka, 1983; Stucky, 1984) have resulted in the recognition of two zones—the *Lambdotherium* Range Zone and the *Palaeosyops borealis* Assemblage Zone. These two zones have been mapped in three separate stratigraphic intervals in the upper part of the Wind River Formation. The vertebrate fauna from the *Lambdotherium* Range Zone can be considered the "type fauna" for the Lostcabinian Land Mammal Subage of the Wasatchian Land Mammal Age (latest Wasatchian). It is characterized by the restricted occurrence of *Lambdotherium popoagicum* and *Hyopsodus walcottianus*, and by the presence of typical late Wasatchian genera such as *Palaeictops, Palaeosinopa, Microsyops, Notharctus, Shoshonius, Viverravus, Didymictis, Miacis, Vulpavus, Esthonyx, Hyopsodus, Phenacodus, Hyracotherium, Heptodon, Diacodexis, Bunophorus, Paramys,* and *Knightomys.* The genera *Armintodelphys, Scenopagus, Nyctitherium, Alveojunctus, Uintasorex, Shoshonius, Mesonyx,* cf. *Orohippus,* and *Pauromys* first occur in the

Fig. 1.—Major fossil vertebrate localities in western North America preserving faunas of the Wasatchian and Bridgerian land mammal ages. Key to localities: 1) Bighorn Basin, Wyoming; 2) Powder River Basin, Wyoming; 3) Wind River Basin, Wyoming; 4) Southwestern Wyoming; 5) Piceance Basin, Colorado; 6) Huerfano Basin, Colorado; 7) Powder Wash, Utah; 8) San Juan Basin (San Jose Formation), New Mexico.

Wind River Formation within this zone, and *Loveina, Meniscotherium, Hyopsodus walcottianus,* and *Lambdotherium popoagicum* last occur or become extinct within this zone. The reports of either *Lambdotherium* (Guthrie, 1967; Korth, 1982) from the Lysite Member (Lysitean) of the Wind River Formation or *Homogalax* from the Lost Cabin

Table 1.—*Generic composition of Middle Wasatchian through Early Bridgerian mammalian faunas of western North America. Occurrences of genera based on original sources except where noted.*

Taxa	San Jose Formation[1] New Mexico	Wind River Formation[2] Lysite Member	Wasatch Formation[3] Dad Local Fauna	Wasatch Formation[3] LaBarge Local Fauna	Wasatch Formation[3] New Fork Tongue	Wasatch Formation, New[4] Fork Tongue, Arkosic Facies	Wasatch Formation, New[4] Fork Tongue, Western Facies	Debeque Formation[5] "Lambdotherium Zone"	Willwood Formation[6] "Lambdotherium Zone"	Huerfano Formation[7] "Lambdotherium Zone"	Wind River Formation[8] Lambdotherium Zone	Wind River Formation[8] Palaeosyops borealis Zone	Huerfano Formation[7] "Palaeosyops borealis Z"	Huerfano Formation[7] "Palaeosyops huerfanensis Z"	Aycross Formation[9] Bighorn Basin	Wasatch Formation[4,10] Cathedral Bluffs Tongue	Wasatch Formation[3] Cathedral Bluffs Tongue	Bridger Formation[4] Bridger A	Bridger Formation[11] Bridger A	Green River Formation[12] Powder Wash (Upper)	Bridger Formation[13] Bridger B
Multituberculata																					
Ectypodus											+										
Marsupialia[14]																					
Peratherium	+	+		+							+	+		+	+	+	+	+	+	+	+
Peradectes				+								+			+			+		+	
Armintodelphys											+	+								+	
Proteutheria																					
Didelphodus	+	+						+			+	+						+		+	
Palaeictops[15]		+	?	+		+		+		+	+	+			+					+	
Prodiacodon	+																				
Palaeosinopa[16]	+				+						+	+					+				
Pantolestes												+								+	+
Apatemys	+	+		+							+	+		+	+	+		+		+	+
Insectivora[17]																					
Diacodon	+																				
Macrocranion	+	+									+				cf.						
Talpavus																				+	+
Scenopagus	+										+	+		+	+	+		+	+	+	+
Nyctitherium	+										+	+		+	+	+		+		+	+

Table 1.—*Continued.*

Taxa	San Jose Formation[1] New Mexico	Wind River Formation[2] Lysite Member	Wasatch Formation[3] Dad Local Fauna	Wasatch Formation[3] LaBarge Local Fauna	Wasatch Formation[3] New Fork Tongue	Wasatch Formation, New[4] Fork Tongue, Arkosic Facies	Wasatch Formation, New[4] Fork Tongue, Western Facies	Debeque Formation[5] "Lambdotherium Zone"	Wilwood Formation[6] "Lambdotherium Zone"	Huerfano Formation[7] "Lambdotherium Zone"	Wind River Formation[8] Lambdotherium Zone	Wind River Formation[8] Palaeosyops borealis Zone	Huerfano Formation[7] "Palaeosyops borealis Z"	Huerfano Formation[7] "Palaeosyops huerfanensis Z"	Aycross Formation[9] Bighorn Basin	Wasatch Formation[4,10] Cathedral Bluffs Tongue	Wasatch Formation[3] Cathedral Bluffs Tongue	Bridger Formation[4] Bridger A	Bridger Formation[11] Bridger A	Green River Formation[12] Powder Wash (Upper)	Bridger Formation[13] Bridger B
Leptacodon	+																				
Myolestes															cf.			+			
Pontifactor															cf.						
Cryptolestes																				+	
Aethomylos																				+	
Plagioctenodon											cf.										
Centetodon[18]											+	+		+				+		+	+
Chiroptera																					
Ageina											+										
Icaronycteris											+	+									
Primates																					
Niptomomys[19]		cf.									cf.										
Uintasorex											+	+			+					+	
Navajovius	+																				
Microsyops	+	+		+	+	+	+	+	+	+	+	+		+	+	+		+	+	+	+
Alveojunctus[20]											+				+	+					
Ignacius/Elwynella											cf.				+						
Phenacolemur	+	+						+		+	+	+				+					
Loveina[21]		+		+			+			+	+		+								
Shoshonius[22]						+					+	+		+	+						
Utahia																				+	

Table 1.—*Continued.*

Taxa	San Jose Formation^1 New Mexico	Wind River Formation^2 Lysite Member	Wasatch Formation^3 Dad Local Fauna	Wasatch Formation^3 LaBarge Local Fauna	Wasatch Formation^3 New Fork Tongue	Wasatch Formation, New^4 Fork Tongue, Arkosic Facies	Wasatch Formation, New^4 Fork Tongue, Western Facies	Debeque Formation^5 "Lambdotherium Zone"	Willwood Formation^6 "Lambdotherium Zone"	Huerfano Formation^7 "Lambdotherium Zone"	Wind River Formation^8 Lambdotherium Zone	Wind River Formation^8 Palaeosyops borealis Zone	Huerfano Formation^7 "Palaeosyops borealis Z"	Huerfano Formation^7 "Palaeosyops huerfanensis Z"	Aycross Formation^9 Bighorn Basin	Wasatch Formation^{4,10} Cathedral Bluffs Tongue	Wasatch Formation^3 Cathedral Bluffs Tongue	Bridger Formation^4 Bridger A	Bridger Formation^{11} Bridger A	Green River Formation^{12} Powder Wash (Upper)	Bridger Formation^{13} Bridger B
Washakius[23]												+						+	+		+
Uintanius/Huerfanius[24]	+											+		+					+	+	
Trogolemur																					+
Chlororhysis			+	+																	
Anemorhysis		+		+							cf.										
Omomys														+	+	+		+	+	+	+
Absarokius		+		+				+	+		+	+		+	cf.		+				
Aycrossia[25]												+			+						
Anaptomorphus																+		+	+	+	+
Gazinius[26]															+						
Cantius/Notharctus[27]	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+
Pelycodus[28]	+							cf.		cf.											
Copelemur[29]	+	+							?		+	+									
Smilodectes[30]												cf.		+				+	+	+	+
Taeniodonta																					
Ectoganus/Stylinodon[31]	+	+		+		+	+	cf.		+	+	+		+		+					
Tillodontia[32]																					
Esthonyx	+	+	+	+	+	+		+	+	+	+	+		+							
Trogosus[33]						?						+		+	+		+		+	+	+
Tillodon																					+
Megalesthonyx[34]									+	+											

Table 1.—*Continued.*

Taxa	San Jose Formation[1] New Mexico	Wind River Formation[2] Lysite Member	Wasatch Formation[3] Dad Local Fauna	Wasatch Formation[3] LaBarge Local Fauna	Wasatch Formation[3] New Fork Tongue	Wasatch Formation, New[4] Fork Tongue, Arkosic Facies	Wasatch Formation, New[4] Fork Tongue, Western Facies	Debeque Formation[5] "Lambdotherium Zone"	Willwood Formation[6] "Lambdotherium Zone"	Huerfano Formation[7] "Lambdotherium Zone"	Wind River Formation[8] Lambdotherium Zone	Wind River Formation[8] Palaeosyops borealis Zone	Huerfano Formation[7] "Palaeosyops borealis Z"	Huerfano Formation[7] "Palaeosyops huerfanensis Z"	Aycross Formation[9] Bighorn Basin	Wasatch Formation[4,10] Cathedral Bluffs Tongue	Wasatch Formation[3] Cathedral Bluffs Tongue	Bridger Formation[4] Bridger A	Bridger Formation[11] Bridger A	Green River Formation[12] Powder Wash (Upper)	Bridger Formation[13] Bridger B
Creodonta[35]																					
Oxyaena/Patriofelis	+	+	+	+		+		+	+	+	+	+		+	+						+
Ambloctonus[36]	+	+	+	+					+												
Arfia[37]														+							
Prolimnocyon	+	+		+	+			+	+		+	+									
Prototomus	+	+		+		?	?		+		+	+									
Tritemnodon	+	+		+		+					cf.	+		+						+	+
Provivera																		?	+		+
Proviverroides															+					+	
Limnocyon[38]												+								+	+
Thinocyon																		+			+
Machaeroides[39]											?	?									+
Carnivora																					
Didymictis	+	+	+	+	+	+	+	+	+	+	+	+		+			+				
Viverravus		+	+	+	+				+	+	+	+	+	+	+		+	+		+	+
Miacis	+	+		+	+	+	+		?		+	+		+						+	+
Oodectes	+											cf.		+						?	+
Vassacyon											cf.	cf.									
Uintacyon	+	+		+	+			+	+		+	+		+	+					+	+
Vulpavus	+	+	+	+	+	+		+	+		+	+		+					+		+
Palaearctonyx																					+

Table 1.—*Continued.*

Taxa	San Jose Formation[1] New Mexico	Wind River Formation[2] Lysite Member	Wasatch Formation[3] Dad Local Fauna	Wasatch Formation[3] LaBarge Local Fauna	Wasatch Formation[3] New Fork Tongue	Wasatch Formation, New[4] Fork Tongue, Arkosic Facies	Wasatch Formation, New[4] Fork Tongue, Western Facies	Debeque Formation[5] "Lambdotherium Zone"	Willwood Formation[6] "Lambdotherium Zone"	Huerfano Formation[7] "Lambdotherium Zone"	Wind River Formation[8] Lambdotherium Zone	Wind River Formation[8] Palaeosyops borealis Zone	Huerfano Formation[7] "Palaeosyops borealis Z"	Huerfano Formation[7] "Palaeosyops huerfanensis Z"	Aycross Formation[9] Bighorn Basin	Wasatch Formation[4,10] Cathedral Bluffs Tongue	Wasatch Formation[3] Cathedral Bluffs Tongue	Bridger Formation[4] Bridger A	Bridger Formation[11] Bridger A	Green River Formation[12] Powder Wash (Upper)	Bridger Formation[13] Bridger B
Condylarthra																					
Harpagolestes																					+
Pachyaena/Mesonyx	+				+							+		+	+						+
Hapalodectes		+			+				+			+	+								
Thryptacodon	+	+		+							+	+									
Chriacus	+							cf.													
Anacodon	+	+																			
Apheliscus	+	+																			
Hyopsodus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Phenacodus[40]	+	+				+	+	+	+	+	+	+									
Ectocion[41]												+									
Meniscotherium[42]	+			+	+	+	+				+										
Pantodonta																					
Coryphodon	+	+	+	+		+		+	+	+	+	+		+							
Dinocerata																					
Bathyopsis/Probathyopsis		+			+	+					+	+		+	+				+		+
Perissodactyla																					
Hyracotherium[43]	+	+	+	+	+	+	+	+	+	+	+	+		+			+			+	+
Orohippus[44]											+	+			+	+		+	+		+
Xenicohippus	+	cf.																			

Table 1.—*Continued.*

Taxa	San Jose Formation[1] New Mexico	Wind River Formation[2] Lysite Member	Wasatch Formation[3] Dad Local Fauna	Wasatch Formation[3] LaBarge Local Fauna	Wasatch Formation[3] New Fork Tongue	Wasatch Formation, New[4] Fork Tongue, Arkosic Facies	Wasatch Formation, New[4] Fork Tongue, Western Facies	Debeque Formation[5] "Lambdotherium Zone"	Willwood Formation[6] "Lambdotherium Zone"	Huerfano Formation[7] "Lambdotherium Zone"	Wind River Formation[8] Lambdotherium Zone	Wind River Formation[8] Palaeosyops borealis Zone	Huerfano Formation[7] "Palaeosyops borealis Z"	Huerfano Formation[7] "Palaeosyops huerfanensis Z"	Aycross Formation[9] Bighorn Basin	Wasatch Formation[4,10] Cathedral Bluffs Tongue	Wasatch Formation[3] Cathedral Bluffs Tongue	Bridger Formation[4] Bridger A	Bridger Formation[11] Bridger A	Green River Formation[12] Powder Wash (Upper)	Bridger Formation[13] Bridger B
Lambdotherium			+	+	+	+	+	+	+	+	+										
Palaeosyops						+						+	+	+	+		+	+	+		+
Limnophyops																					+
Homogalax[45]	+	+	cf.																		
Parisectolophus																					+
Heptodon[46]		+	+	+	+	+	+	+	+	?	+	+			+						?
Helaletes[46]											+	+		+		?			+	+	+
Selenaletes												+									
Hyrachyus					+	+						+		+	+	+	+	+	+	+	+
Artiodactyla[47]																					
Diacodexis[48]	+	+	+	+	+	+	+	+	+	+	+	+						+			+
Bunophorus/Wasatchia[49]	+	+	+	+	+		+	+	+	+	+	+		+							
Antiacodon									+	+		+		+	+	+		+		+	+
Hexacodus[50]	cf.	+	+	+	+												+				
Helohyus												+						+			+
Homacodon[51]												+									
Microsus[52]												cf.						+	+	+	+
Rodentia[53]																					
Paramys	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+
Pseudotomus								+							cf.					+	
Thisbemys		+						+		+		+		+	+		+	+			+

Table 1.—*Continued.*

Taxa	San Jose Formation^{1} New Mexico	Wind River Formation^{2} Lysite Member	Wasatch Formation^{3} Dad Local Fauna	Wasatch Formation^{3} LaBarge Local Fauna	Wasatch Formation^{3} New Fork Tongue	Wasatch Formation, New^{4} Fork Tongue, Arkosic Facies	Wasatch Formation, New^{4} Fork Tongue, Western Facies	Debeque Formation^{5} "Lambdotherium Zone"	Willwood Formation^{6} "Lambdotherium Zone"	Huerfano Formation^{7} "Lambdotherium Zone"	Wind River Formation^{8} Lambdotherium Zone	Wind River Formation^{8} Palaeosyops borealis Zone	Huerfano Formation^{7} "Palaeosyops borealis Z"	Huerfano Formation^{7} "Palaeosyops huerfanensis Z"	Aycross Formation^{9} Bighorn Basin	Wasatch Formation^{4,10} Cathedral Bluffs Tongue	Wasatch Formation^{3} Cathedral Bluffs Tongue	Bridger Formation^{4} Bridger A	Bridger Formation^{11} Bridger A	Green River Formation^{12} Powder Wash (Upper)	Bridger Formation^{13} Bridger B
Leptotomus														?	cf.				+		+
Notoparamys	+																				
Quadratomus														+				+			
Reithroparamys		+						+						+	+	+	+	+			+
Acritoparamys								+			+	+						+			+
Microparamys	+										+				+	+	+	+		+	+
Lophiparamys	+	+									+										
Ischyrotomus																					+
Franimys	+	+																			
Mytonomys		+							?		+										
Sciuravus					+							+				+	+	+	+	+	+
Knightomys	+	+		+				+	+		+	+		+		+					
Pauromys											+	+				+				+	+
Tillomys																+		+			+
Taxymys															+			+			+
Dawsonomys				+																	
Mysops																+					+
Mattimys											+	+									
Palaeanodonta																					
Tubulodon											+	+									

Table 1.—*Continued.*

Taxa	San Jose Formation[1] New Mexico	Wind River Formation[2] Lysite Member	Wasatch Formation[3] Dad Local Fauna	Wasatch Formation[3] LaBarge Local Fauna	Wasatch Formation[3] New Fork Tongue	Wasatch Formation, New[4] Fork Tongue, Arkosic Facies	Wasatch Formation, New[4] Fork Tongue, Western Facies	Debeque Formation[5] "Lambdotherium Zone"	Willwood Formation[6] "Lambdotherium Zone"	Huerfano Formation[7] "Lambdotherium Zone"	Wind River Formation[8] Lambdotherium Zone	Wind River Formation[8] Palaeosyops borealis Zone	Huerfano Formation[7] "Palaeosyops borealis Z"	Huerfano Formation[7] "Palaeosyops huerfanensis Z"	Aycross Formation[9] Bighorn Basin	Wasatch Formation[4,10] Cathedral Bluffs Tongue	Wasatch Formation[3] Cathedral Bluffs Tongue	Bridger Formation[4] Bridger A	Bridger Formation[11] Bridger A	Green River Formation[12] Powder Wash (Upper)	Bridger Formation[13] Bridger B
Pentapassalus				+																	
Tetrapassalus																					+
Palaeanodon	?	+																			
Metacheiromys																					+

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[1] Lucas et al. (1981).
[2] Guthrie (1967).
[3] Gazin (1952, 1962).
[4] West (1973*a*).
[5] Kihm (1984).
[6] Schankler (1980). Faunal list includes only those genera which are reported from the same interval as *Lambdotherium* (670–725 m Levels).
[7] Robinson (1966).
[8] Stucky (1982, 1984).
[9] Bown (1982).
[10] West and Dawson (1973).
[11] McGrew and Sullivan (1970).
[12] Krishtalka and Stucky (1984).
[13] Gazin (1976).
[14] Krishtalka and Stucky (1983*b*).
[15] Gazin (1962:23) indicates that the specimens from the Dad local fauna represent either *Palaeictops* or *Diacodon.*
[16] Gazin's (1962:25) discussion of the specimens from the New Fork and Cathedral Bluffs tongues suggests that they represent *Palaeosinopa* rather than *Pantolestes* (see Matthew, 1909).
[17] Occurrences of *Macrocranion, Talpavus, Scenopagus,* and *Nyctitherium* are based on Krishtalka (1976*a*, 1976*b*).
[18] Krishtalka and West (1979) report *Centetodon* from the upper Huerfano Formation.
[19] Wind River Formation records are based on CM 36968, CM 39488, and CM 54210 from the Lysite Member and an uncatalogued specimen in the CM collections from the Red Creek Facies (UCM Loc. 81008).
[20] Bown (1982).
[21] Type materials and other specimens of *Omomys minutus* and *O. sheai* are here referred to *Loveina* (Robinson, written communication; personal observations; see Simpson, 1940).
[22] Szalay (1976).
[23] Originally reported as cf. *Washakius* (Stucky, 1982); further study suggests that the generic allocation is correct.

Table 1.—*Continued.*

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[24] Although *Huerfanius* and *Uintanius* are closely related to one another, they are here considered distinct genera. The suggestion by Szalay (1976) that the P_{3-4} on the type of *U. turriculorum* are deciduous, is in error (Robinson, oral communication; personal observations).

[25] *Aycrossia* and *Strigorhysis* are morphologically very similar to one another and may be synonymous (Bown, oral communication, 1982). However, *Aycrossia* would appear to be generically distinct from *Absarokius* (contra Szalay, 1982) and *Anaptomorphus* (contra Gingerich, 1981*a*) as detailed by Bown (1979*b*).

[26] *Gazinius* is retained as a distinct genus of anaptomorphid primate. Szalay (1982) has recently suggested that it is a junior synonym of *Anaptomorphus*.

[27] *Cantius* (=*Pelycodus* of authors prior to 1982; see Gingerich and Haskin, 1981) and *Notharctus* are here considered together because of the difficulty of assigning individual specimens to either genus.

[28] Gingerich and Haskin (1981).

[29] Gingerich and Simons (1977).

[30] Gingerich (1979).

[31] Schoch (1981).

[32] McKenna (1976); Gingerich and Gunnell (1979); Stucky and Krishtalka (1983).

[33] FM PM 15602, an incisor fragment of large size with a restricted band of enamel is tentatively referred to *Trogosus.* This specimen was formerly referred to the Taeniodonta (West, 1973*a*).

[34] Robinson (oral communication, 1982).

[35] Species formerly referred to "*Sinopa*" are allocated to creodont genera as proposed by Van Valen (1965).

[36] Record from the Lysite Member of the Wind River Formation based on CM 43800.

[37] Kihm (1984).

[38] Record of *Limnocyon* from the Wind River Formation based on CM 22277.

[39] Record of *Machaeroides* based on CM 37342 and Stucky (1982).

[40] Although *Phenacodus* is not known from Bridger A or B, West and Atkins (1970) report this genus from later Bridgerian Tabernacle Butte (McGrew, 1959).

[41] *Ectocion superstes* is tentatively retained in *Ectocion.*

[42] Occurrence of *Meniscotherium* in the Wind River Formation is based on White (1952) and PU 14875.

[43] Kitts (1957) noted the close similarity of *Hyracotherium craspedotum* and *Orohippus major.* Specimens of these species are virtually identical and are here considered to represent the same species, which is allocated to *Hyracotherium* on the basis of P^4 morphology (see Kitts, 1957).

[44] Korth and Evander (1982); Stucky (1982, 1984).

[45] Record from the Lysite Member of the Wind River Formation based on CM 36094.

[46] New specimens of tapiroids recovered since the most recent review of these North American taxa (Radinsky, 1963) indicate that a review of Eocene *Helaletes* and *Heptodon* is needed. I recognize both *Helaletes nanus* and *Heptodon ventorum* from the Wind River and Bridger formations. *Helaletes nanus* (including *H. boops* and the type specimen of *Heptodon calciculus*) is characterized by oblique lophs and a rounded preentocristid on the lower molars, the absence of P_1, a small hypoconulid on M_3, and curved lophs and a concave metacone on M^3. In contrast, *Heptodon ventorum* is characterized by relatively transverse lophs and a ridge-like preentocristid on the lower molars, presence of P_1, a large hypoconulid on M_3, and relatively straight lophs on the upper molars and a concave metacone on M^3. *H. posticus* is tentatively retained in the genus *Heptodon,* although the expanded postmetacone crista of the upper molars may ally this species more closely with *Hyrachyus.* On the basis of these characters, a specimen from the Aycross Formation referred to *Helaletes* (Bown, 1982) and USNM 363978 from the Bridger Formation are referred to *Heptodon.*

[47] A revision of early and middle Eocene artiodactyls is now in progress by Krishtalka and Stucky, which will result in some taxonomic changes at the generic level. Original generic allocations are here retained.

[48] CM 51656 represents an addition record of *Diacodexis* from the Bridger Formation (see West, 1973*a*).

[49] FM PM 15509, a specimen originally referred to *Phenacodus* (West, 1973*a*) is here referred to the *Wasatchia*/*Bunophorus* group.

[50] Occurrence of *Hexacodus* in the Lysite Member of the Wind River Formation is based on CM 42175, ACM 2800, and ACM 2404.

[51] Record from *Palaeosyops borealis* Zone of the Wind River Formation is based on CM 42126.

[52] Record from the Wind River Formation based on CM 40785. Zone uncertain; specimen may also represent *Hexacodus.*

[53] Identifications of rodents are based on Korth (1981, 1984, and written communications, 1982) and original sources.

Member (Guthrie, 1971) are either an error in identification or a questionable occurrence (Stucky, 1984).

The abrupt appearance of *Palaeosyops borealis, Microsyops lundeliusi, Hyrachyus, Trogosus,* and *Antiacodon* in the uppermost part of the Wind River Formation is used to mark the base of the *Palaeosyops borealis* Assemblage Zone. In addition to the above taxa, the first appearances of *Homacodon, Helohyus, Pantolestes, Huerfanius* (=?*Uintanius*), *Washakius,* cf. *Smilodectes, Selenaletes,* and *Sciuravis* sp. are documented within this zone. All of the above taxa, exclusive of *Selenaletes* and *Homacodon,* are common elements of the fauna from the lower part of the Bridger Formation (Bridger A and B, Gazin, 1976). Mammals typical of the late Wasatchian continue to be common in the *Palaeosyops borealis* zone and include *Hyracotherium, Phenacodus, Notharctus* (*s.l.*), *Esthonyx, Ectocion, Hyopsodus, Heptodon ventorum, Diacodexis, Bunophorus, Paramys, Knightomys,* and *Pauromys.*

The only locality where *Lambdotherium* and *Palaeosyops* may occur together in the Wind River Formation is 48FR76 (White, 1952). However, the lithosympatric (defined in Stucky, 1984) occurrence of these taxa at this locality is at present not determinable; the fossil materials were collected from a stratigraphic interval of several hundred feet rather than a fossiliferous horizon (as defined by Stucky, 1984).

Several localities in the Wind River Basin appear to preserve a more typical Bridgerian fauna (Tourtelot and Thompson, 1948; Black 1969; West and Atkins, 1970; Wallace, 1980; Stucky, 1984). The occurrence of *Palaeosyops huerfanensis* suggests this and may also indicate that additional Eocene biostratigraphic zones can be defined in the Wind River Basin.

SOUTHWESTERN WYOMING

LaBarge fauna of the Wasatch Formation.—The LaBarge fauna reported by Gazin (1952, 1962) contains approximately 35 genera of mammals which were recovered from an approximate 100 ft (30 m) interval. The fauna is similar to the *Lambdotherium* zone fauna of the Wind River Formation but may be slightly older and more similar in age to the *Lambdotherium*-bearing horizons of the Willwood Formation reported by Schankler (1980). Biostratigraphically important genera in the LaBarge fauna include *Ambloctonus, Didymictis, Thryptacodon, Meniscotherium, Esthonyx, Coryphodon, Hyracotherium, Lambdotherium, Bunophorus, Diacodexis, Hexacodus,* and *Knightomys.* All of these genera are now known from the Wind River Formation (CM 42115 and CM 43800, respectively, represent *Hexacodus* and *Ambloctonus*). Wood et al. (1941) included the LaBarge local fauna in their characterization of the Wasatchian.

Dad local fauna of the Wasatch Formation.—The Dad local fauna is less diverse than the LaBarge, consisting of approximately 20 genera (Gazin, 1952, 1962). The presence of *Lambdotherium popoagicum* and *Hyopsodus* sp., cf. *H. walcottianus* suggests a correlation with the *Lambdotherium* zone of the Wind River Formation. This is also suggested by the lack of the first appearances recorded in the *Palaeosyops borealis* zone of the Wind River Formation. *Homogalax* has also been reported, but it is not typical of Graybull *Homogalax* (Gazin, 1962; Radinsky, 1963), probably representing a taxon distinct from *H. protapirinus.* Nothing can be added to Gazin's (1962) discussion of the relationships of the Dad local fauna.

New Fork Tongue of the Wasatch Formation fauna.—Gazin (1962) and West (1973a) have summarized the mammalian fauna of the New Fork Tongue of the Wasatch Formation with slightly differing results. Geographic and stratigraphic differences between the areas from which they recovered the faunas may account for the discrepancies. Gazin (1962) suggested that the New Fork fauna differed from the LaBarge by the first appearances of *Hyopsodus walcottianus, Hapalodectes, Bathyopsis* and *Hyrachyus,* and a different species of *Meniscotherium, M. chamense.* He noted that the species of *Microsyops, Notharctus, Prolimnocyon* and *Bunophorus* had "evolved more appreciably" than the LaBarge species. In general, the fauna reported by Gazin closely resembles the *Lambdotherium* zone fauna of the Wind River Formation. The important exception is the occurrence of *Hyrachyus,* a genus apparently restricted to the *Palaeosyops borealis* zone in the Wind River Formation. Data provided by Gazin (1962) are not sufficient to determine whether *Hyrachyus* occurred either in lithosympatry or lithoparapatry with the taxa typical of the *Lambdotherium* zone of the Wind River Formation.

West (1973*a*) divided the New Fork Tongue in the New Fork-Big Sandy area into two intertonguing facies: a Western Facies and an Arkosic Facies. Approximately 17 mammalian genera have been recovered from localities in the Western Facies, each of which is a fossiliferous horizon. All reported genera are typical of the *Lambdotherium* zone of the Wind River Formation and include both *Lambdotherium popoagicum* and *Meniscotherium.* Neither *Coryphodon* and *Esthonyx,* nor the taxa that first appear in the *Palaeosyops borealis* zone of the Wind River Formation, are reported.

The Arkosic Facies, however, contains approximately 25 genera, some of which are restricted to either the *Lambdotherium* zone or the *Palaeosyops borealis* zone of the Wind River Formation. Two reported mammalian localities, Steele Butte Breaks (BS-1) and East Fork Rim (BS-2), each represent 200 ft (60 m) of stratigraphic section, and it is not known whether all specimens came from the same fossiliferous horizon or were collected over a stratigraphic interval (West, 1973*a,* written communication, 1981). *Hyrachyus* and *Lambdotherium* are known from the Steele Butte Breaks locality and *Palaeosyops borealis* and *Lambdotherium* occur at the East Fork Rim locality. *Coryphodon* is known from both localities and *Esthonyx* only occurs at the latter locality. A specimen from East Fork Rim may also represent *Hyopsodus walcottianus* (FMNH, PM 15318); cf. *Trogosus* (FMNH, PM 15602, this specimen is not included in Schoch and Lucas' (1981) review of *Stylinodon*) may be present at Steele Butte Breaks. Although the biostratigraphic relations of the taxa at these localities are presently unknown, the fauna is of considerable interest. These localities could represent a situation similar to that at locality 48FR76 (White, 1952) in the Wind River Formation where *Lambdotherium* may co-occur with *P. borealis*; alternatively, the situation may be similar to that recorded in the Buck Spring, Red Creek and Deadman Butte stratigraphic sections of the Wind River Formation, where *Hyrachyus* and *Palaeosyops borealis* do not overlap with *Lambdotherium* in 100 ft (30 m) of section (Stucky, 1984). These two localities represent an opportunity to test the validity and possible extension of the *Lambdotherium* and *Palaeosyops borealis* zones in areas outside of the Wind River Basin.

Cathedral Bluffs Tongue of the Wasatch Formation fauna.—Morris (1954), Gazin (1962), West (1973*a*), and West and Dawson (1973) have reported the mammalian fauna of the Cathedral Bluffs Tongue of the Wasatch Formation, which consists of approximately 25 genera. The faunas reported by Morris (1954) and Gazin (1962) and those reported by West (1973*a*) and West and Dawson (1973) are from different basins (Gazin, 1976). This may account for some of the faunal differences, although variation due to age, correlation and sampling may also be important. Genera in common to the Cathedral Bluffs fauna and the *Palaeosyops borealis* zone of the Wind River Formation include *Trogosus, Palaeosyops, Hyrachyus,* and *Antiacodon. Palaeosyops* is, however, represented by a different, larger species, *P. huerfanensis* (Wallace, 1980). Genera in the Cathedral Bluffs fauna that are absent from the *Palaeosyops borealis* zone of the Wind River Formation include *Omomys carteri* and *Anaptomorphus.* The Cathedral Bluffs Tongue fauna, other than the report of *Lambdotherium,* would appear to be younger than the *Palaeosyops borealis* zone fauna of the Wind River Formation. It may correlate with the fauna from strata in the Wind River Formation, where Tourtelot and Thompson (1948) report *P. huerfanensis* (Wallace, 1980), and probably correlates well with the fauna from the upper Huerfano Formation (Robinson, 1966), despite the occurrence of *Coryphodon* and *Esthonyx* in the latter.

Robinson (UCM) and Honey (USGS) have recently recovered fossil mammals from the Cathedral Bluffs Tongue along the East Flank of the Washakie Basin; 1200 ft (365 m) of sediments have been mapped. *Lambdotherium* has been recovered from a locality approximately 190 ft (58 m) above the base of the Cathedral Bluffs Tongue (contact of Tipton Mbr, Green River Formation), and a fauna of Gardnerbuttean age which includes *Omomys* (UCM Loc. 83120) has been recovered 200 ft (61 m) below the contact of the Cathedral Bluffs Tongue and the Laney Shale Member of the Green River Formation.

Lower Bridger Formation fauna.—McGrew and Sullivan (1970), West (1973*a*), and Gazin (1976) have discussed the mammalian fauna (approximately 60 genera) from the lower Bridger Formation. There is no doubt that this fauna is younger than all faunas in southwestern Wyoming discussed above, according to lithostratigraphic relations (West, 1973*a*).

McGrew and Sullivan (1970) provide excellent biostratigraphic data for 35 fossiliferous horizons in Bridger A. Importantly, the Bridger A fauna includes *Omomys, Uintanius, Anaptomorphus,* and *Proviverra,* which are not known from the Wind River Formation. All other genera are represented in the *Palaeosyops borealis* zone of the Wind River Formation (that is, if cf. *Smilodectes* is correctly referred in the Wind River sample, see Stucky, 1982), but some of the species are different—both *Bathyopsis middleswarti* and *Palaeosyops fontinalis* (=*P. paludosus,* see Wallace, 1980) occur in the Bridger A fauna. Typical Wasatchian genera of the *Palaeosyops borealis* zone in the Wind River Formation are absent from this Bridgerian sample—*Esthonyx, Ectocion, Coryphodon, Hyracotherium* and *Bunophorus.*

The lower Bridger Formation fauna from the New Fork-Big Sandy area (West, 1973*a*) is similar to the Bridger A fauna of McGrew and Sullivan (1970), but differs primarily in the greater diversity of small mammals which were recovered by the use of screen washing. Genera not known in the Bridger A fauna of McGrew and Sullivan (1970) include *Thinocyon, Tillomys, Taxymys, Reithroparamys, Helohyus,* and *Diacodexis. Diacodexis* was previously thought to be restricted to the Wasatchian. One additional specimen of *Diacodexis* (CM 51636) is known from the lower Bridger Formation (Bridger B).

Gazin's (1976) lower Bridger sample is based primarily on the collections of the USNM, and includes Matthew's (1909) Bridger A and Bridger B fauna. Most of Gazin's fauna came primarily from Bridger B horizons. Genera that are represented in addition to those reported by both West (1973*a*) and McGrew and Sullivan (1970) include *Tillodon, Ischyrotomus, Harpagolestes, Limnohyops,* and *Parisectolophus.* The derived state of these genera suggests that the fauna is younger than that reported from Bridger A. Other lower Bridger genera are either too poorly known or may be represented in faunas from the

Wind River Formation (*Entomolestes, Thinocyon, Limnocyon, Machaeroides, Synoplotherium, Metacheiromys,* and *Tetrapassalus*; see Stucky, 1982; Table 1).

BIGHORN BASIN, WYOMING

Recent studies by Schankler (1980) in the Willwood Formation and Bown (1982) in the Aycross Formation, as well as other studies of rock units exposed in the Bighorn Basin, suggest a faunal relationship with the *Lambdotherium* and *Palaeosyops borealis* zones of the Wind River Formation.

Schankler (1980) listed approximately 25 genera of mammals in what he defined as the Upper *Heptodon* Range Zone of the Willwood Formation. The generic composition of the fauna from the Upper *Heptodon* Range Zone is quite similar to that from the *Lambdotherium* Range Zone of the Wind River Formation, although small mammals are poorly represented. Species differences appear to be of either paleobiogeographic, paleoecologic, and/or temporal significance. Schankler reports that the common species of *Lambdotherium* is *L. primaevum* (=*L. popoagicum,* according to Wallace, 1980), and that *Esthonyx* is represented by *E. bisulcatus* and *E. acutidens. E. bisulcatus* is not known from the *Lambdotherium* zone of the Wind River Formation. The fauna is undoubtedly older than that from the *Palaeosyops borealis* zone of the Wind River Formation, as it lacks *Palaeosyops, Trogosus, Hyrachyus, Selenaletes,* and other taxa. *Antiacodon* is now known from Yale Localities 162 and 163 (YPM 28020, 28640; Stucky and Krishtalka, in preparation), both of which are in the Upper *Heptodon* Range Zone (Schankler, 1980).

The mammalian fauna of the Aycross Formation of the Absaroka Range, Wyoming, consists of 40 mammalian genera recovered from 28 localities (Bown, 1982). These localities are presumably distributed over a stratigraphic interval, but each locality represents a fossiliferous horizon. Stratigraphic relations of the fossiliferous horizons were not specified. Typical Wasatchian genera, such as *Ectocion, Esthonyx, Coryphodon, Hyracotherium, Lambdotherium,* and *Bunophorus,* are absent. Importantly, a number of the reported genera also occur in the *Palaeosyops borealis* zone of the Wind River Formation, including *Aycrossia, Trogosus, Palaeosyops, Hyrachyus,* and *Antiacodon.* A large species of *Palaeosyops* is, however, represented from one locality—*P. fontinalis* (?=*P. paludosus*). Wallace (1980) has suggested that the *Eotitanops borealis* specimen reported by Bown (1982) may represent either "*Eotitanops*" *minimus* (referred to a new genus by Wallace) or *P. borealis.* Genera in the Aycross fauna not known from the upper part of the Wind River Formation include *Omomys* and *Gazinius.* The faunas in Bown's localities D-1018 and D-1033 compare remarkably well with the fauna from UCM Loc. 79040 of the *Palaeosyops borealis* zone of the Wind River Formation (although the latter locality also preserves *Bunophorus* and *Coryphodon*). The Aycross Formation fauna (in part?) would appear to be slightly younger than the fauna from the *Palaeosyops borealis* zone of the Wind River Formation, based on the presence of *Omomys* and *P. fontinalis.*

Other faunas from the Aycross Formation (McKenna, 1980*a*; Eaton, 1980) compare well with Bown's (1982). Eaton (1982) has also reported mammals from several fossil localities in Aycross-like beds, the Tepee Trail Formation, the Blue Point Marker, the Wapiti Formation, and an unnamed sequence. The mammals are similar to those from Bridger B. *Phenacodus primaevus, Diacodexis, Trogosus,* cf. *Palaeosyops, Omomys carteri, Anaptomorphus, Washakius insignis, Sciuravus, Hyrachyus,* and *Helohyus* are reported.

Torres and Gingerich (1983) have shown that *Lambdotherium* and *Palaeosyops* do not overlap in stratigraphic distribution in the Jim Mountain area of the Bighorn Basin.

HUERFANO BASIN, COLORADO

Robinson (1966) provided the most recent comprehensive review of the mammalian fauna from the Huerfano Formation of southern Colorado. Gingerich (1979, 1981*c*) has discussed some of the primates and horses from this formation. Robinson (1966), following Osborn (1909), orginally divided the Huerfano Formation into two faunal levels, the Lostcabinian and the Gardnerbuttean. Since his review, Robinson and students have recovered a considerable number of specimens (UCM collections) from this formation which substantiate his earlier conclusions. Robinson has recently revised the faunal succession and now recognizes four zones (oral communications, 1981–1982). The lower zone, probably Lysitean in age, includes his localities VIII, IX and XII (provenience on file in UCM locality file). The lower intermediate zone includes his localities IV, VI and XI (=VIIIa of 1966), which is very similar in faunal composition to the *Lambdotherium* zone of the Wind River Formation. The upper intermediate zone includes locality VII and the University of Michigan locality, which contains *Palaeosyops borealis.* The upper zone includes localities I, II, III and V, which were originally used to define the Gardnerbuttean subage (Robinson, 1966). This new faunal zonation conforms with the biostratigraphic data reported in 1966 and in many ways mirrors the faunal zonation proposed for the Wind River Formation (Stucky, 1984).

The lower intermediate zone fauna includes *Lambdotherium popoagicum* and *Hyopsodus walcottianus* in abundance, a specimen of *Megalesthonyx* (Locality VI, Robinson oral communication, 1983), and other typical Wasatchian genera. *Microsyops lundeliusi, Trogosus,* *Palaeosyops borealis,* and *Hyrachyus* are absent. A new, primitive species of *Antiacodon* is now known from this part of the Huerfano Formation (Stucky and Krishtalka, in preparation).

A rather small assemblage of species is associated with *P. borealis* in the upper intermediate zone, which includes *Loveina zephryi, Paramys copei, Viverravus gracilis,* and *Hyoposodus wortmani.* To this list can be added *Hapalodectes,* based on AMNH 17558 from "Apodoch Gulch" (sic). The presence of *Loveina zephryi* represents a discrepancy with the *Palaeosyops borealis* zone of the Wind River Formation. The rarity of this washakiine primate in the Wind River and Huerfano formations and the depauperate fauna of the Huerfano upper intermediate zone make comparison difficult. About the only conclusion that can be drawn is that *Lambdotherium popoagicum* and *Palaeosyops borealis* are not known to be lithosympatric or lithoparapatric in the Huerfano Formation (see Wallace, 1980).

The fauna from Robinson's (1966) upper zone of the Huerfano Formation, on which he based the Gardnerbuttean, is very well represented. Neither *Lambdotherium* nor *Hyopsodus walcottianus* is reported. Taxa in abundance in this upper zone, which are also known from the *Palaeosyops borealis* zone and *not* the *Lambdotherium* zone in the Wind River Formation, include *Microsyops lundeliusi, Trogosus, Palaeosyops, Helaletes, Hyrachyus,* and *Antiacodon.* Other taxa, which are probably represented in the *Palaeosyops borealis* zone, include *Huerfanius, Thisbemys,* and *Mesonyx*; the latter genus also occurs in the *Lambdotherium* zone. Specific differences for *Palaeosyops* (*P. huerfanensis*) and *Didymictis* (*D. vancleveae*) are of importance and may suggest a younger age. "*Eotitanops*" *minimus* (referred to a new genus by Wallace, 1980) is not known from the Wind River Formation. If the evolutionary development of *P. huerfanensis* was isochronous throughout western North America, the horizon from which Tourtelot and Thompson (1948) recovered *P. huerfanensis* in the Wind River Formation would generally correlate with this upper zone fauna of the Huerfano Formation. Gingerich (1979) has recently reported new species of *Smilodectes* and *Notharctus, S. mcgrewi* and *N. robinsoni,* from the upper Huerfano Formation (Locality II), both of which may be present in the *Palaeosyops borealis* zone of the Wind River Formation (see Stucky, 1982, reported as cf. *Smilodectes* sp. and *Notharctus* sp., cf. *N. robinsoni*). *Smilodectes gracilis* may also be represented at Huerfano Locality I (Gingerich, 1979). *Omomys carteri* is also known from the upper Huerfano Formation (UCM 23499, Loc. II).

There is no doubt that typical Wasatchian taxa are also known in the upper zone of the Huerfano Formation (Gardnerbuttean) as Robinson (1966) and McKenna (1976) have shown. These include *Esthonyx acutidens, Bunophorus* and *Coryphodon,* which are represented in the *Palaeosyops borealis* zone of the Wind River Formation as well.

PICEANCE BASIN, COLORADO

The mammalian fauna of the Debeque Formation of the Piceance Basin, Colorado has recently been documented by Kihm (1984). The fauna from the Debeque ranges in age from the Clarkforkian, throughout the Wasatchian, into the Bridgerian. Kihm (1984) divides the Wasatchian into early, middle and late zones, corresponding to the Graybullian, Lysitean, and Lostcabinian. Only the Lostcabinian fauna is discussed here. The late Wasatchian of the Piceance Basin is restricted to the stratigraphic occurrence of *Lambdotherium* in the upper part of the Debeque Formation. Twenty-nine genera are reported from this interval. The fauna is similar to that from the *Lambdotherium* zone of the Wind River Formation (Stucky, 1984) and the upper part of the Willwood Formation (Schankler, 1980). None of the genera which first appear in the *Palaeosyops borealis* zone of the Wind River Formation are present in Kihm's late Wasatchian sample. Kihm indicates that previous reports of *Palaeosyops* from the Debeque Formation were in error.

OTHER NORTH AMERICAN AREAS

"Wasatch" Formation, Powder River Basin, Wyoming.—Whitmore (in Soister, 1968) reports a lower deciduous premolar of *Lambdotherium* along with *Coryphodon* and *Hyracotherium* from Pumpkin Buttes in upper strata of the so called "Wasatch" formation of the Powder River Basin. Delson (1971) has demonstrated that the major part of this rock unit is early Wasatchian in age (Graybullian).

Uinta Basin, Utah.—Burke (1935) reported a single molar (CM 13426) of *Lambdotherium* from the lower of two fossiliferous horizons at the Powder Wash locality in the Douglas Creek Member of the Green River Formation, Uinta Basin, Utah. This specimen has been abraded by fluvial transport, suggesting that it is allochthonous. The fauna from the upper fossiliferous horizon is typically Bridgerian, as indicated by the rodents *Sciuravus* and *Pauromys* (Dawson, 1968), the primates *Utahia, Omomys,* and *Smilodectes* (Gazin, 1958; Szalay, 1976), a large tillodont, a large tapiroid, and the artiodactyls *Antiacodon* and *Microsus.* The insectivores (Krishtalka, 1976*a,* 1976*b*) and marsupials (Krishtalka and Stucky, 1984) are too poorly known among Eocene faunas to contribute to the determination of the age of the fauna from the upper horizon at Powder Wash. Krishtalka and Stucky (1984) have provided a faunal list for the Powder Wash locality and determined the age of this locality as early Bridgerian. Of interest are the insectivore genera *Cryptolestes* and *Aethomylos,* which were previously known only from Eocene localities in California. *Hyracotherium* is the only equid represented at Powder Wash.

Montana.—Wallace (1980) reports that Alan Tabrum (University of Montana) recovered specimens which compare favorably with *P. huerfanensis* and *P. borealis* from the same stratigraphic level in the Sage Creek Beds of Montana.

British Columbia.— Russell (1935) reported *Trogosus* from coal deposits in British Columbia (see Gazin, 1953).

Ellesmere Island, Canada.—A vertebrate fauna, in part homotaxic with early to middle Eocene vertebrate faunas of the western interior of North America, has been recovered over the past decade from localities within the Arctic Circle, Ellesmere Island, Canada (Dawson et al., 1976; West and Dawson, 1978; McKenna, 1980*b*). *Pantolestes, Phenacolemur*-like paramomyids, *Coryphodon,* a tillodont, *Lambdotherium, Hyrachyus, Manteoceras,* a diversity of dermopterans, and rodents, as well as a number of lower vertebrates, invertebrates, and plants, have been reported from several horizons. Hickey et al. (1983) have reported a Clarkforkian age for this fauna based on magnetostratigraphic correlations. However, reexamination of the paleomagnetic data has indicated that samples show overprinting, and there is some doubt as to the validity of the original results (Dawson, oral communication, 1984). Most of the mammals suggest a late Wasatchian or early Bridgerian age.

THE WASATCHIAN-BRIDGERIAN BOUNDARY

Biostratigraphic relations of the late Wasatchian through early Bridgerian faunas of the western interior of North America are sufficiently documented to suggest several alternative definitions for a boundary between these land mammal ages. The faunal studies and systematic reviews, published after Wood et al. (1941) defined the Wasatchian and Bridgerian, have substantially refined and modified the concepts of these ages (see West et al., in press). Range extensions and the clarification of phylogenetic relations (along with correlative nomenclatorial changes) of key taxa as well as the descriptions of new taxa have altered the nature and composition of the faunas ascribed to these ages. Not surprisingly, the basic utility and definitions of the Wasatchian and Bridgerian have remained intact; they still serve as important biochronologic units.

Recent studies detailed above have confirmed that marked faunal turnover occurred across the Wasatchian-Bridgerian boundary. Some taxa, characteristic of the late Wasatchian (Lostcabinian), persist for some time and overlap in occurrence with the first biostratigraphic records of other taxa that become major components of typical Bridgerian faunas. As such, the time interval encompassing the Wasatchian-Bridgerian transition is of theoretical interest in studying faunal turnover and the internal dynamics of paleocommunity evolution. Any boundary should maintain the historical basis and foundations of the land mammal ages laid down by Wood et al. (1941) as well as focus on major, easily recognized events in the fossil record. This may result in minor shifts in the biostratigraphic placement of some faunas; for example, faunas previously classified as late Wasatchian may now be accepted as early Bridgerian. But if these shifts focus attention directly on those events of Eocene vertebrate history which represent turning points in the course of faunal evolution, then the utility of establishing a boundary has been served.

Tedford (1970) suggested that the land mammal ages could become less complex and confusing, and as a result, more utilitarian, if they were based on detailed biostratigraphic studies. Current workers have followed this practice, and have suggested that boundaries are best placed at the record of first occurrences of exotic taxa (immigrant species; Repenning, 1967; Tedford, 1970; Rose, 1981; Stucky, 1984). This practice is followed here.

The lithostratigraphically independent faunal sequences of the early and middle Eocene fossil record from the Big Horn, Huerfano, Green River, and Wind River basins show a common pattern of generic association through the late Wasatchian and early Bridgerian, suggesting a regional level chronofaunal development throughout the western interior of North America. Biostratigraphy remains, at present, the primary means of correlating these sequences. Several alternative boundaries are implied by historical precedent and documented faunal transitions. However, a major emphasis is here placed on the faunal record of the Wind River Formation, because it has classically defined the late Wasatchian and is one of the best documented records of this time period. In order to more fruitfully discuss the alternatives for the Wasatchian-Bridgerian boundary, the major changes in the Wasatchian and Bridgerian land mammal age faunas are discussed in some detail.

Wood et al. (1941:9–10) originally defined the Wasatchian and Bridgerian land mammal ages as follows:

> *Wasatchian* age—new provincial time term, based on at least the upper part of the Wasatch group of southwestern Wyoming (modified to Wasatchian series by C. R. Keyes). As a functional term, the typical areas and faunas must be regarded as those of the Bighorn and Wind River basins of Wyoming. The Wasatchian covers the time during which the faunas of the Sand Coulee, Gray Bull, Lysite and Lost Cabin were deposited. If technical justification for assigning the Lost Cabin to Wasatchian time is required, it is supplied by the discovery of the LaBarge local fauna (q.v., in the Glossary) in the type area of the Wasatch.
> Principal additional correlatives: upper Canyon Largo and lower Huerfano.
> Index fossils: *Ambloctonus, Anacodon, Diacodexis, Diacodon, Didelphodus, Heptodon, Homogalax* (*"Systemodon"*), *Hyracotherium* (*"Eohippus"*), *Lambdotherium, Meniscotherium, Pachyaena, Palaeonictis,* genus cf. *Paramys, Pelycodus, Prolimnocyon, Teilhardella.*

First appearance: *Anaptomorphus, Eotitanops, Hyopsodus, Miacis, Sinopa, Viverravus, Vulpavus.*
Last appearance: *Chriacus, Coryphodon, Didymictis, Dissacus, Ectocion, Ectypodus, Esthonyx,* Multituberculata, *Oxyaena, Palaeosinopa, Phenacodus, Probathyopsis, Psittacotherium.*
Bridgerian age—new provincial time term, based on the Bridger formation of southwestern Wyoming (or a redefinition of Bridgerian "series" of C. R. Keyes), or, more specifically, the time of deposition of Bridger A–D, inclusive, with the enclosed faunas.
Principal correlative: Washakie A with Bridger C + D.
Index fossils: *Apatemys, Helaletes, Helohyus, Homacodon, Hyrachyus affinus, H. princeps, Mysops, Orohippus, Palaeosyops, Patriofelis, Thinocyon, Tillomys, Tillotherium, Uintatherium.*
First appearance: *Harpagolestes, Limnocyon, Mesonyx, Notharctus, Paramys* (proper), *Sciuravus, Telmatherium.*
Last appearance: *Vulpavus.*
Characteristic fossils: *Hyopsodus, Hyrachyus, Miacis.*

Among the index fossils listed for the Wasatchian by Wood et al. (1941), *Diacodexis, Didelphodus, Heptodon, Hyracotherium,* and *Paramys* are known from the *Lambdotherium* zone and *Palaeosyops borealis* zone of the Wind River Formation. These genera may all be represented in the lower part of the Bridger Formation as well (Gazin, 1976; see notes to table 5). Species formerly included in *Pelycodus* have now been assigned to *Cantius, Copelemur, Pelycodus,* and *Notharctus* (Gingerich and Simons, 1977; Gingerich and Haskin, 1981). *Pelycodus* is restricted to the middle part of the Wasatchian. *Cantius* and *Notharctus* appear to represent evolutionary stages of a single lineage and *Copelemur* may represent the ancestor of *Smilodectes.* The notharctine primates from across the Wasatchian-Bridgerian boundary are in need of restudy. *Ambloctonus* and *Meniscotherium* last occur in horizons that preserve *Lambdotherium. Anacodon, Diacodon, Palaeonictis,* and *Tetonius* (=*Anaptomorphus* of Wood et al., 1941) occur only in the early and middle parts of the Wasatchian and are not known to be associated with *Lambdotherium. Teilhardella* has been synonymized with *Apatemys* (West, 1973*b*), which ranges throughout the Bridgerian and Wasatchian. Among the first appearances listed by Wood et al., *Eotitanops* has been synonymized with *Palaeosyops* (Wallace, 1980), and is restricted to non-*Lambdotherium*-bearing fossiliferous horizons. *Palaeosyops* is found associated with genera more characteristic of the Bridgerian than the Wasatchian (*Antiacodon, Hyrachyus,* and *Trogosus*). *Hyopsodus, Miacis, Viverravus,* and *Vulpavus* are known in both typical Wasatchian and Bridgerian assemblages and *Sinopa* has been divided into several genera, the ranges of which are not as yet clearly established (Van Valen, 1965; Gingerich, 1981*b*).

Among the last appearances listed by Wood et al. for the Wasatchian, *Ectocion* is restricted to the *Palaeosyops borealis* zone, and *Ectypodus* is known from the *Lambdotherium* zone of the Wind River Formation. These restricted occurrences in this formation are artifacts of the fossil record, as *Ectocion* occurs in the earlier Wasatchian (Schankler, 1980) and *Ectypodus* is known from the late Eocene (Krishtalka and Black, 1975), and early Oligocene (Krishtalka et al., 1982). All other genera listed as last occurrences are known in either both zones of the upper Wind River Formation (*Coryphodon, Didymictis, Esthonyx, Oxyaena* (s.l.), *Palaeosinopa, Phenacodus*) or neither zone (*Chriacus, Dissacus, Probathyopsis, Psittacotherium*), the latter set being restricted to the early and middle parts of the Wasatchian.

Similar temporal range extensions and systematic changes have been described for the mammalian genera used by Wood et al. (1941) to describe the Bridgerian. Among the index fossils, *Apatemys* is known from the Wasatchian, *Patriofelis* is closely related to *Oxyaena,* and *Tillomys* is closely related to *Knightomys.* A small creodont, possibly related to *Thinocyon,* is known from the Wind River Formation (Stucky, 1982), and *Helaletes* (see table 5), *Helohyus, Homacodon, Hyrachyus, Palaeosyops,* and *Trogosus* (=*Tillotherium*) are all known from the *Palaeosyops borealis* zone of the Wind River Formation. Four of the latter five genera (excluding *Helohyus*) are known from the Huerfano B fauna (Robinson, 1966) as well. *Orohippus* occurs in both the *Lambdotherium* and *Palaeosyops borealis* zones of the Wind River Formation (Korth and Evander, 1982; Stucky, 1982; see Table 1). *Mysops, Uintatherium* and *Telmatherium* are restricted to the upper part of the Bridger Formation (Gazin, 1976; Korth, 1981, 1984).

Among the first appearances listed by Wood et al. (1941) for the Bridgerian, *Harpagolestes* and *Mesonyx* are rare in the Bridger Formation (Gazin, 1976), and the latter is known in the Wind River Formation and Huerfano Formation from several specimens. Both *Paramys* and *Notharctus* are represented in faunas of Wasatchian age (Stucky, 1982). *Sciuravus* is known from Badwater Locality 17 in association with *Phenacodus* and *Antiacodon,* and from UCM Loc. 81010 in association with *Palaeosyops* and *Washakius* in the Wind River Basin. It is also known from Wasatchian deposits in southwestern Wyoming (Gazin, 1962; Korth, 1984).

Savage (1977:439) defined the term Wasatchian as a chronostratigraphic "stage" of worldwide scope, and the "*Lambdotherium* concurrent range zone" for the late Wasatchian of the western interior of North America. He defined these as:

> the lower limit of the Wasatchian stage is defined by the lowest joint occurrence of the following genera: *Hyracotherium, Coryphodon, Haplomylus, Pelycodus, Apatemys, Didelphodus, Palaeosinopa, Prototomus, Viverravus, Miacis, Pachyaena, Hyopsodus, Homogalax* and *Diacodexis.* The upper limit of the Wasatchian is subjacent to the lowest joint occurrence of *Anaptomorphus, Smilodectes, Uintanius,*

> *Washakius, Hemiacodon, Mesonyx, Uintatherium, Palaeosyops, Orohippus, Helaletes, Trogosus, Leptotomus* and *Homacodon* (North American recognition) and is the highest occurrence of *Hyracotherium, Esthonyx, Palaeosinopa, Meniscotherium* and *Coryphodon* (North American and Eurasian recognition) . . . . The lower limit of the *Lambdotherium* zone is defined by the lowest stratigraphic location of the following: *Shoshonius, Patriofelis, Hyrachyus, Eotitanops* [=*Palaeosyops*], *Lambdotherium, Bathyopsis* and *Antiacodon.* The upper limit coincides with the upper limit of the Wasatchian.

Importantly, Savage defined a boundary between the Wasatchian and Bridgerian land mammal ages of North America which can be further refined on the basis of new information. The "*Lambdotherium* concurrent range zone" would appear to be based on the Lost Cabin Member Fauna as described by Guthrie (1971), although a stratotype was not indicated. As shown by Stucky (1984), this fauna represents a composite assemblage of species derived from several superimposed fossiliferous horizons. New biostratigraphic data indicate that *Lambdotherium* does not occur in lithosympatry with *Palaeosyops* (=*Eotitanops*; Wallace, 1980) or *Hyrachyus. Bathyopsis, Antiacodon,* and *Shoshonius* occur in lithosympatry with either *Lambdotherium* or *Palaeosyops.* Their occurrences could be useful in defining the latter part of the Wasatchian as well as the early part of the Bridgerian.

According to the criteria of Savage (1977), the upper limit of the Wasatchian (or the lower limit of the Bridgerian, equivalent to the Wasatchian-Bridgerian boundary) would fall between Bridger B and C, as *Hemiacodon* and *Uintatherium* are restricted to Bridger C and D (Gazin, 1976). Cf. *Smilodectes, Uintanius* (including *Huerfanius*), *Washakius, Mesonyx, Palaeosyops, Orohippus, Helaletes, Homacodon,* and *Trogosus* are now known in the *Palaeosyops borealis* zone of the Wind River Formation. Many of these occur in lithosympatry or lithoparapatry with *Hyracotherium, Esthonyx, Palaeosinopa,* and *Coryphodon* in the Wind River and Huerfano formations. With some minor modifications, Savage's upper limit of the Wasatchian can be used to define the Wasatchian-Bridgerian boundary.

Wood et al. (1941) indicated that the upper Huerfano Formation fauna was early Bridgerian. Robinson (1966) restudied this fauna and used it as the basis for defining the Gardnerbuttean subage of the Wasatchian Land Mammal Age. This fauna, like that now known from the *Palaeosyops borealis* zone of the Wind River Formation, contains genera that are typical of the Wasatchian and the Bridgerian; it appears to be intermediate in age and composition between more typically Wasatchian and Bridgerian faunas. The Gardnerbuttean was characterized by Robinson (1966) by genera with Wasatchian affinities, including *Coryphodon, Absarokius, Palaeosyops, Didymictis, Bunophorus,* and *Diacodexis,* and by those with Bridgerian affinities, including

Patriofelis, Oodectes, Mesonyx, Palaeosyops, Antiacodon, Metacheiromys, Helaletes, and *Trogosus.* McKenna (1976) added *Esthonyx* to the list of genera that were more typical of the Wasatchian. All of these genera, except *Metacheiromys* describe equally well the *Palaeosyops borealis* zone fauna of the Wind River Formation. The upper Huerfano Formation fauna includes several taxa, which are not recorded in the *Palaeosyops borealis* zone of the Wind River Formation: *Omomys carteri* (UCM 23499, Loc. II), *Didymictis vancleveae, Eotitanops minimus* (referred to a new genus by Wallace, 1980) and *Palaeosyops huerfanensis.* These taxa are more advanced than closely related species in the *Palaeosyops borealis* zone of the Wind River Formation, suggesting that most of the Huerfano B fauna is slightly younger. The genera *Helohyus, Ectocion* and *Selenaletes* and any of the homacodontine artiodactyls (*Hexacodus, Microsus* or *Homacodon*), known from the upper part of the Wind River Formation, are absent in Huerfano B.

Classically the presence of *Lambdotherium* has been used to define the late Wasatchian or Lostcabinian (Osborn, 1909; Sinclair and Granger, 1911; Wood et al., 1941; Van Houten, 1945; Gazin, 1952, 1962; Robinson, 1966; Guthrie, 1971; West, 1973*a*; Stucky and Krishtalka, 1982). Importantly, when *Lambdotherium* is known in a fauna, it is abundant. Other taxa that are found in association with *Lambdotherium* and are useful in defining the late Wasatchian include *Hyopsodus walcottianus, Esthonyx, Megalesthonyx, Didymictis, Coryphodon, Thryptacodon, Phenacodus, Diacodexis, Bunophorus, Hyracotherium,* and *Heptodon.* Among these, *H. walcottianus* and *Megalesthonyx* first occur in the North American record in the Lostcabinian. As such, faunas of Lostcabinian or late Wasatchian age would include the *Lambdotherium* Range Zone of the Wind River Formation, the Dad and LaBarge local faunas of the Wasatch Formation, and those from the Western Facies and, in part, the Arkosic Facies of the New Fork Tongue of the Wasatch Formation, the upper *Heptodon* Range Zone of the Willwood Formation, the upper horizons of the Debeque Formation, the lower Huerfano Formation and perhaps the upper part of the "Wasatch" formation of the Powder River Basin.

Although the Gardnerbuttean has not been generally accepted as a useful term in understanding early to middle Eocene faunas in North America, data now available on the fauna from the uppermost part of the Wind River Formation (*Palaeosyops borealis* zone), combined with Robinson's (1966) assessment of this subage, suggest that it has a great deal of utility. The Gardnerbuttean is best characterized by the first occurrences of *Palaeosyops, Hyrachyus, Helaletes,* and *Trogosus,* in conjunction with relict taxa of the Lostcabinian. As such, the Gardnerbuttean would include the faunas from the *Palaeosyops borealis* zone of the Wind River Formation, the upper Huerfano Formation (Huerfano B), the upper part of the Cathedral Bluffs Tongue of the Wasatch Formation (of Gazin, 1962), and, in part, the Arkosic facies of the New Fork Tongue of the Wasatch Formation. If, as advocated here, the concept of the Gardnerbuttean is accepted as earliest Bridgerian and redefined to include those faunas that contain *Palaeosyops borealis,* this subage is useful and important in understanding the chronofaunal changes from the Wasatchian to the Bridgerian. Middle Bridgerian faunas would include those from the Aycross Formation, Bridger A, the Cathedral Bluffs fauna of West and Dawson (1973) and the fauna from the upper Powder Wash locality in the Green River Formation.

The data presently available on late Wasatchian to early Bridgerian faunas summarized above suggest three alternative solutions for a boundary between these two Land Mammal Ages. The ranges of biostratigraphically important taxa from late Wasatchian to early Bridgerian faunas of western North America are presented in Table 2 and all genera known in these faunas are listed in Table 1.

A first alternative would place the boundary at the beginning of the Gardnerbuttean as emended above (i.e., including the occurrence of *Palaeosyops borealis*). This boundary would be determined by the first appearances of *Palaeosyops* (also first appearance of Brontotheriidae), *Trogosus, Hyrachyus, Helaletes, Helohyus, Pantolestes, Omomys, Homacodon, Microsus, Washakius,* and/or *Smilodectes.* The absence of *Lambdotherium* would also be of importance, although its discovery as a relict in Gardnerbuttean faunas would not be surprising. The advantages of this boundary are: 1) the appearances of these exotic taxa in association with typical late Wasatchian taxa (for example, *Coryphodon, Esthonyx, Hyracotherium,* and *Bunophorus*) are relatively easy to recognize in the fossil record; 2) the immigration of these exotic taxa appears to be nearly synchronous, although it was by no means simultaneous; 3) the reliance on stratigraphically well documented collections from the Wind River, Huerfano, Green River and Big Horn basins (Gingerich, personal communication, 1983); 4) the indirect advantage of detailed comparisons of the morphologic variation of taxa from both Wasatchian and Bridgerian sequences. The major disadvantage of the use of the boundary is that it would apparently not be recognizable in the rocks on which the Bridgerian and Wasatchian were originally based. It would seem, however, better to define a boundary that depends on the major features and nature of the fossil record in areas where it can actually be documented. At present, I consider the Gardnerbuttean valid and recognizable in many areas of the western interior of North America.

A second, alternative boundary could be defined on the first ap-

Table 2.—*Occurrences of selected genera in late Wasatchian through early Bridgerian mammalian faunas. Occurrences of different genera within a Land Mammal Subage do not necessarily imply lithosympatry or lithoparapatry (see Stucky, 1984). Key to symbols: CF, tentative identification; ± apparent first occurrence; *, apparent last occurrence; (?), questionable identification; (+), gap in fossil record; +, occurrence.*

	Wasatchian		Bridgerian	
Genera	Lysitean	Lostcabinian	Gardnerbuttean	Bridger A-B
Anacodon	*			
Apheliscus	*			
Xenicohippus	*			
Franimys	*			
Diacodexis	+	+	+	*
Hyracotherium	+	+	+	*
Heptodon	+	+	+	CF*
Phenacodus	+	+	+	(+)
Esthonyx	+	+	*	
Ectocion	(+)	(+)	*	
Prolimnocyon	+	+	*	
Prototomus	+	+	*	
Didymictis	+	+	*	
Hapalodectes	+	+	*	
Coryphodon	+	+	*	
Bunophorus	+	+	*	
Knightomys	+	+	*	
Palaeosinopa	+	+	*	
Thryptacodon	+	+	*	
Absarokius	±	+	*	
Loveina	±	+	*	
Hexacodus	±	+	CF*	
Meniscotherium	+	*		
Ambloctonus	+	*		
Homogalax	+	CF*		
Lambdotherium		±*		
Megalesthonyx		±*		
Shoshonius		±	*	
Orohippus		±	+	+
Pauromys		±	+	+
Antiacodon		±	+	+
Sciuravus		±	+	+
Helaletes		(?)	+	+
Machaeroides		CF	CF	+
Pantolestes			±	+
Washakius			±	+
Omomys			±	+
Smilodectes			±	+
Trogosus			±	+
Palaeosyops			±	+
Hyrachyus			±	+
Helohyus			±	+
Homacodon			±	(+)
Leptotomus			±	+

Table 2.—*Continued.*

Genera	Wasatchian		Bridgerian	
	Lysitean	Lostcabinian	Gardnerbuttean	Bridger A-B
Limnocyon			CF	+
Microsus			CF	+
Anaptomorphus				±
Proviverra				±
Parisectolophus				±
Palaearctonyx				±

pearance of *Limnohyops, Parisectolophus, Ischyrotomus, Taxymys,* and *Tillomys,* and the last appearances of *Esthonyx, Bunophorus, Palaeosinopa, Coryphodon, Ectocion, Didymictis,* and perhaps *Shoshonius.* This boundary has the advantages of the use of both the first occurrence of exotic taxa and the extinction of relict taxa, in addition to the direct relation of the boundary to the rock unit on which the Bridgerian was based (Bridger Formation). The disadvantages of this boundary are that (1) the stratigraphic interval over which it may occur is at present poorly documented, and (2) a heavy reliance would be placed on the absence rather than the presence of taxa.

A final alternative could be the raising in rank of the Gardnerbuttean to full Land Mammal Age status, defined by the first alternative above at its earlier boundary and the second alternative at its later boundary. This would have the advantage of emphasizing the co-occurrence of exotic and primitive taxa, but would de-emphasize the relationships of Gardnerbuttean taxa to either Wasatchian or Bridgerian taxa.

The first alternative represents the better choice, primarily because this boundary: 1) is apparently preserved in several areas where continued biostratigraphic studies could result in a finer record of the faunal change across western North America; 2) fits well into the modern philosophical foundations of systematic analysis, where derived characteristics represent the primary basis for establishing phylogenetic relationships, and exotic taxa represent the primary basis for biostratigraphic relationships; 3) emphasizes the evolutionary patterns of the Bridgerian by focusing on those species which later become dominant elements of the Bridgerian chronofauna; and 4) indirectly shifts the paleontological analysis from the identification of species to an emphasis on the patterns of variation of taxa through time and geographic extent. As such, I advocate that the Wasatchian-Bridgerian boundary be placed at the first occurrences in the fossil record of *Palaeosyops borealis, Hyrachyus,* and *Trogosus.* Continued stratigraphic field studies across the Wasatchian-Bridgerian boundary will not only provide a more refined clarification of age relations between the early to middle

Ecoene faunas of the western interior of North America, but will also contribute to a more realistic understanding of the processes of faunal turnover and vertebrate evolution.

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VERTEBRATES FROM ARCHAEOLOGICAL SITES ON BARBUDA, WEST INDIES

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Abstract

We report our identifications of fish, reptile, bird, and mammal bones from three prehistoric sites on Barbuda. The sites of Indiantown Trail, Sufferers, and Overview Cave contain few examples of the distinctive ceramics associated with the initial Saladoid colonization of the Lesser Antilles in the first centuries A.D. All of Barbuda's sites represent more recent, post-Saladoid occupation except for a possible late Saladoid (Mill Reef) component at the Sufferers site. Marine vertebrate remains from these sites represent bony fish, shark, manatee (*Trichechus manatus*), and a shearwater (*Puffinus lherminieri*). Most of the species of fish occur either in inshore waters or over shallow reefs, two habitats that abound near Barbuda. Terrestrial vertebrates are represented by two species of lizards (notably including the extinct iguanid, *Leiocephalus cuneus*), two species of doves, and an extinct oryzomyine rodent. Fragmentary turtle remains could represent either marine species (Cheloniidae) or the tortoise *Geochelone carbonaria.* Of the 2516 bones in the sample, 2503 (MNI = 147) are from uncontaminated units. By count, fish

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remains constitute 95% of the bones from uncontaminated units; 27% of the fish remains were identifiable to family or lower taxa. This sample reveals some important new records for the vertebrate fauna of Barbuda. The vertebrate assemblage from Indiantown Trail (MNI = 136) contains the greatest number of specimens and diversity of species of the three sites.

INTRODUCTION

Vertebrate assemblages from prehistoric archaeological sites on Barbuda are important to archaeologists and zoologists for several reasons. First, the vertebrate remains establish the contemporaneity of prehistoric human populations with species now extirpated on Barbuda. Second, they indicate the kinds of habitats that existed on Barbuda at the time of human colonization. Third, the remains provide information about the species that people exploited and thus generate data for interpreting human subsistence patterns. Fourth, remains from Barbuda can be compared to those found in prehistoric sites elsewhere in the West Indies. This paper pertains mainly to the first two points. Interpretations about subsistence patterns are constrained by the small number of bones presently available from Barbuda's prehistoric sites. Comparisons with other West Indies faunal assemblages are limited in scope in this paper because a broader treatment of the topic is planned in the future, when the mollusk and crab assemblages have been analyzed and published.

PHYSICAL SETTING

Barbuda is a flat and dry limestone island located between lat. 17°31′ to 17°45′N and long. 61°44′ to 61°53′W in the eastern Caribbean. It lies about 40 km north of Antigua in the outer arc of the northern Lesser Antilles (Fig. 1) and has an area of about 160 km^2 (62 mi^2). Barbuda's name has long been a source of confusion because of its similarity to Barbados, which is located some 500 km SSE. Both names are derived from the Spanish word for "bearded" though why that term was applied to either island remains uncertain (Sauer, 1966:193).

Barbuda and Antigua are the only emergent features on the Barbuda Bank, which is one of the larger and shallower banks in the Lesser Antilles, having an area within the 200 m isobath of about 3600 km^2 (Martin-Kaye, 1969:187). Only 20% of the bank's surface lies at depths greater than 40 m below sea level (Detjen, 1978:54). Deep-water passages separate the Barbuda Bank from other banks in the northern Lesser Antilles. Four marine environments, reef, backreef, sandy bank, and lagoon, are found around Barbuda (Wigley, 1977:299-302). Of the many reefs, the most spectacular one fronts the east coast for almost 35 km (Adey and Burke, 1976:103). Seagrass beds are very extensive to the west and south of Barbuda (ECNAMP, 1980: Map 6).

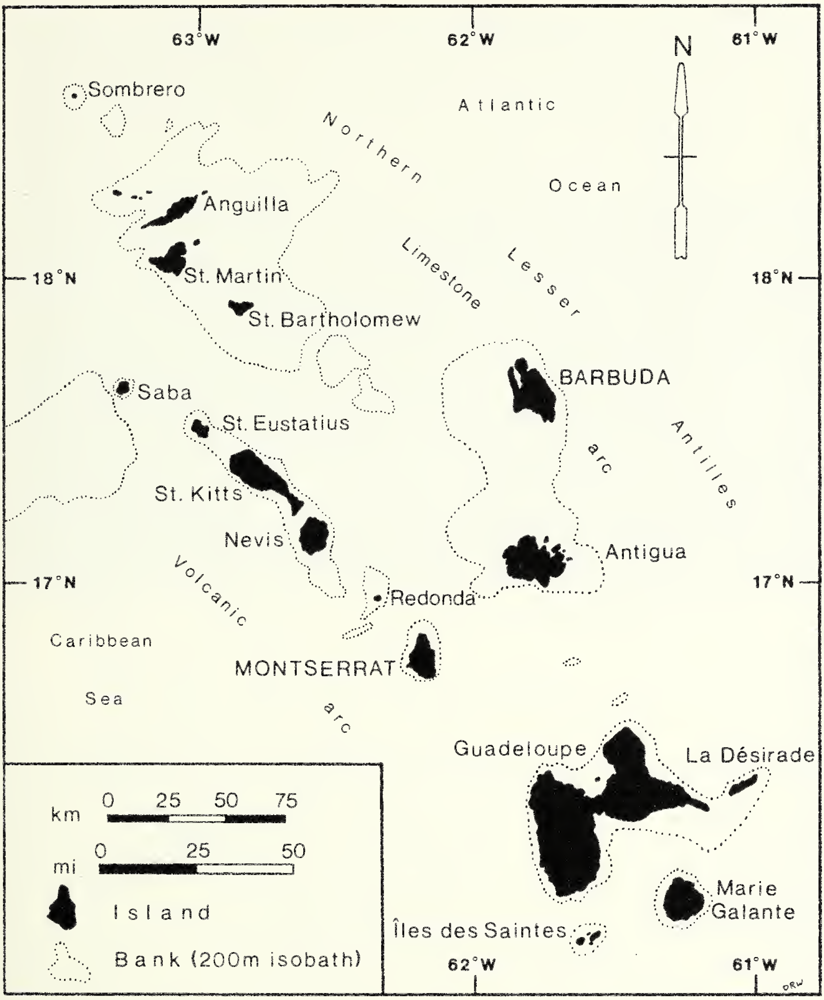

Fig. 1.—Islands and banks of the northern Lesser Antilles, showing the relationship of Barbuda to surrounding islands.

Two major topographic units are present on Barbuda. The first is the "Highlands," a plateau-like feature in the east-central sector occupying about 25% of the landmass (Fig. 2). The edge of the Highlands on the east, north, and northwest faces is marked by distinct, almost vertical escarpments. These escarpments range from 15 to 30 m high, usually rise from the 50-ft contour, and, being former sea cliffs, are

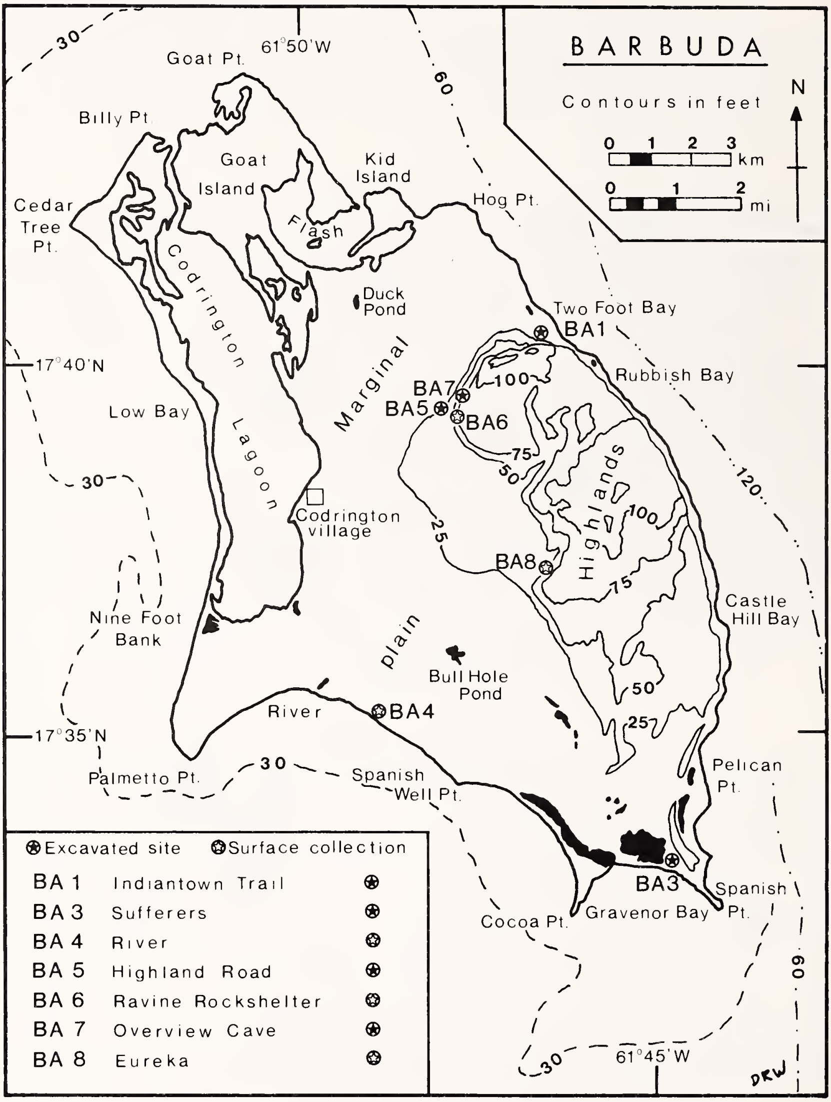

Fig. 2.—Topographic units and prehistoric site locations on Barbuda.

penetrated by numerous caves (Fig. 3). The greatest elevation on Barbuda, which has never been accurately determined or agreed upon, is less than 46 m (150 ft), more than 38 m (125 ft), and occurs at a few isolated areas of the north and central Highlands. In the southern part

Fig. 3.—Escarpments at the east face of the Highlands near Rubbish Bay.

of the Highlands, escarpments are smaller, more gradually inclined, and less commonly encountered.

The other major topographic unit, the Marginal plain, flanks the Highlands on the north, west, and south and generally is level or slopes slightly. The terrain rises above the 25-ft contour at the base of the Highlands (notably to the west) and at a few isolated ridges located elsewhere on the plain. Land is but a meter or two above sea level along most of the coast as well as by Codrington Lagoon and Goat Island Flash, the large saltwater bodies that intrude on the Marginal plain (Fig. 2). Ponds and swamps have formed at inland depressions on the plain and at its fringes.

Brasier and Mather (1975) recognize three limestone units, the Beazer and Codrington formations on the Marginal plain, and the Highlands formation in the Highlands topographic area. A fourth formation (Palmetto Point) includes the coastal sand deposits. Vernon and Lang (1966) identify four soil series. Codrington Clay and Blackmere Clay Loam occur on the Marginal plain, while Barbuda Clay Loam and Highland Ridge Clay Loam occur in the Highlands. "Land type" categories (beach sands, mangrove swamp soil, salina) are also noted. Barbuda's soils are generally shallow with bare limestone pavement being exposed in many areas.

Fig. 4.—Goat Island Trail remained impassable to vehicles for a week after it was inundated on 20 November 1978. Such unusual and ephemeral pools of standing water are formed in depressions on Barbuda's limestone surface after especially heavy rains.

There are no streams anywhere on Barbuda. Rainfall is dispersed mainly through infiltration into solution fissures and sinkholes (which abound in the karstic Highlands) and evaporation. Standing water is common after heavy rains (Fig. 4). The water table is near the surface on the Marginal plain; groundwater tends to be somewhat saline (Mather, 1971).

Barbuda is fringed with extensive white-sand beaches along the south, west, and north coasts. Palmetto Point peninsula and Cedar Tree Point are two major prograding shores with actively accumulating sand deposits. The east coast is solid limestone from Hog Point to Spanish Point except where pocket beaches have formed between rocky headlands. Large dune ridges occur just inland of the east coast at several points.

Harris (1965:25–59) classifies Barbuda's vegetational communities as evergreen woodland, swamp, grassland, and coastal. The latter includes manchineel, mangrove, strand, and rock pavement communities. Barbuda's vegetation tends to be xerophytic and diminutive. Spiny succulents such as cacti and agave are common, and thorny trees and shrubs, many of which possess the physiognomic feature of smaller

Fig. 5.—Large trees are rare on Barbuda. They occur mainly in moisture retaining features such as Darby Sink Cave, a sinkhole located in the northern Highlands.

leaf size to reduce transpiration, tangle and form impenetrable thickets. The few large trees on Barbuda are restricted to moisture-retaining sinkholes for the most part (Fig. 5). Dense mangrove stands border Codrington Lagoon and Goat Island Flash.

In many ways, Barbuda's environments contrast sharply with those of the volcanic islands in the inner arc of the Lesser Antilles, and the contrast between a low limestone island and a high volcanic one was a major theme of the archaeological research undertaken by Watters in 1978–79 on Barbuda and nearby Montserrat (Fig. 1), part of the results of which is discussed herein. Vertebrate remains from Montserrat's sites have been described already (Steadman et al., 1984), and papers on the molluscan fauna of each island's sites are being prepared. Contrasts between the marine and terrestrial fauna of these physiographically dissimilar islands will be discussed in detail in future papers.

ARCHAEOLOGY

The European discoverer of Barbuda is not known and perhaps never will be, yet it seems assured that Columbus did not sight the island in 1493 when his fleet traversed the Lesser Antilles, because the island would have lain too low in the eastern horizon to have been observed.

The first European attempt at colonization for which we have documentation, occurred in 1628 when a party of English under Master Littleton briefly settled but eventually abandoned Barbuda because it was a "barren rocke" (Smith, 1930:65–66). In the 1680s, Barbuda was leased by the Codrington family, who retained the leasehold until the 1870s. It is not known whether Indians resided on Barbuda at the time of European colonization, but it is certain that Caribs from other islands raided the early settlers on a number of occasions in the 17th century (Watters, 1980*a*:84–96). Because of limited and unreliable rainfall and the poor quality of the shallow soil, Barbuda never produced plantation crops such as tobacco or sugarcane, as was the usual case in the volcanic Lesser Antilles. Instead, Barbuda became a "provisioning station" supplying domesticated animals, foodstuffs, hides, charcoal, and other items to Antigua and other nearby islands (Watters, 1980*b*:125).

Very little was known of the prehistoric archaeology of Barbuda prior to the completion of a year-long project by D. R. and C. L. Watters, the results of which are reported elsewhere (Watters, 1980*a*). No published accounts dealt solely with Barbuda's archaeology, although brief comments have appeared in other published works (for example, Harris, 1965:72–73, plate 18; Russell and McIntire, 1966:37). Ceramic assemblages from Barbuda's archaeological sites contain very few examples of the distinctive white-on-red (WOR) and zone-incised-crosshatch (ZIC) ceramics, which are generally regarded as excellent indicators of the initial colonization by ceramic-bearing Amerindians of the Lesser Antilles in the first centuries A.D. WOR and ZIC pottery characteristic of this Saladoid colonization is known from nearby Montserrat, St. Kitts, St. Eustatius, Antigua, and Guadeloupe as well as from the volcanic Lesser Antilles situated further south, nearer the origin area of the distinctive ceramics in South America. Because these ceramics are so widely distributed in the Lesser Antilles, their almost complete absence from the known prehistoric sites of Barbuda is perplexing.

Not only are distinctive WOR and ZIC ceramics largely absent from Barbuda, but the ceramics that have been recovered are generally undiagnostic, being mainly plain sherds. Most of Barbuda's ceramics are referable to the post-Saladoid, for they appear to be more similar to later materials from nearby islands than to the earlier Saladoid assemblages. Rouse and Allaire (1978) have proposed the term "Elenoid" to cover the ceramics in the northern Lesser Antilles and eastern Greater Antilles that are more recent than the Saladoid assemblages. We cannot refer the Barbuda materials to that series with any degree of certainty, since the Elenoid ceramic series is based on materials from Puerto Rico with which we are not sufficiently familiar.

Apart from the very few WOR or ZIC sherds, the only other ceramics from Barbuda that can be regarded as Saladoid are from the Sufferers (BA3) site. These few sherds are most similar to Mill Reef ceramics, which represent a later Saladoid phase known from Antigua (Hoffman, 1979). The late Saladoid ceramics from Sufferers were not found in primary context but instead in bulldozed dirt piles (see site discussion below). If the Sufferers site actually contained a late Saladoid component, this would suggest that Barbuda was occupied around the middle of the first millenium A.D. Sites containing mainly post-Saladoid materials could date to the latter centuries of the first millenium or the beginning of the second millenium A.D.

Seven prehistoric sites were identified during the 1978–79 project. Test pits, excavated at four sites, were dug in 10-cm units within natural strata and the sediments were dry-screened through ⅛-in. mesh. Materials were segregated by 10-cm unit and stratum. Three excavated sites, Indiantown Trail (BA1), Sufferers (BA3), and Overview Cave (BA7), yielded vertebrate remains. No vertebrates were found at the fourth site excavated, Highland Road (BA5), or at three surface collected sites, River (BA4), Ravine Rockshelter (BA6), and Eureka (BA8). (BA2, a designation applied by the Antigua Archaeological Society to extensive piles of *Strombus gigas* at Gravenor Bay, is not presently recognized by us as an archaeological site because cultural remains were not found in association with the shells.)

A single 2 by 2 m test pit excavated in the center of the Indiantown Trail site revealed two strata. Stratum I is a compacted, dark yellowish brown (Munsell notation dry 10YR4/4, wet 7.5YR3/4) soil reaching a depth of slightly more than 60 cm in the eastern part of the test pit. Stratum II is a yellow red (dry 5YR5/8, wet 5YR6/8) soil that presents a striking and unmistakable color contrast with Stratum I. Part of Stratum II was dug to about 120 cm without encountering bedrock. Stratum I contains units 1–7; Stratum II units 8–12 (Fig. 6). Total volume of soil removed from test pit 1 was approximately 4.8 m^3. Stratum I corresponds to Vernon and Lang's (1966) Blackmere Clay Loam and Stratum II to their Barbuda Clay Loam. Artifacts are most abundant in units 2 and 3. No cultural remains occur in Stratum II. One local informant said that some parts of the Indiantown Trail site had been cultivated by Barbudans in this century. No historic artifacts or other indicators of disturbance were found in this particular test pit however, and thus we regard the artifacts and faunal remains to be in primary context. The faunal assemblage from BA1 includes vertebrates coral, crab, and mollusks.

Sufferers (BA3) is the site most difficult to interpret because it has been greatly disturbed. The site's current size appears to be quite large when judging from the distribution of cultural remains on the surface. However, its size is decidedly artificial because much of the area was

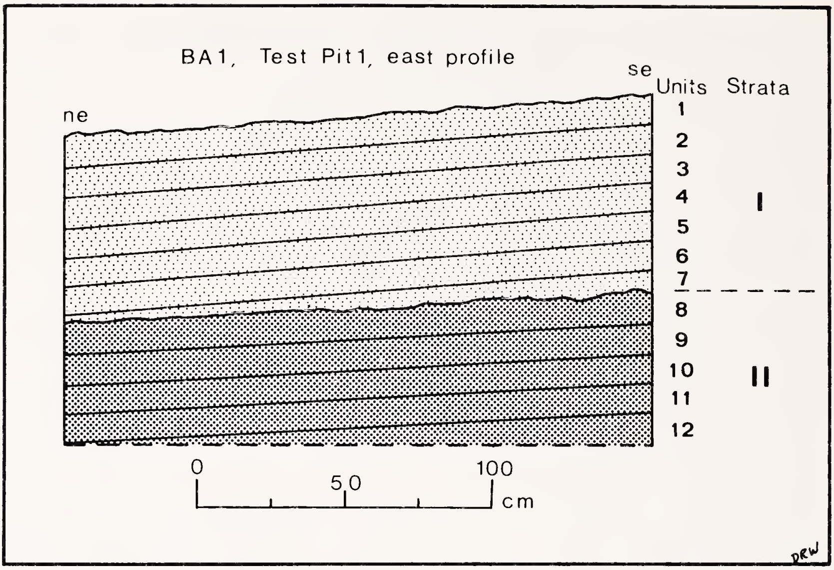

Fig. 6.—Stratigraphic profile of Test Pit 1 at Indiantown Trail, Barbuda.

bulldozed in the 1970s in a scheme to promote cultivation. Exactly how much of the site was destroyed is uncertain, although at least the upper portion must have been displaced because many artifacts were observed in bulldozed dirt piles at the margins of the site. Problems of interpretation are compounded further by the perplexing stratigraphy of test pit 1.

A 1 by 2 m test pit was excavated and three strata were identified at BA3 (Fig. 7). Stratum I reaches a depth of about 35 cm (units 1–4) in the eastern two-thirds of the test pit but extends to about 60 cm (units 1–6) in the western third. Stratum II underlies Stratum I only in the eastern portion. Units 7–9 of Stratum II and units 5–6 of Stratum I are at roughly the same depth. Stratum III begins at about 60 cm throughout the test pit and extends to 110 cm (units 10–13) without revealing bedrock. Stratum I is a pale brown (dry 10YR6/3, wet 10YR4/3), very compacted soil; Stratum II, dark yellowish brown (dry 10YR5/4, wet 10YR4/4), is similarly colored but much less compacted; Stratum III is reddish yellow (dry 7.5YR6/6, wet 10YR7/6) and compacted. We segregated Strata I and II principally on the basis of difference in compactness and secondarily on the color change. Strata I and II probably are Blackmere Clay Loam, whereas III seems to be Barbuda Clay Loam. About 2.2 m^3 of deposit was removed from test pit 1.

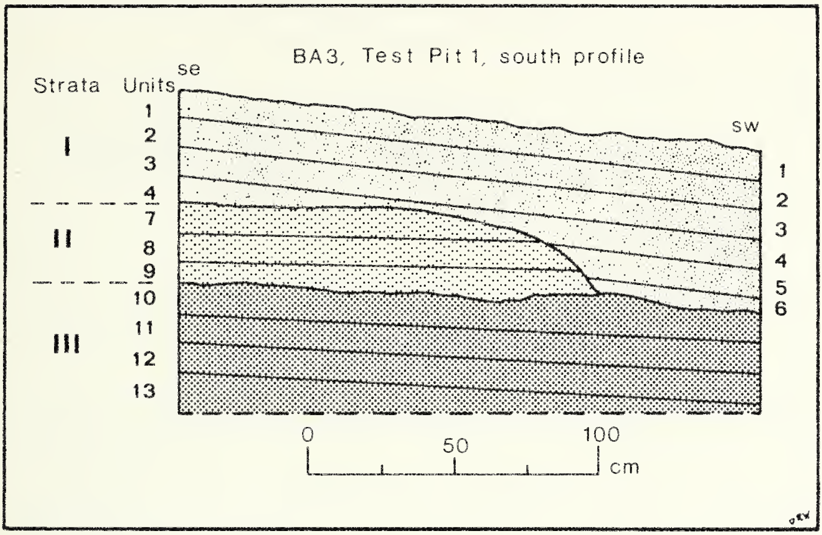

Fig. 7.—Stratigraphic profile of Test Pit 1 at Sufferers, Barbuda.

Knowing beforehand that the site had been bulldozed, we were especially attentive to indications of disturbance while digging test pit 1. The strata did not seem disturbed, and we therefore regard the artifacts and faunal remains as being in primary context throughout the test pit. In our view, the bulldozer probably removed additional units that were in place above the present surface level of the test pit. How much soil was displaced is not known. There is no evidence that the bulldozer disturbed any deposits beneath unit 1. In short, it appears that the dozer blade cut into the original site surface displacing some upper deposits but spared the deeper strata.

The Sufferers site has been bulldozed again according to a report in the *Barbuda Voice* (1983) newspaper. If the site has been totally destroyed, as the report implies, then it is unlikely that we will ever be able to establish confidently the original extent of the site, the actual depth of deposit, or the degree of previous destruction.

Ceramics from test pit 1 at Sufferers are most abundant in units 1–4, whereas vertebrate remains are most numerous in units 2–5 of Stratum I and 7–8 of Stratum II. The quantities of ceramics and vertebrates from Sufferers are minuscule when compared to those from Indiantown Trail. No cultural materials or faunal remains were found in Stratum III. Other faunal remains from the test pit include coral, mollusks, crab, and a single chiton valve.

Overview Cave (BA7) is located about 2.5 km from the east coast

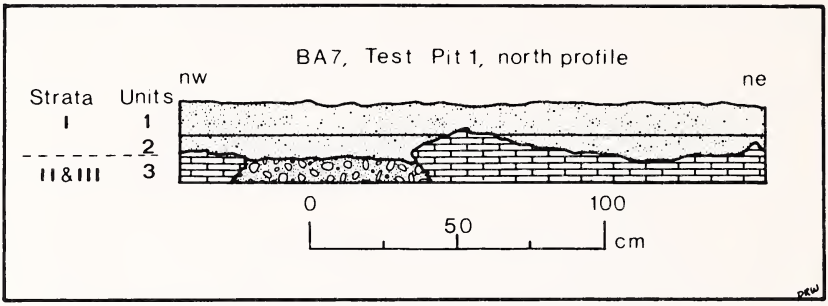

Fig. 8.—Stratigraphic profile of Test Pit 1 at Overview Cave, Barbuda.

at the northwest face of the Highlands escarpment. This is the only inland site where vertebrate remains were recovered. Limestone pavement predominates in the vicinity of the cave. Soil has accumulated in crevices in the limestone but is very shallow. A 1 by 2 m test pit was dug on the slope in front of the cave's dripline. Three strata were identified (Fig. 8). Stratum I, a dark brown (dry 7.5YR3/2, wet 5YR5/2) and very loose soil having much humus, has a maximum depth of about 20 cm (units 1–2) and seems to be Blackmere Clay Loam. Stratum II underlies Stratum I though only in a small portion of the test pit. Stratum II contains only one unit (3), a thin layer of limestone pebbles that grades into bedrock. Solid limestone bedrock (Stratum III) occurs beneath Stratum I in most of the test pit, and beside and under Stratum II in the remainder (Fig. 8). The total volume of deposit removed was 0.5 m^3.

Faunal remains and artifacts occur only in Stratum I and predominantly in unit 1. However, unit 1 is definitely contaminated because it yielded teeth from a non-indigenous animal, the goat. This finding tends to corroborate an informant's statement that the cave was used in the past by persons hunting goats (Watters, 1980*a*:229). Contamination of unit 2 (11–20 cm) in Stratum I is not definite. Unit 2 contains no vertebrate remains that can be ascribed unequivocally to post-Columbian introduced species. We regard artifacts and faunal remains in unit 2 (but not unit 1) to be in undisturbed context. Only 14 vertebrate bones of all kinds were recovered at BA7. Coral, crab, and mollusk remains likewise were limited in number at Overview Cave.

THE VERTEBRATE FAUNA

Species accounts of vertebrate remains from Indiantown Trail, Sufferers, and Overview Cave are presented below in standard systematic order. Test pits are not specified in the "Material" portion of the species accounts because only one test pit was excavated at each site. Fish identifications and interpretations are by Reitz, those of reptiles by Pregill, and those of birds and mammals are by Steadman. All specimens are catalogued in the collections of the Department of Paleobiology of the National Museum of Natural History, Smithsonian Institution (USNM). The six-digit catalogue number appears for each taxon under "Material."

The Minimum Number of Individuals (MNI) was determined using paired elements, size, age, and excavation provenience as criteria. In calculating MNI, the vertebrate sample from each Stratum was considered to be a single, homogenous unit. This consideration rests upon the relative uniformity of the sediment within each Stratum. Not included in MNI calculations are bones from the surface and disturbed level (unit 1) at Overview Cave. These bones were excluded because our main interest is with the fauna that can be associated definitely with Amerindian occupation. Faunal remains from contaminated units cannot be related with certainty to the prehistoric occupation because some of these bones could have been introduced into the sediments during the historic period.

Two basic problems confront zooarchaeological use of MNI. First, MNI usually is based upon paired elements such that two left dentaries, for example, indicate two animals. Occasionally, however, a species is identified only from non-paired elements such as vertebrae or scales, and when this occurs the number of individuals may be underestimated in MNI tabulations. Second, MNI is subject to sample size bias. Samples with fewer than 200 individuals or 1400 bones may be too small for certain interpretations (Grayson, 1979; Wing and Brown, 1979). The sample discussed herein contains 2503 bones from uncontaminated units, but 1858 (74%) are fragmentary remains identifiable only as "Fish sp." or "Vertebrate sp.," and the sample's MNI (at 147) is less than 200 individuals. Until a larger sample is acquired through additional excavations, it is not possible to determine with confidence the nature or extent of sample size bias in our present sample, or to correct for it. Our data, however, do document the contemporaneity of certain species with the aboriginal inhabitants.

Our interpretation of the faunal remains is complicated further by the paucity of information about the modern fauna of Barbuda. Thorough surveys are needed before definitive statments are made about the current status of vertebrates on the island. From 16 to 24 January 1983, Pregill, Steadman, and Watters were part of a team that visited Barbuda to begin such surveys. Birds, reptiles, and mammals collected during that period have been deposited in the San Diego Natural History Museum and the National Museum of Natural History, Smithsonian Institution. We hope to continue with a more complete survey of Barbuda's vertebrates in the future.

FISH

The fish were identified using the comparative skeletal collection of the Zooarchaeological Laboratory, Florida State Museum, Gainesville. Five atlases from uncontaminated units could be measured (width of atlas in mm—*Albula vulpes,* 11.0; *Epinephelus* spp., 6.7, 8.9; *Mycteroperca* spp., 10.3; *Haemulon* spp., 7.5), and the estimated weights of the fish range from 713 to 1966.7 g (1.57 to 4.34 pounds). Another atlas of *Epinephelus* is noticeably larger (16.3 mm) and came from a fish that could have weighed as much as 4598.9 g (9.7 pounds). That atlas, however, came from the surface of the Overview Cave site and thus cannot be indubitably associated with prehistoric occupation. Weights for all the fish bones have been recorded and are available on request from Reitz. Modifications observed on the bones included an enlarged notochord foramen on the shark vertebra. Habitat and behavioral information summarized below by species comes from Randall (1968) and Fischer (1978).

Order Squaliformes
Family Carcharhinidae
Carcharhinidae sp.—requiem shark

Material.—Sufferers, Stratum II: unit 7—vertebra (359456). MNI = 1.

Six species of requiem sharks occupy inshore Caribbean waters and others are found in deeper waters. Sharks are more active at night than by day but will feed whenever the opportunity arises. They can be taken with hook and line, spears, or nets. The individual identified from Sufferers was at least one meter long. Sharks are known to have been consumed by aboriginal peoples elsewhere in the West Indies (Wing and Reitz, 1982), although the modified vertebra identified here may not document a subsistence related activity.

Order Elopiformes
Family Albulidae
Albula vulpes (Linnaeus)—bonefish

Material.—Indiantown Trail, Stratum I: unit 1—vertebra (359457); unit 2—5 teeth row fragments (359458); unit 3—atlas, 9 teeth row fragments (359459); unit 4—vertebra (359460); unit 7—2 vertebrae (359461). MNI = 2. Overview Cave, Stratum I: unit 1—vertebra (359462). MNI = 0.

This is a carnivorous fish that inhabits sand or mud flats in shallow coastal waters. It feeds on bottom-dwelling invertebrates and may be caught on light tackle. Bonefish are especially plentiful in Codrington Lagoon and Goat Island Flash according to residents of Barbuda.

Order Atheriniformes
Family Belonidae
Belonidae sp.—needlefish

Material.—Indiantown Trail, Stratum I: unit 1—maxilla (359463). MNI = 1.

Needlefishes are pelagic species occupying offshore surface waters or coastal environments, depending on the species. These carnivores are caught with nets and by hook and line.

Order Perciformes
Family Serranidae
***Epinephelus* sp.**—grouper

Material.—Indiantown Trail, Stratum I: unit 1—atlas, epihyal, maxilla (359464); unit 2—8 articulars, 10 dentaries, 3 maxillae, premaxilla, opercular (359465); unit 3—epihyal, premaxilla, maxilla, 2 dentaries, 2 quadrates (359466); unit 4—2 articulars, dentary, (359467); unit 7—articular, quadrate (359468). MNI = 7. Sufferers, Stratum I: unit 6—atlas (359469). MNI = 1. Overview Cave, Surface—atlas (359470). MNI = 0.

***Mycteroperca* sp.**—grouper

Material.—Indiantown Trail, Stratum I: unit 2—dentary (359471); unit 3—atlas, articular (359472). MNI = 1.

Serranidae sp.—sea basses

Material.—Indiantown Trail, Stratum I: unit 1—quadrate, pharyngeal, epihyal (359473); unit 2—basioccipital, maxilla (359474); unit 3—preopercular (359475); unit 4—2 fragments (359476). MNI = 0. Sufferers, Stratum I: unit 3—maxilla (359477). MNI = 0.

Groupers are dermersal carnivores that occupy a variety of habitats. Many members of this family are found over deep, dead coral banks or rock ledges, whereas others are found over shallow reefs. They are caught with spears, handlines, and traps.

Family Lutjanidae
***Lutjanus* sp.**—snapper

Material.—Indiantown Trail, Stratum I: unit 2—2 articulars (359478); unit 3—articular (359479). MNI = 2.

Snappers are one of the most abundant Caribbean fish families and tend to be found over banks rather than shallow reefs; some species school. They are carnivorous, active at night, and can be taken with handlines, traps, or nets, depending upon the species.

Family Haemulidae
***Haemulon* sp.**—grunt

Material.—Indiantown Trail, Stratum I: unit 2—atlas (359480); unit 3—maxilla (359481). MNI = 1.

***Orthopristis* sp.**—pigfish

Material.—Indiantown Trail, Stratum I: unit 1—maxilla, articular (359482). MNI = 2.

Grunts are a diverse family, generally abundant in deep reefs in the Caribbean. Individuals feed on invertebrates over sand and grass flats at night. They are caught using seines, traps, and handlines.

Family Sparidae

Sparidae sp.—porgies

Material.—Indiantown Trail, Stratum I: unit 2—pterotic (359483). MNI = 1. Overview Cave, Stratum I: unit 2—fragment (359484). MNI = 1.

Porgies are a group of bottom-dwelling species that live primarily over rocky areas, deep reefs, or flat bottoms. They are taken with traps and handlines.

Family Labridae

***Bodianus* sp.**—wrasse

Material.—Indiantown Trail, Stratum I: unit 2—pharyngeal, maxilla, premaxilla (359485). MNI = 1.

***Halichoeres* sp.**—wrasse

Material.—Indiantown Trail, Stratum I: unit 3—premaxilla (359486). MNI = 1.

Wrasses are a family of generally carnivorous fishes. This group is one of the most diverse in the Caribbean, and some of the species are among the most numerous fishes on shallow coral reefs. They are diurnal and feed primarily on benthic invertebrates. Wrasses are captured using handlines or traps.

Family Scaridae

***Scarus* sp.**—parrotfish

Material.—Indiantown Trail, Stratum I: unit 1—dentary, premaxilla, 7 pharyngeal fragments (359487); unit 2—70 pharyngeal fragments, 6 hyomandibulars, 12 dentaries, 14 premaxillae, 4 quadrates (359488); unit 3—63 pharyngeal fragments, 10 dentaries, 4 premaxillae, articular, quadrate, 3 maxillae, 2 basioccipitals, 5 hyomandibulars, 5 operculars, 2 fragments (359489); unit 4—vertebra, basioccipital, opercular, 8 pharyngeal fragments, maxilla, dentary, 4 fragments (359490); unit 5—maxilla, opercular, vertebra, 6 pharyngeal fragments, dentary, premaxilla, fragment (359491); unit 6—premaxilla, 6 pharyngeal fragments, fragment (359492); unit 7—4 pharyngeal fragments (359493). MNI = 36.

***Sparisoma* sp.**—parrotfish

Material.—Indiantown Trail, Stratum I: unit 1—6 pharyngeal fragments, 2 maxillae, 2 dentaries (359494); unit 2—10 pharyngeal fragments, 2 articulars, quadrate, 10 dentaries, 6 premaxillae (359495); unit 3—13 pharyngeal fragments, 11 dentaries, 9 premaxillae, basioccipital (359496); unit 5—2 pharyngeal fragments (359497); unit 6—2 pharyngeal fragments, quadrate, articular (359498); unit 7—pharyngeal fragment (359499). MNI = 15. Overview Cave, Stratum I: unit I—pharyngeal fragment, dentary (359500). MNI = 0.

Scaridae sp.—parrotfish

Material.—Indiantown Trail, Stratum I: unit 2—9 vertebrae, 4 operculars, 2 hyomandibulars, 4 dentaries, 2 fragments (359501); unit 3—6 fragments (359502); unit 5—2 teeth (359503); unit 7—basioccipital, pharyngeal fragment, opercular (359504). MNI = 0.

Parrotfishes are herbivorous animals that occur very commonly over shallow coral reefs and are active during daylight hours. They will seldom take a hook and are most often captured in traps or speared. They can be trapped in sizable numbers.

Family Sphyraenidae

Sphyraena barracuda (Walbaum)—barracuda

Material.—Indiantown Trail, Stratum I: unit 1—vertebra (359505); unit 2—3 premaxillae, vertebra (359506); unit 3—3 vertebrae (359507). MNI = 2.

Barracudas are pelagic carnivores found in a variety of habitats depending upon age. Young fishes live inshore whereas solitary adults live over reefs and in offshore waters. Handlines or nets are used to capture barracudas.

Family Acanthuridae

***Acanthurus* sp.**—surgeonfish

Material.—Indiantown Trail, Stratum I: unit 2—11 cleithra, 56 spines (359508); unit 3—16 spines, cleithrum (359509); unit 4—4 spines (359510); unit 5—6 spines (359511); unit 6—3 spines (359512); unit 7—spine (359513). MNI = 43.

Most surgeonfishes live over shallow coral reefs or rocky areas. They are diurnal feeders on benthic algae and sea grasses. They will not take a hook. They compose a major portion of catches in traps.

Family Scombridae

Scombridae sp.—mackerals

Material.—Indiantown Trail, Stratum I: unit 1—vertebra (359514). MNI = 1.

Mackerals are pelagic fishes generally found in offshore waters although some species enter reef areas. They are usually taken with hook and line although nets and traps can be used.

Order Tetradontiformes

Family Balistidae

***Balistes* sp.**—triggerfish

Material.—Indiantown Trail, Stratum I: unit 2—spine, premaxilla (359515); unit 4—

2 spines (359516); unit 5—spine (359517). MNI = 4. Sufferers, Stratum II: unit 8—spine (359518). MNI = 1.

Triggerfishes are generally solitary inhabitants of reefs although some species occur over sand, rubble, or seagrass beds. They usually feed on benthic invertebrates and are caught in traps or by using handlines.

Family Diodontidae
Diodon hystrix Linnaeus—porcupinefish

Material.—Indiantown Trail, Stratum I: unit 1—dentary (359519); unit 2—dentary (359520). MNI = 2.

Diodontidae sp.—porcupinefish

Material.—Indiantown Trail, Stratum I: unit 3—spine (359521). MNI = 0.

Porcupinefishes occur in a variety of habitats including shallow reefs and inshore waters. They feed on benthic invertebrates and may be caught using traps or handlines.

Fish sp.

Material.—Indiantown Trail, Stratum I: unit 1—141 fragments (359522); unit 2—945 fragments (359523); unit 3—407 fragments (359524); unit 4—91 fragments (359525); unit 5—89 fragments (359526); unit 6—61 fragments (359527); unit 7—56 fragments (359528). MNI = 0. Sufferers, Stratum I: unit 2—8 fragments (359529); unit 3—9 fragments (359530); unit 4—vertebra (359531); unit 5—4 fragments (359532); unit 6—vertebra (359533). Stratum II: unit 7—4 vertebrae (359534); unit 8—6 fragments (359535); unit 9—2 fragments (359536). MNI = 0. Overview Cave, Stratum I: unit 1—6 vertebrae (359537). MNI = 0.

REPTILES

Fragmentary and mostly unidentifiable remains of turtles were found at Indiantown Trail (BA1) and Sufferers (BA3). Two species of lizards were identified from isolated elements recovered from Indiantown Trail. The bones were compared with skeletons in the osteological collections of the Department of Herpetology, San Diego Natural History Museum.

Order Testudines
Family indeterminate—turtles

Material.—Indiantown Trail, Stratum I: unit 1—metacarpal fragment (359538); unit 2—scrap of plastron or carapace (359539). MNI = 1. Sufferers, Stratum I: unit 1—4 scraps of plastron and/or carapace (359540); unit 2—scrap of plastron or carapace (359541); unit 3—3 scraps of plastron and/or carapace (359542); unit 5—11 scraps of plastron and/or carapace (359543). MNI = 1.

The referred material consists of thumbnail size scraps of bones that are inadequate even for confident identification to family. Quite probably they represent marine turtles (Cheloniidae). The Hawksbill *Er-*

etmochelys imbricata and the Green Turtle *Chelonia mydas* are not uncommon in archaeological sites from the West Indies, having been reported in cultural contexts from Antigua (Wing et al., 1968), St. Kitts, Marie Galante (Wing, 1973), and Montserrat (Steadman et al., 1984). Sea turtles nest on a number of Barbuda's beaches today.

Conceivably, some of the bones could belong to the tortoise *Geochelone carbonaria.* The species is a native of northern South America (Williams, 1960) that presumably has been introduced in the West Indies, primarily the Lesser Antilles, although it is unclear when or by whom. The literature on the subject is scattered and vague (Grant and DeSola, 1934; Lescure, 1979; Underwood, 1962), but supposes that Amerindians migrating north from South America may have transported these animals. The species has never been documented in an archaeological context. *Geochelone carbonaria* occurs throughout Barbuda today, although it is cryptic and infrequently encountered in the field. Barbudans still gather and eat this tortoise.

Order Squamata
Family Iguanidae
Leiocephalus cuneus Etheridge (1964)—curly-tailed lizard (Extinct)

Material.—Indiantown Trail, Stratum I: unit 6—right dentary, right femur (359544). MNI = 1.

Leiocephalus cuenus is an extinct lizard known only from fossils collected in several caves near Two Foot Bay on the east coast of Barbuda (Etheridge, 1964). The cave deposits were presumed to be of latest Pleistocene age. The fossils came from paleontological rather than archaeological context. The dentary and femur from the Indiantown Trail archaeological site differ in no significant way from the fossil type material. The Indiantown Trail site is located within 1 km of the Two Foot Bay caves (Fig. 2). The Indiantown Trail specimens are the first *L. cuneus* bones recovered from archaeological context.

More recently, fossils of *L. cuneus* along with a number of other extinct vertebrates were found in sediments at Burma Quarry, a fissure deposit located on the northeast coast of Antigua. This material was associated with five stratigraphically concordant radiocarbon dates ranging from 2560 ± 70 years B.P. to 4300 ± 150 years B.P. In an analysis of the paleontology of Burma Quarry, Steadman et al. (manuscript) conclude that the arrival of Amerindians on the island, and the subsequent colonization by Europeans, caused massive extinctions in the vertebrate fauna of Antigua because of habitat destruction. Among those species was *L. cuneus.* The contemporaneity of *L. cuneus* with the Amerindian occupation and the essentially modern extirpation of the species from Antigua are now confirmed for Barbuda as well by the evidence from Indiantown Trail. The specific causes pertaining to the extinction of *L. cuneus* are unclear.

Leiocephalus cuneus is the largest species of the genus known, either fossil or living. The dentary from BA1 has a tooth row length of 18.6 mm and came from an individual approximately 160 mm in snout–vent length. Large adults of this species, however, may have obtained a snout–vent length of as much as 200 mm. The largest of the 22 living species, all restricted to the Greater Antilles, are at most 120 to 130 mm snout–vent length.

Elsewhere in the Lesser Antilles, recently extinct species of *Leiocephalus* are known from Anguilla (Pregill, personal observation) and Martinique, the latter having become extinct sometime in the 19th century (Pregill et al., manuscript).

Family Teiidae
Ameiva* cf. *griswoldi Barbour (1916)—
ameiva or ground lizard

Material.—Indiantown Trail, Stratum I: unit 2—right humerus (359545). MNI = 1.

This specimen is from a small *Ameiva* probably no more than 65 mm snout–vent length. The epiphyses are missing from both ends of the bone, suggesting that it came from a juvenile. The epiphyses normally do not fuse to the shaft until adult size is reached. The deep olecranon fossa is preserved, however, and will serve to distinguish the humerus of *Ameiva* from those of the other small Lesser Antillean lizards. *Ameiva griswoldi* is endemic to the Barbuda Bank and common throughout Barbuda today. Adults reach an average snout-vent length of approximately 110 mm.

On some islands of the Lesser Antilles, *Ameiva* have been subjected to intense predation pressure by mongooses (*Herpestes* spp.), even to the point of extinction. Although the mongoose has effectively extirpated *A. griswoldi* from Antigua in the past few decades (Steadman et al., manuscript), the lizard survives on Barbuda and some of Antigua's offshore cays that are free of mongoose predation. The species was also reported from archaeological deposits at Mill Reef, Antigua (Wing et al., 1968).

BIRDS

Nine bird bones were recovered, all from the Indiantown Trail site. Identifications were made using the skeletal collection of the Division of Birds, USNM. The last faunal report on the ornithology of Barbuda is that of Danforth (1935). Barbudan birds are covered by Bond (1956, and supplements) in a general sense, but a thorough treatment of the modern Barbudan avifauna is not presently available.

Order Procellariiformes
Family Procellariidae
Puffinus lherminieri Lesson—Audubon's Shearwater

Material.—Indiantown Trail, Stratum I: unit 2—humerus, tarsometatarsus (359428); unit 3—ulna, 2 carpometacarpi (359429); unit 4—humerus (359430). MNI = 1.

P. lherminieri is readily distinguished from all other West Indian procellariids by its small size. There are no historic records of Audubon's Shearwaters from Barbuda. Brodkorb (1963:246) reported *P. lherminieri* as a fossil from caves on Barbuda of presumed late Pleistocene age, based on unspecified collections at the University of Florida. *P. lherminieri* is known from the late Holocene Burma Quarry site and other archaeological sites on Antigua (Steadman et al., manuscript), where *P. lherminieri* is also apparently extinct today, or at least has not been recorded historically. Some combination of predation by rats (*Rattus*) and humans probably accounts for the loss of *P. lherminieri,* which probably nested along the east coast of Barbuda in prehistoric times.

Order Columbiformes
Family Columbidae
Columba leucocephala Linnaeus—White-crowned Pigeon

Material.—Indiantown Trail, Stratum I: unit 3—carpometacarpus (359431); unit 4—humerus (359432). MNI = 1.

This and the next identification are based upon the comparative osteology of northern Lesser Antillean columbids outlined in Steadman et al. (1984). *C. leucocephala* occurs commonly as a fossil in the West Indies, although the nearest prehistoric record to Barbuda is from St. Croix (Brodkorb, 1971:196; Olson and Hilgartner, 1982). This pigeon of many habitats is widespread in the Antilles today, and is known commonly from Barbuda (Riley, 1904; Danforth, 1935; Steadman, personal observation, 1983).

Geotrygon mystacea (Temminck)—Bridled Quail-dove

Material.—Indiantown Trail, Stratum I: unit 4—femur (359433). MNI = 1.

The only other prehistoric record of *G. mystacea* is from Montserrat (Steadman et al., 1984). This dove may be extinct now on Barbuda, for it has been reported only by Cory (1892), who provided no details for the record. Elsewhere in the Lesser Antilles, *G. mystacea* prefers a moist canopied forest. Some of the forest found today in the Highlands of Barbuda would seem to be adequate to support this species. Nevertheless, the occurrence of *G. mystacea* in an archaeological context may suggest that Barbuda's forests were less disturbed prehistorically than in post-Columbian times.

MAMMALS

As was the case on Montserrat (Steadman et al., 1984), all species of mammals recorded from archaeological sites on Barbuda owe their current status to the activities of humans, who either introduced or extirpated each species. Specimens in the Division of Mammals, USNM, were used for comparisons, as were paleontological and archaeological remains of rodents from many other Lesser Antillean islands. Sequence and nomenclature follow Varona (1974).

Order Primates
Family Hominidae
Homo sapiens Linnaeus—man

Material.—Indiantown Trail, Stratum I: unit 4—2 femoral fragments (359435). MNI = 1.

These specimens are from the femoral shaft of an adult. The bones are from an uncontaminated unit, and therefore are from an Amerindian rather than a European or African.

Order Sirenia
Family Trichechidae
Trichechus manatus Linnaeus—manatee

Material.—Indiantown Trail, Stratum I: unit 2—humerus (359434). MNI = 1.

The manatee is known historically from the Greater Antilles. It is rare and local there today. To our knowledge, this specimen is the first record of *T. manatus* from Barbuda. Elsewhere in the Lesser Antilles, manatees are known from archaeological contexts on Antigua (Wing et al., 1968) and on St. Lucia, and from historical accounts on Marie Galante and Martinique (Ray, 1960).

Order Artiodactyla
Family Bovidae
Capra hircus Linnaeus—goat

Material.—Overview Cave, Stratum I: unit 1—upper premolar, 2 upper molars, lower molar (359436). MNI = 0.

These teeth are the only specimens from any Barbudan prehistoric site that represent an animal introduced in post-Columbian times. Therefore, the upper 10 cm of sediment at the Overview Cave test pit cannot be considered to be of a purely prehistoric context. Goats were brought to Barbuda in early historic times, by the middle of the seventeenth century if not earlier.

Order Rodentia
Family Cricetidae
Tribe Oryzomyini
Undescribed extinct species
("Undescribed species B" of Steadman et al., 1984)

Material.—Indiantown Trail, Stratum I: unit 1—maxilla with M*1-3,* humerus (359437); unit 2—5 mandibles with 0 to 3 molars (359439); 2 pelves, 4 femura, 3 tibiofibulae (359438); unit 3—3 pelves, 6 femora, 2 tibiofibulae (359440); unit 4—femur, tibiofibula (359441); unit 5—2 mandibles with 1 and 3 molars (359442); unit 6—femur, tibiofibula, metatarsal or metacarpal (359443). MNI = 6. Sufferers, Stratum I: unit 2—femur (359444); unit 3—humerus, 2 femora (359445); unit 4—humerus (359446). MNI = 3. Stratum II: unit 7—lower incisor (359447); unit 8—3 mandibles with all molars (359448); unit 9—metacarpal or metatarsal (359449). MNI = 3.

This extinct rodent has been reported previously from paleontological sites on Barbuda that are late Pleistocene or Holocene in age (Wing et al., 1968). This widespread but still undescribed extinct species is also known from prehistoric archaeological sites on Antigua, Montserrat, Guadeloupe, and Marie Galante (Steadman et al., 1984).

Vertebrate sp.

Material.—Indiantown Trail, Stratum I: unit 2—2 fragments (359452); unit 3—2 fragments (359450), 359451). MNI = 0. Sufferers, Stratum I: unit 4—21 fragments (359455). Stratum II: unit 7—8 fragments (359453, 359454). MNI = 0.

These fragmentary scraps of bone are wholly undiagnostic and cannot be allocated even to class.

Compilations of our analyses are presented in Tables 1 and 2.

DISCUSSION

Indiantown Trail (BA1), the largest known prehistoric site on Barbuda, yielded far more ceramics than Sufferers (BA3) and Overview Cave (BA7), and the site's vertebrate assemblage also contains by far the greatest number of specimens and diversity of species of any excavated site on Barbuda. The quantity and diversity of vertebrate remains at BA1 are not unusual in view of the range of terrestrial and marine habitats in its vicinity. The abundance of artifacts and faunal materials recovered from the test pit indicates that BA1 was used extensively by Barbuda's early inhabitants. Indiantown Trail would have been a location preferable in many ways to other areas of Barbuda.

The site is situated on the Marginal plain at the base of the Highlands escarpment some 700 m inland from the east coast. Indiantown Trail

Table 1.—*The vertebrate fauna from Indiantown Trail, Sufferers, and Overview Cave, Barbuda, segregated by Stratum. The first number is the quantity of specimens identified. The second number is the MNI. Stratum I(D) is the disturbed unit at Overview Cave. Remains from that contaminated unit constitute no MNI, as they cannot be associated unequivocally with Amerindian occupation.*

Taxa	Indiantown Trail	Sufferers		Overview Cave	
		I	II	I(D)	I
Fish					
Carcharhinidae sp.			1, 1		
Albula vulpes	19, 2			1, —	
Belonidae sp.	1, 1				
Epinephelus sp.	38, 7	1, 1			
Mycteroperca sp.	3, 1				
Serranidae sp.	8, 0	1, 0			
Lutjanus sp.	3, 2				
Haemulon sp.	2, 1				
Orthopristis sp.	2, 2				
Sparidae sp.	1, 1				1, 1
Bodianus sp.	3, 1				
Halichoeres sp.	1, 1				
Scarus sp.	252, 36				
Sparisoma sp.	80, 15			2, —	
Scaridae sp.	32, 0				
Sphyraena barracuda	8, 2				
Acanthurus sp.	98, 43				
Scombridae sp.	1, 1				
Balistes sp.	5, 4		1, 1		
Diodon hystrix	2, 2				
Diodontidae sp.	1, 0				
Fish sp.	1790, 0	23, 0	12, 0	6, —	
Reptiles					
Turtle sp(p).	2, 1	19, 1			
Leiocephalus cuneus	2, 1				
Ameiva cf. *griswoldi*	1, 1				
Birds					
Puffinus lherminieri	6, 1				
Columba leucocephala	2, 1				
Geotrygon mystacea	1, 1				
Mammals					
Homo sapiens	2, 1				
Trichechus manatus	1, 1				
Capra hircus				4, —	
Oryzomyini sp.	34, 6	5, 3	5, 3		
Vertebrate sp.	4, 0	21, 0	8, 0		
Total fish	2350, 122	25, 1	14, 2	9, —	1, 1
Total reptiles	5, 3	19, 1			
Total birds	9, 3				
Total mammals	37, 8	5, 3	5, 3	4, —	
Grand total (includes "Vertebrate sp.")	2405, 136	70, 5	27, 5	13, —	1, 1

Table 2.—*The vertebrate fauna from Indiantown Trail, Sufferers, and Overview Cave, Barbuda, combining all undisturbed strata. These figures represent MNI of taxa definitely associated with Amerindian occupation.*

Taxa	Indiantown Trail	Sufferers	Overview cave	All sites
Fish				
Carcharhinidae sp.		1		1
Albula vulpes	2			2
Belonidae sp.	1			1
Epinephelus sp.	7	1		8
Mycteroperca sp.	1			1
Lutjanus sp.	2			2
Haemulon sp.	1			1
Orthopristis sp.	2			2
Sparidae sp.	1		1	2
Bodianus sp.	1			1
Halichoeres sp.	1			1
Scarus sp.	36			36
Sparisoma sp.	15			15
Sphyraena barracuda	2			2
Acanthurus sp.	43			43
Scombridae sp.	1			1
Balistes sp.	4	1		5
Diodon hystrix	2			2
Reptiles				
Turtle sp(p).	1	1		2
Leiocephalus cuneus	1			1
Ameiva cf. *griswoldi*	1			1
Birds				
Puffinus lherminieri	1			1
Columba leucocephala	1			1
Geotrygon mystacea	1			1
Mammals				
Homo sapiens	1			1
Trichechus manatus	1			1
Oryzomyini sp.	6	6		12
Total fish	122	3	1	126
Total reptiles	3	1		4
Total birds	3			3
Total mammals	8	6		14
Grand total	136	10	1	147

has soil markedly deeper and moister than in the surrounding terrain where exposed limestone prevails. The wetter condition of the soil results from accumulation of runoff from the nearby Highlands escarpment, and the retention of moisture is enhanced by the fact that the site is out of the path of prevailing winds, being protected by the mass of the Highlands. This combination of increased accumulation and decreased evaporation produces soil conditions that are more favorable for cultivation at Indiantown Trail than elsewhere on this semiarid and drought-prone island.

Evergreen woodland and coastal vegetational communities predominate on the Marginal plain in the vicinity of Indiantown Trail. Denser forest is found on the Highlands plateau above the site. Caves are plentiful in the escarpment as are sinkholes in the Highlands above. East of BA1 are several marine and coastal environments including part of the 35-km coral reef that is less than 200 m from shore, the backreef area with patch coral, and sandy pocket beaches interspersed with limestone headlands at the shoreline. A large dune ridge and brackish swamp lie just north of the site.

Our discussion considers only those taxa recorded from uncontaminated units at the three sites. The only disturbed level is unit 1 of Stratum I at Overview Cave (BA7), where teeth from an animal introduced in post-Columbian times (the goat, *Capra hircus*) were found. All of the other species from that contaminated unit also were recovered in primary (undisturbed) contexts at Sufferers or Indiantown Trail. The goat is the only unique species from BA7.

By far the most abundantly represented vertebrate remains are bony fish, and most of these remains were recovered at Indiantown Trail. The small samples from Sufferers and Overview Cave contain few species. With the single exception of a worked shark vertebra from Sufferers, all of the fish taxa identified from that site and Overview Cave were also recovered at Indiantown Trail. The differences in the fish faunas from the three sites might reflect subsistence preferences among the groups living there, but these variations also may reflect nothing more than biases due to small sample sizes. The same may be said for the reptiles, birds, and mammals recovered.

The fish identified are found in a variety of Caribbean habitats, but the three major genera represented (the parrotfish *Scarus* and *Sparisoma* and the surgeonfish *Acanthurus*) occur predominantly over shallow reefs (Randall, 1968; Fischer, 1978). The coral reefs that are a major feature near the Indiantown Trail site seem to have been exploited extensively. Most of the other species may be found either in inshore waters or over shallow reefs. Analysis of the identified fish suggests the use of several capture techniques. Parrotfishes and surgeonfishes will not readily take hooks and therefore probably were caught in traps or speared. The remaining fishes may have been trapped as well, although many could have been taken with hook and line. It is doubtful that nets were used, at least not over reefs and rocky outcrops where they could become entangled or snagged.

Turtle remains from Indiantown Trail and Sufferers are not remarkable in extent, diversity, or quality of preservation, and their very fragmentary nature does not permit confident identification even to family. They could represent either marine turtles or a tortoise.

The presence of the iguanid *Leiocephalus cuneus* in secure archaeological context is significant, as it verifies the contemporaneity of that now extinct species with prehistoric human inhabitants of Barbuda. The occurrence of the lizard *Ameiva griswoldi* in a prehistoric archaeological site on Barbuda is not unexpected as it occurs throughout Barbuda today and has been reported previously from a prehistoric site on Antigua. The Indiantown Trail specimen does confirm the presence of this lizard on both islands of the Barbuda Bank, to which it is endemic, during Amerindian occupation.

Avian remains were recovered only from the Indiantown Trail site, and only three species were identified. Mammals are the second most abundant of the vertebrate remains recovered both in terms of bone count and MNI, but they are quite sparsely represented when compared to fish remains. With 34 bones representing 12 individuals, rodents outnumber all other mammals and birds combined.

The limited remains of birds and mammals nevertheless include three species extinct on Barbuda today—the shearwater *Puffinus lherminieri,* the manatee *Trichechus manatus,*and the oryzomyine rodent. These animals represent potentially abundant sources of readily available food for the early inhabitants of Barbuda, who may well have overexploited the first two of these species. In addition, the present status of *Geotrygon mystacea* on Barbuda is unclear, but it also may be extinct or rare.

The limestone cliffs lining the east coast of Barbuda, with their many recesses, crevices, and solution pits, would seem to be an ideal place for *P. lherminieri* to roost and nest. The current absence of these shearwaters from Barbuda can hardly be a natural phenomenon, but probably can be attributed to predation by humans and/or introduced rats (*Rattus*). The loss of manatees (*T. manatus*) from Barbuda's waters is almost certainly due to predation by man, whether pre- or post-Columbian. Barbuda is only one of the many areas throughout the manatee's range where it has become rare or extinct because of human predation.

The loss of native oryzomyine rodents on Barbuda, as well as on other islands in the Lesser Antilles, is probably related to the post-Columbian introduction of Old World rats (*Rattus*), although the mechanism involved is not clear. Pending completion of a review of the systematics, paleontology, and evolution of West Indian oryzomyines being prepared by D. W. Steadman and M. D. Carleton, it is premature to make any definitive statements about this extinct species.

It is fortunate that materials from the three test pits were screened through ⅛-in. mesh rather than the ¼-in. mesh more often used by archaeologists. Many vertebrate remains that would have passed through the larger mesh were retained in the ⅛-in. screen. Use of even finer mesh screens would retain even smaller bones and thus could add to the diversity of the faunal sample. Such efforts are planned for future excavations on Barbuda in areas where higher than normal concentrations of bone have been identified. Although they can be very time consuming, these efforts will provide us with a more complete picture of the relationships between prehistoric human inhabitants and terrestrial and marine animals of Barbuda.

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EARLY WOODLAND CERAMIC AND PERISHABLE FIBER INDUSTRIES FROM THE NORTHEAST: A SUMMARY AND INTERPRETATION

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Abstract

The previous recognition of Early Woodland period ceramics and associated perishable fiber industries has been limited and less often well reported in the wide Northeast. This paper offers a summary of Early Woodland ceramics and perishables from the Northeast, including discussion of "Vinette I" ceramics, other related and possibly unrelated ceramic forms, perishables reconstructed from negative impressions, and actual perishables preserved in rare cases. Particular emphasis is given to the behavioral implications of these data in terms of industrial consistency and variability as an indication of social interaction and continuity during the Early Woodland period.

Introduction

The previous recognition of Early Woodland ceramic remains has been limited and less often well reported in the broad Northeast. In the case of Early Woodland perishable fiber remains, the record is even more abysmal, with recognition and recovery of fiber perishables rare and detailed analyses rare to nonexistent (Adovasio and Carlisle, 1982; Doyle et al., 1982).

In light of these conditions, this paper initially offers a summary and discussion of what we can currently say about Early Woodland ceramic

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and perishable fiber industries in the Northeast. Particular emphasis is given here to identification of Early Woodland perishable fiber industries because they have been so little studied, but like ceramics (for example, Brashler, 1981; Deetz, 1965; Petersen, 1981), potentially provide highly sensitive population specific attributes (for example, Adovasio, 1977, 1983, various). The behavioral implications of the combined ceramic and perishables data are ultimately examined here in terms of technological consistency and variability as possible indicators of social interaction and continuity within and subsequent to the Early Woodland period.

As used herein, the Northeast is loosely defined following Trigger (1978:1) as the area from Virginia and North Carolina in the south to the boreal forest of Ontario and Quebec in the north and from the prairie grasslands in the west to the Atlantic Ocean in the east. The Early Woodland period is likewise loosely and somewhat arbitrarily defined as the 1000 year interval from ca. 1200 (1000) B.C. to 200 B.C. (A.D. 1), following traditional convention (for example, Griffin, 1967, 1978; Ritchie, 1965), but with recognition of alternative designations (for example, Sanger, 1979; Snow, 1980; Stoltman, 1978; Willey, 1966).

EARLY WOODLAND CERAMIC INDUSTRIES

The onset of the Early Woodland period in the Northeast, as elsewhere, has been traditionally marked by the first general appearance of ceramic technology at sometime slightly before about 1200–1000 B.C. In at least one portion of the Northeast, however, early ceramics were apparently present (in what we would call uncertain contexts) during the preceding Transitional or Terminal Archaic period in association with steatite vessels in the Orient and Frost Island phases of New York (Lopez, 1957; Ritchie, 1959; Ritchie and Funk, 1973; Smith, 1950). Likewise, the early presence of ceramic vessels has been demonstrated in the coastal Mid Atlantic region before 1000 B.C., some of which exhibit modelled bowl forms (lug handles, flat bottoms and low "trough shaped") directly analogous to the earlier steatite vessels and often including actual steatite temper in the clay paste. Other forms, more like beakers (with a variety of other attributes) have been identified in the Mid Atlantic region, giving rise to a plethora of type designations. Although "Bushnell Plain" beaker forms have been dated to 1100 ± 60 B.C. and "Marcey Creek Plain" bowl and beaker forms have been dated to 950 ± 95 B.C., both in the Potomac River drainage, dated associations for such ceramics are extremely rare and consequently these forms have been generally guess dated to the period from about 750 B.C. to 1200 B.C. (Egloff and Potter, 1982; Kraft, 1976; Gardner and McNett, 1971; Stewart, 1982). Poorly understood steatite tempered ceramics have been also recovered in the Connecticut River, Merrimack River, and Hudson River drainages to the north (Brumbach, 1979; Kenyon, 1979, 1981; Weeks, 1971). In the latter case, "fired clay" fragments recovered at the Schuylerville site can probably be associated with rudimentary ceramic developments in this area (Brumbach, 1979; various personal communications).

On the basis of current evidence, however, it seems safe to say that the first widely distributed form of ceramics in the Northeast was rather different than its apparent predecessor in the Mid Atlantic and southern New England coastal areas. Variability in vessel form and surface finish is characteristic of the earliest, widely distributed ceramics across the Northeast, but nonetheless they can be generally characterized as exhibiting some combination of exterior/interior surface finish applied with perishable fiber industries (such as cordage, netting and basketry or fabrics), a conoidal (pointed bottom) bowl vessel form, coarse grit temper and often coiled construction. The "classic" form, with exterior/interior perishable fiber impressions, was given the "Vinette I" type designation in New York State (Ritchie and MacNeish, 1949:100). "Vinette I" or closely related ceramics have been subsequently identified (or are identifiable) over a considerable portion of the far Northeast, including Pennsylvania (Kinsey, 1958, 1971), New Jersey (Kinsey, 1972, 1974), Connecticut (Lavin, 1980; Pope, 1953), Maine (Borstel, 1982; Byers, 1959; Doyle et al., 1982; Spiess et al., 1983), Massachusetts (Bullen, 1948; Byers and Rouse, 1960; Dincauze, 1975; Fowler, 1966; Moffett, 1959; Ritchie, 1969), New Hampshire (Dincauze, 1976; Kenyon, 1979, 1981), Rhode Island (Fowler, 1952, 1956), and Vermont (Petersen, 1979; Petersen and Basa, n.d.). Dated associations for "Vinette I" ceramics in this area are relatively rare, however, and only include 998 ± 100 B.C. at the Oberlander No. 2 site, 870 ± 60 B.C. at the Scaccia site, 841 ± 68 B.C. at the Hunter site, and 630 ± 100 B.C. and 563 ± 250 B.C. at the Morrow site, all Meadowood Phase components in New York (Ritchie, 1965; Ritchie and Funk, 1973). In the Delaware River drainage, "Vinette I" ceramics have been dated to 480 ± 80 B.C. at the Miller Field site and presumably to 810 ± 100 B.C., 750 ± 100 B.C., 400 ± 95 B.C., and 100 ± 95 B.C. at the Faucett site (Kinsey, 1972, 1974). Well associated dates for "Vinette I" ceramics in New England include 590 ± 105 B.C., 520 ± 120 B.C., 430 ± 80 B.C., and 360 ± 100 B.C. at the Peterson and Pratt sites on Martha's Vineyard (Ritchie, 1969) and 600 ± 60 (Beta-6852, C-13 corrected) and 365 ± 130 B.C. at the Great Diamond Island site in Casco Bay on the Maine coast (Hamilton and Yesner, 1981; Doyle et al., 1982).

In addition, classic "Vinette I" ceramics have been identified in the adjoining Canadian provinces of Nova Scotia (Ellen Foulkes, personal communication, August 1982), Ontario (Finlayson, 1977; Mitchell, 1963; Ridley, 1954; Spence et al., 1978; Wright, 1967, 1972; Wright and Anderson, 1963), and Quebec (Clermont, 1978; Clermont and Chapdelaine, 1982; Levesque et al., 1964; Wright, 1979). Unfortunately, few dates can be clearly associated with "Vinette I" ceramics in Canada, although some of the early dates from the Donaldson site in Ontario, ca. 600–700 B.C., may possibly be associated with "Vinette I" ceramics recovered there (Finlayson, 1977; Wright and Anderson, 1963). In addition, two dates of A.D. 130 ± 100 and 80 ± 100 B.C. from a site near Deep River, Ontario, may well date associated "Vinette I" ceramics (Mitchell, 1963; Wilmeth, 1978), although these dates seem too recent.

A closely associated (and presumably synonymous) form to "Vinette I" exhibits smoothing over the interior and/or exterior perishable impressed surfaces. While this latter form has been often isolated as a separate type (for example, Kinsey, 1972; Lavin, 1980; Levesque et al., 1964; Lopez, 1957; Salwen, 1968), this may be an arbitrary distinction since partially smoothed and unsmoothed forms co-occur, frequently intergrade and are often indistinguishable under current definition in areas as widespread as Maine, Pennsylvania, New Jersey, Connecticut, Kentucky, and Quebec (for example, Clay, 1980; Doyle et al., 1982; Kinsey, 1958; Kraft, 1976; Petersen and Basa, n.d.; Pope, 1953; Ritchie, 1969; Smith, 1950; Spence et al., 1978).

Other very similar ceramic forms, with perishable fiber impressed (or paddled) surfaces, have been defined over the wide extent of the Northeast as discrete contemporaneous ceramic types. These forms are seemingly separable as distinct types on the basis of precise attributes of temper, paste, and form. In the Mid Atlantic area, these include "Marcey Creek Cord Marked," "Seldon Cord Marked," "Accokeek Creek Cord Marked," and "Stony Creek Cord Marked," of which none seem well dated (Egloff and Potter, 1982; Manson, 1948; Stephenson and Ferguson, 1963). Likewise, an analogous but distinct form from "Vinette I" ceramics, "Juaniata Thick" beaker form ceramics have been identified in interior Pennsylvania (Michels and Smith, 1967), as have been "Wolfe Neck Cord Marked" and "Cobourn Cord Marked" ceramics in Delaware. The latter two forms have associated dates of 505 ± 60 B.C., 500 ± 85 B.C., 380 ± 85 B.C. and 375 ± 65 B.C. at the Wolfe Neck and Dill Farm sites (Griffith, 1982).

Still other forms which are roughly similar to "Vinette I" include "Wolfe Neck Net Marked," "Cobourn Net Marked," "Accokeek Creek Net Impressed," "Popes Creek Net Impressed" and "Stoney Creek Net Marked," all of which were roughly contemporaneous with and closely related to other Mid Atlantic types noted above. Another form, "Brod Head Net Marked," has been actually recovered with "Vinette I" ceramics and associated with dates of 480 ± 80 B.C., 400 ± 95 B.C., and 100 ± 95 B.C. at the Miller Field and Faucett sites, respectively, in the Delaware River drainage (Kinsey, 1972, 1974). Distinctive but similar cordage, fabric and net impressed ceramic beaker forms, which occur in Virginia and adjoining North Carolina, have been dated to 660 ± 60 B.C. at the Currituck site (Egloff and Potter, 1982; Painter, 1977).

Broad relationships are also shared with a host of other named ceramic types in the Midwest Ohio River and Great Lakes drainages. These include "Half Moon Cord Marked" beaker forms (Mayer-Oakes, 1955), well dated at Meadowcroft Rockshelter with a series of dates as early as 1115 ± 80 B.C. and 865 ± 80 B.C. and younger dates before 200 B.C. (Johnson, 1977, 1982). Another early beaker form in the upper Ohio drainage of Pennsylvania, Ohio, and Kentucky, "Fayette Thick" has been dated to at least 855 B.C. and possibly before 1020 B.C. at the Rais-Swartz Rockshelter and 520 ± 310 B.C. at the Leimbach site (Clay, 1980; Griffin, 1945; Ozker, 1982). Further north, "Schultz Thick," has been defined at the Schultz site in the Lake Huron drainage and dated to 530 ± 150 B.C., as the earliest form in the Upper Great Lakes (Fischer, 1972; Ozker, 1982). Further west in Minnesota, exterior/interior "corded" ceramics are represented by the undated "LaMoille Thick" (Anfinson, 1979). Very similar ceramics occur as the "Marion Thick" and "Baumer" types in the Mississippi River drainage (Griffin, 1952; Linder, 1974; Ozker, 1982), the first of which has been dated to 560 ± 100 B.C. at the Larson site. Still elsewhere in the Upper Mississippi drainage, "Hilgen Cord Marked" beaker forms have been dated to 840 ± 65 B.C., 525 ± 65 B.C., and 460 ± 55 B.C. at the Hilgen Mounds in Wisconsin (Ozker, 1982; Van Langen and Kehoe, 1971).

The presence of plain, smooth surfaced vessels has also been noted for Early Woodland components in the upper Ohio River drainage as "Adena Plain," with a distribution paralleling that of "Fayette Thick" ceramics (Dragoo, 1963; Griffin, 1945; Ozker, 1982). Additional "plain" forms with zone incised decoration (e.g., "Montgomery Incised") are also present, which along with "Adena Plain" seem to be late ceramic developments of the Early Woodland period (Clay, 1980; Griffin, 1978). Another, somewhat enigmatic development of plain surfaced ceramics (with occasional punctate decoration) is recorded from the Maritime Province of New Brunswick at about 500–600 B.C. (Allen, 1980, 1981; Turnbull, 1976).

In summary, the earliest ceramics in the broad Northeast seem to clearly predate 1000 B.C. in the Mid Atlantic area, where they appear to be an indigenous development modelled after earlier and likely coexistent steatite vessels. The development of these flat or round bottomed bowl forms is quite possibly due to "stimulus diffusion," or broad scale information exchange networks with the Southeast, where distinctive fiber tempered ceramics clearly predate 2000 B.C., or may well be an independent development in the Northeast (Griffin, 1978; Kraft, 1976; Stoltman, 1978; Tuck, 1978; Wright, 1979). Shortly after the development of ceramics in the Mid Atlantic area at about 1200 B.C., a more northern and extremely widespread development is represented by the appearance of "Vinette I" and related ceramic forms, with a characteristic surface finish of perishable fiber industries (cordage, netting, and basketry or fabrics) applied on both exterior and interior surfaces. These forms were widespread over nearly the entire Northeast and beyond, from Maine to Minnesota and Kentucky to Ontario. These representations may have been influenced by the earlier, more restricted forms of the Mid Atlantic or may represent another independent indigenous development.

These early ceramics in the Northeast are most clearly native developments in the context of aboriginal hunter-gatherer populations in eastern North America (Griffin, 1978; Tuck, 1978) and not likely influenced by Asiatic or European developments as previously speculated (Kehoe, 1962; Ritchie, 1955; Willey, 1966; Wright, 1967). In any case, a rapid spread of early exterior/interior perishable fiber impressed ceramics seems well documented in the archaeological record after ca. 1000 B.C. with their persistence as late as 100–200 B.C.

The nature of subsequent later Early Woodland and Middle Woodland ceramic developments is another complicated topic, beyond the scope of this paper. Suffice it to say, however, that later forms seem to have been developed from the antecedent forms discussed in this paper in nearly all areas where ceramics were ever adopted in the Northeast (Braun, 1980; Mason, 1981; Petersen, n.d.a; Petersen and Power, 1983; Ritchie, 1965; Stoltman, 1978).

EARLY WOODLAND PERISHABLE FIBER INDUSTRIES

The earliest evidence of perishable fiber industries greatly predates the antiquity of ceramics in the broad Northeast. In point of fact, perishable fiber industries have been clearly identified in Early Archaic period contexts in Alabama (Griffin, 1974), Missouri (Logan, 1952), and Tennessee (Chapman and Adovasio, 1977), well dated to before 7000 B.C. in the latter case, and possibly to Paleoindian contexts in Pennsylvania (Adovasio et al., 1978; Stile, 1982). Likewise, perishable fiber industries were clearly present in the Great Lakes drainage by at least the Middle Archaic period (Adovasio and Andrews [with Carlisle], 1980). It has been well demonstrated that perishable fiber industries have a comparable antiquity in western North America, Mexico, and South America, with the production of cordage and twined basketry apparently well established for the length and breadth of the New World by the 8th millenium B.C. at the latest (Adovasio, 1970, 1974, various; Adovasio and Carlisle, 1982; Adovasio and Maslowski, 1980).

The early development and ultimate complexity of perishable fiber industries can not be over emphasized for northeastern aboriginal populations and more broadly for eastern North America on the basis of both the fragmentary archaeological and ethnographic records (for example, Bower, 1980; Brasser, 1975; Gilliland, 1975; Harper, 1956; Holmes, 1884, 1896; Mason, 1981; Michels and Smith, 1967; Snow, 1980; Trigger, 1978; Willoughby, 1935). Examination of collections from sites such as Burrs Hill in Rhode Island, Sheep Rock Shelter in Pennsylvania, and Key Marco in Florida reveals the wide array of perishable fiber industries employed by native aboriginal populations across this wide area.

More specifically to the present case, a variety of actual perishables (nearly all fragmentary) have been recovered from a limited number of Early Woodland components in the wide Northeast. These are worthy of further detailed discussion here, along with positive casts of perishables reconstructed from ceramics and other clay remains (Adovasio, 1982; Adovasio and Andrews [with Carlisle], 1980; Dincauze, 1975; Doyle et al., 1982; Dragoo, 1963; Johnson, 1982; King, 1968; Kraft, 1976; Petersen, n.d.a.; Petersen and Basa, n.d.; Ritchie, 1949, 1965; Watson, 1969). It should be emphasized that in spite of the characteristic usage of fiber perishables in surface finish of Early Woodland ceramics (and thus their preservation as negative impressions), the number of sites which have produced Early Woodland perishables is very small and well studied samples even smaller (<12) for the entire Northeast. Consequently, all extant reported samples have been given consideration and are discussed here in varying detail.

Although only mentioned briefly, Early Woodland perishables were first given broad consideration by Webb and Snow in 1945, who suggested a series of characteristic perishable fiber industries for the classic "Adena Culture" in the upper Ohio River drainage. These forms included simple plaiting, twill plaiting, close simple twining, open simple twining, and open diagonal twining with characteristic S wefts, where present. In addition, close simple twining with S and Z wefts and cordage of various single ply, double ply and multiple ply elements were considered characteristic of Adena perishables (Webb and Snow, 1945; see also Adovasio and Andrews [with Carlisle], 1980; Rachlin, 1960; Webb and Baby, 1957; Willoughby, 1938).

The available inventory of variably studied Early Woodland fiber perishables known to us includes samples discussed by Webb as well as others from Salts Cave and Mammoth Caves (Watson, 1969; King, 1974), the Jean Rita site in southern Illinois (Linder, 1974), the Blanton

Table 1.—*Distribution of Early Woodland perishable fiber industries in the Northeast.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Salt's Cave	Green R., KY	simple (?) plaited, 1/1 interval (?) "slipper" (14+) twill plaited, 2/2 interval (?) fragment (2) close twined "slipper," S and S & Z wefts and plaited, 1/1 interval (1) close twined "slipper," S & Z wefts and plaited, 1/1 interval (3) close twined "slipper," S & Z wefts, (52+) open twined "slipper," unknown wefts (1) close twined fragment, unknown wefts (1) open simple twined fragment, S wefts (2) open twined fragment, unknown wefts (16+) open twined bag, ? spin, S twist cordage (1) cordage, 2 ply, ? spin, S twist (52+) cordage, 2 ply, ? spin, Z twist (2+) cordage, 3 ply, ? spin, ? twist (1) cordage, braided (73+)	A.D. 30 ± 160 10 B.C. ± 160 290 B.C. ± 200 320 B.C. ± 140 400 B.C. ± 140 480 B.C. ± 140 560 B.C. ± 140 570 B.C. ± 140 620 B.C. ± 140 710 B.C. ± 100 740 B.C. ± 140 770 B.C. ± 140 890 B.C. ± 150 990 B.C. ± 120 1125 B.C. ± 140 1190 B.C. ± 150 1410 B.C. ± 220 1460 B.C. ± 220 1540 B.C. ± 110	Watson, 1969:36–41 plates 5, 9, 13A–13B, 1974:211–212 King, 1974:31–40, Figs. 4.1–4.9
Mammoth Cave	Green R., KY	simple (?) plaited, 1/1 interval (?) "slipper" (21) close (?) twined "slipper" (43) twill plaited, 2/2 interval basket (1)	280 B.C. ± 40 420 B.C. ± 60 1050 B.C. ± 70 2170 B.C. ± 70	Watson, 1969:36–41, 1974:183, Figs. 22.1–22.2

Table 1.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Newt Kash	Licking R., KY	"slipper" (2) open simple twined fragment, S wefts (1+) cordage, 2 ply (?) cordage, braided	650 B.C. ± 300 700 B.C. ± 300	Funkhouser and Webb, 1936:116–123, Figs. 7–14, 19 Watson, 1969:70 Webb and Baby, 1957: 32–38
Red-Eye Hollow	Kentucky R., KY	close twined "slipper," S & Z wefts (4) open and close simple (?) twined "slipper" S wefts (3) open twined bag, S wefts (1) cordage	—	Funkhouser and Webb, 1929:49, 86–100, Figs. 10–11, 38–39, 41, 43–61 Webb and Baby, 1957: 32–38
Steven DeHart	Red R., KY	close twined "slipper," S & Z wefts (1) cordage, braided (1+)	—	Funkhouser and Webb, 1930:283–294 Webb and Baby, 1957: 32–38
Jean Rita	Mississippi R., IL	cordage, Z twist in unknown form (2+)*	A.D. 35 ± 60	Linder, 1974:113–121
Morgan Stone Mound	Licking R., KY	simple plaited, 1/1 interval fragment (1) twill plaited, 2/1 interval fragment (3+) close simple twined fragment, S & Z wefts (1) open simple twined fragment, S wefts (7) open diagonal twined fragment, S wefts (3+) open simple and diagonal twined fragment, S wefts (1) cordage, 3 ply, ? spin, Z twist (2+)	—	Carey, 1941*a*:268–281, Figs. 19–20 Webb and Snow, 1945: 27–28, 103, 105

Table 1.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Drake Mound	Kentucky R., KY	twill plaited, 2/1 interval (1) open simple wrapped twined fragment, S wefts (1)	—	Carey, 1941*b*:185–190, Fig. 27 Webb and Snow, 1945: 27–28, 103, 105
Wright Mound	Licking R., KY	open simple twined fragment, S wefts (1+) open diagonal twined fragment, S (?) wefts (1+)	—	Webb and Haag, 1940: 70, Figs, 46–48
Hartman Mound	Ohio R., KY	close simple (?) twined fragment, S wefts (1+)	—	Webb, 1943:539–540, Fig. 15D Webb and Snow, 1945: 27–28, 103, 105
Adena Mound	Scioto R., OH	close simple twined fragment, S wefts (1)	—	Willoughby, 1938:287
Westenhaver Mound	Scioto R., OH	twill plaited, 2/1 interval fragment (1) open simple twined fragment, S wefts (1)	—	Willoughby, 1938:280, 286, Fig. 1h, 1n
15J035	Levisa Fork, KY	close diagonal twined fragment, S wefts (1)*	—	Adovasio, 1982:830–844
Blanton	Levisa Fork, KY	fishnet knot netting, 2 ply, S spin, Z twist cordage (1)* squareknot netting, 2 ply, Z spin, S twist cordage (1)* unknown basketry or netting (1)*	—	Adovasio, 1982:830–844
Natrium Mound	Ohio R., WV	close simple twined fragment, S wefts (1)	—	Solecki, 1953:374, plate 25b

Table 1.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Cresap Mound	Ohio R., WV	close (?) twined or plaited fragment (1)	—	Dragoo, 1963:32–33, 35, 122, 128–129 Adovasio and Carlisle, 1982:847
Northern Thorn Mound	Monongahela R., WV	close simple twined fragment, S wefts (3)* close simple twined fragment, S & Z wefts (2)* open diagonal twined fragment, S wefts (13)* open and close diagonal twined fragment, S & Z wefts (1)* cordage, 2 ply, Z spin, S twist (7)* cordage, braided (composed of 3 strands of 2 ply, Z spin, S twist) (1)*	—	Adovasio and Andrews [with Carlisle], 1980: 33–72, Figs. 1–27
McKees Rocks Mound	Ohio R., PA	open simple twined fragment, S wefts (1)	—	Dragoo, 1963:156, Plate 49 Adovasio and Carlisle, 1982:847
Meadowcroft Rockshelter	Cross Creek, PA	simple plaited, 1/1 interval fragment (6) open simple twined fragment, Z wefts (2)* unknown basketry or cordage, Z twist (1)*	340 B.C. ± 90 375 B.C. ± 75 535 B.C. ± 350 705 B.C. ± 120 865 B.C. ± 80 870 B.C. ± 75 910 B.C. ± 80 980 B.C. ± 75 1100 B.C. ± 85 1115 B.C. ± 80	Johnson, 1982:142–162 Stile, 1982:130–141, Figs. 1–2

Table 1.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Riverside	Lake Huron, MI	open twined fragment, S weft (1) open wrapped simple twined fragment, S weft (1)	A.D. 1 ± 130 100 B.C. ± 140 130 B.C. ± 140 140 B.C. ± 140 510 B.C. ± 140 1081 B.C. ± 300	King, 1968:117–123, Figs. 1–6
Picton	Lake Ontario, ONT	cordage, 2 ply, ? spin, Z twist (1+) unknown "hair" or "fur fabric" (1)	—	Ritchie, 1949:38, Fig. 11p
Bruce Boyd	Lake Erie, ONT	cordage, 2 ply, ? spin, Z twist (1+)* cordage, 3 ply, ? spin, Z twist (1)*	—	Spence et al., 1978:38
Morrow	Honeoye Lake, NY	close simple (?) twined fragment, Z wefts (1) knotted netting, 2 ply, ? spin, S twist cordage (1)	563 B.C. ± 250 630 B.C. ± 100	Ritchie, 1965:186–187, 194–196, Plates 67, 70
Van Orden	Hudson R., NY	cordage, details unknown (1+)	—	Ritchie, 1958:100–101
Muskalonge	Muskalonge Lake, NY	cordage, 2 ply, ? spin, S twist (1+) cordage, 1 ply, S twist (1)	—	Ritchie, 1955:37, 40, Plates 8, 11.7–11.8
Canton	Atlantic Coast, NJ	cordage, 3 ply, Z spin, S twist (1) cordage, ? ply, ? spin, S twist (1)	—	Mounier, 1981:59–60, Plate 6
Rosenkrans	Delaware R., NJ	twill plaited, 2/1 interval fragment (1) open twined fragment, S wefts (2) cordage, 2 ply, Z spin, S twist (1) unknown "fabric" (1)	610 B.C. ± 120	Kraft, 1976:18, 21, 23–25, 31–32, Figs. 9f, 9g, 11f, 11g, 14

Table 1.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Clap's Landing	Charles R., MA	cordage, ? ply, ? spin, S twist in unknown form (4)* unknown cordage or twined fragment (2)*	—	Dincauze, 1975:7
Boucher	Missisquoi R., VT	open simple twined fragment, S wefts (3+) knotted netting, 2 ply, Z spin, S twist cordage (1)* cordage, 2 ply, Z spin, S twist (4+) cordage, 1 ply, Z twist unknown cordage or twined fragment (4+)*	—	Petersen and Basa, n.d.
Augustine Mound	Miramichi R., NB	open simple (?) twined fragment, S wefts (1+) cordage, 2 ply, ? spin, S twist (1+)	380 B.C. ± 110	Turnbull, 1976:54–55, Plate 3

* Specimen derived from negative ceramic or packed clay remains.

Table 2.—*Distribution of Early Woodland perishable fiber industries in Maine.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Great Diamond Island	Casco Bay	open simple twined fragment, S wefts (1)* close simple twined fragment, Z wefts (2)* interlinked fabric fragment, 2 ply, Z spin, S twist cordage (1)* cordage, 2 ply, S spin, Z twist cordage (2 +)*	365 B.C. ± 130 600 B.C. ± 60	Hamilton and Yesner, 1981 Doyle et al., 1982
Great Moshier Island	Casco Bay	close simple twined fragment, Z wefts (1)*	260 B.C. ± 320	Petersen, n.d.a.
Hamilton		open simple twined fragment, Z wefts (3)* close simple (?) twined fragment, Z wefts (1)* close simple (?) twined fragment, S wefts (4)*	—	Doyle et al., 1982 Petersen, n.d.a.
Tidal Presumpscot	Presumpscot R.	close simple (?) twined fragment, S wefts (1)*	—	Petersen, n.d.a.
Taylor	Boothbay Harbor	interlinked fabric (?) fragment, 2 ply, S spin, Z twist cordage (1)*	—	Petersen, n.d.a.
ME16-37	Boothbay Harbor	cordage, 2 ply, S spin, Z twist in unknown form (1)*	—	Petersen, n.d.a.
Nahanada	Boothbay Harbor	open simple (?) twined fragment, Z wefts (1)*	—	Petersen, n.d.a.
Lime Island	Penobscot Bay	open simple (?) twined fragment, Z wefts (1)*	—	Petersen, n.d.a.
Fernald Point	Penobscot Bay	cordage, 2 ply, S pin, Z twist in unknown form (1)*	—	Petersen, n.d.a.

Table 2.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
Turner Farm	Penobscot Bay	open simple twined fragment, Z wefts (1)* open simple twined fragment, S wefts (2)* close simple (?) twined fragment, Z wefts (1)* cordage, 2 ply, Z spin, S twist in unknown form (3)* cordage, 2 ply, S spin, Z twist in unknown form (1)*	—	Petersen, n.d.a.
Basin Island	Sebago Lake	open simple twined fragment, S wefts (1)*	—	Doyle et al., 1982 Petersen, n.d.a.
White's Bridge	Sebago Lake	close simple (?) twined fragment, S wefts (1)*	—	Doyle et al., 1982 Petersen, n.d.a.
Outlet 1	Cobbosseecontee Stream	close simple twined fragment, Z wefts (1)* open simple twined fragment, S wefts (4)*	—	Petersen, n.d.a.
Outlet 2	Cobbosseecontee Stream	cordage, 2 ply, 2 spin, S twist in unknown form (1)*	—	Petersen, n.d.a.
Rips	Cobbesseecontee Stream	close simple (?) twined fragment, S wefts (2)*	—	Petersen, n.d.a.
Vassalborough	Kennebec R.	close simple (?) twined fragment, S wefts (1)*	—	Doyle et al., 1982 Petersen, n.d.a.
Sebasticook I	Sebasticook R.	open simple twined fragment, S wefts (1)*	—	Doyle et al., 1982 Petersen, n.d.a.
Sebasticook II	Sebasticook R.	close simple (?) twined fragment, Z wefts (1)*	—	Doyle et al., 1982 Petersen, n.d.a.

Table 2.—*Continued.*

Site name	Location	Structural form(s) and twist or weft slant	Date	References
		close simple (?) twined fragment, S wefts (1)*		
Evergreens	Kennebec R.	open simple twined fragment, S wefts (1)* close simple (?) twined fragment, S wefts (1)*	—	Spiess et al., 1983 Petersen, n.d.a.
Carratunk Falls	Kennebec R.	close simple (?) twined fragment, S wefts (2)* cordage, 2 ply, Z spin, S twist in unknown form (1)*	—	Petersen, n.d.a.
Hirundo	Pushaw Stream	open simple twined fragment, S wefts (1)* close simple (?) twined fragment, S wefts (1)*	—	Petersen, n.d.a.
Young	Pushaw Stream	cordage, 2 ply, Z spin, S twist in unknown form (2+)* cordage, unknown ply and twist in unknown form (4+)*	—	Borstel, 1982 Petersen, n.d.a.
Rhoda	Sebec R.	open simple twined fragment, Z wefts (1+)*	—	Petersen, n.d.a.
Brockway	Sebec R.	cordage, 2 ply, Z spin, S twist in unknown form (1+)*	—	Petersen, n.d.a.
Schoodic Stream	Piscataquis R.	close simple (?) twined fragment, S wefts (1)*	—	Petersen, n.d.a.
Junior Stream	West Grand Lake	open simple twined fragment, S wefts (1)* cordage, 2 ply, Z spin, S twist in unknown form (1)*	—	Petersen, n.d.a.

* Specimen derived from negative impression on Vinette I-like ceramics.

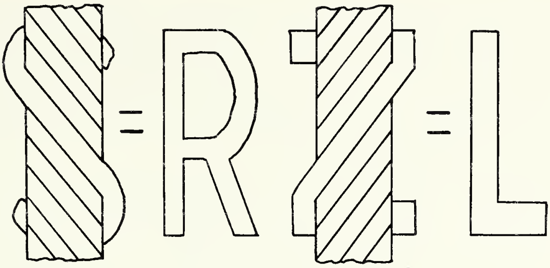

Fig. 1.—Direction of twist, spin or weft slant and symbols employed in their description (after Hurley, 1979).

site and 15JO35 in eastern Kentucky (Adovasio, 1982), and the Natrium Mound in West Virginia (Solecki, 1953). Other sites from the upper Ohio drainage include Cresap Mount in West Virginia and McKees Rocks Mound in Pennsylvania (Dragoo, 1963), Northern Thorn Mound in West Virginia (Adovasio and Andrews [with Carlisle], 1980), and Meadowcroft Rockshelter in Pennsylvania (Johnson, 1982; Stile, 1982). In the Mid Atlantic region, samples are available from the Canton Site in southern New Jersey (Mounier, 1981) and the Rosenkrans site in western New Jersey (Kraft, 1976). In New England, samples include material from the Clap's Landing site in eastern Massachusetts (Dincauze, 1975), the Great Diamond Island site in southwestern Maine (Hamilton and Yesner, 1981), 25 other variably known sites from coastal and interior Maine (Doyle et al., 1982; Petersen, n.d.a.; Spiess et al., 1983), as well as the Boucher site in northwestern Vermont (Petersen and Basa, n.d.) and the East Creek site in western Vermont (Louise Basa and Stephen Loring, personal communication, March 1983). Samples are also known from the Augustine Mound in New Brunswick (Turnbull, 1976), the Muskalonge Lake and Morrow sites in northern New York (Ritchie, 1955, 1965), and the Bruce Boyd site in southwestern Ontario (Spence et al., 1978). Two other possibly Early Woodland period sites in the Northeast which produced actual fiber perishable include the Picton site in Ontario (Ritchie, 1949) and the Riverside site in Michigan (King, 1968; Adovasio and Andrews [with Carlisle], 1980).

To briefly summarize the inventories from these sites, there were at least seven different structural types of cordage, two types of netting, two structural types of plaited fabrics or basketry, and nine structural types of twined fabrics, basketry or sandals represented (see Tables 1 and 2). Raw materials apparently included paw paw (*Aimina triloba* L.), canary grass (*Phalaris caroliniana*), and rattlesnake master (*Eryn-*

gium yuccifolium) in Kentucky, bovid hair (Bovidae sp.) in New Brunswick and more commonly over the broad region, relatively fine Indian hemp (*Apocynum cannibinum* L.) and milkweed (*Asclepias* sp.) as well as more coarse inner bark, apparently basswood (*Tilia americana* L.) for many of the indentifiable specimens (Turnbull, 1976:55; Watson, 1969:38; Whitford, 1941).

It should be obvious from the preceding summary that Early Woodland perishable fiber industries remain incompletely known across the entire Northeast due to rare conditions of preservation, recovery, and adequate study. The cumulative data on fiber perishables nonetheless indicate the highly diversified and sophisticated nature of Early Woodland perishable fiber industries in the Northeast. Furthermore, the sum of these data is obviously reflective of a long span of prior development in the region (see Adovasio and Andrews [with Carlisle], 1980; Adovasio and Carlisle, 1982).

Clearly recognizing the limited extent of the available perishable data, one tentative observation seems inescapable. That is, Z twist cordage and twined fabrics or basketry with Z wefts only occur in contexts which are clearly not attributable to classic Adena or Adena-related Middlesex phase contexts. Adena and Middlesex perishable fiber industries share a highly preferred usage of S-twist cordage and twined fabrics or basketry with S wefts (see Fig. 1). Thus, an intriguing technological correlation seems apparent between Adena and Middlesex fiber industries, a correlation which is borne out by a variety of other more commonly noted aspects of their respective technological inventories, such as use of Ohio fire clay tubular pipes, native copper beads and lithic tools manufactured from Midwestern raw materials.

Before embarking on some far reaching diffusionary scheme however, it should also be noted that S twist cordage and fabrics or basketry with S wefts occur in other Early Woodland contexts which do not seem to be classic Adena or Middlesex related, such as the interior sites in Maine mentioned previously or the Clap's Landing site in Massachusetts. Consequently, we may ultimately be able to specify that S twist cordage and/or S weft fabrics are necessary but not sufficient conditions for the definition of Adena or Adena-related fiber perishables, whereas Z twist cordage and/or Z wefts were rare to nonexistent in such contexts during the Early Woodland period.

BEHAVIORAL IMPLICATIONS

At this juncture, the behavioral implications of the aforementioned Early Woodland ceramic and perishable fiber industries will be given some further consideration. All of the available data allow suggestion of broadly similar ceramic, cordage, netting, and basketry (or fabric) industries over much of the broad Northeast during the Early Woodland period. Although such uniformity has been previously noted by a variety of researchers (for example, Braun, 1980; Griffin, 1978; Ozker, 1982; Stoltman, 1978; Willey, 1966), few archaeologists have ventured to explain the widespread technological millieu of the Early Woodland period in other than sketchy terms. The well known, if no longer tenable, reconstruction offered by Ritchie and Dragoo suggested that direct and broad scale "splinter migration" best accounted for the wide spread of classic Adena technologies in much of the Northeast, particularly manifest in the burial ceremonialism of the Middlesex phase (Ritchie and Dragoo, 1959, 1960). While no longer supported by more recent research and current interpretive fashion, the mechanics of the commonly accepted alternative of an Early Woodland trading network (for example, Granger, 1978; Kraft, 1976; Snow, 1980; Thomas, 1970; Turnbull, 1976) remain poorly developed and less well understood. We can be reasonably sure that raw materials and presumably finished goods and perishable materials were in some way moved across the northeastern countryside, but the mechanisms responsible for such movement and the motivation behind it need better explication. Although reconstruction of an Early Woodland trade (or exchange) network lies beyond the scope of this presentation, one potentially valuable and possibly analogous discussion has been well formulated by David Clarke (1979) in his consideration of the Bell Beaker network in western Europe. Clarke's treatment emphasizes the varied economic and social roles which material culture, including textiles and ceramics, may play within and between social groups. His valuable treatment well compliments similar considerations about cultural styles offered by a variety of other archaeologists, including, for example, Braun (1980), McPherron (1967), and Wobst (1977). Still other, more ecological-economic considerations could likewise be used to better examine this matter, including treatments offered by Brose (1979), Dalton (1977), and Ericson (1977), for example. Suffice it to say here that this matter bears further investigation in the context of trade and exchange as well as the more nebulous matter of cultural styles reflected in the archaeological record of the Early Woodland period and the broader span of prehistory and history.

We are in a better position to reflect on a matter of smaller regional scale, but of no less importance, however. Using data drawn from a variety of recent detailed analyses conducted in northern New England (Doyle et al., 1982; Hamilton and Yesner, 1981; Petersen, 1977*a,* 1977*b,* 1978, 1980, n.d.a.; Petersen and Basa, n.d.; Petersen and Power, 1981, 1983), we can begin to go beyond subjective reconstruction to examine and evaluate important matters of cultural continuity and identity in this portion of the Northeast. (We would like to reiterate the word begin here since detailed, problem-oriented technical analyses are a slow, sometimes painful, but nonetheless needed process.)

Individual and combined research in Maine and Vermont permits tentative demonstration of long lasting continuities in both areas on the basis of preserved technologies, specifically including ceramics and fiber perishables. Ceramic data from the Lake Champlain and Connecticut River drainages of Vermont have permitted the tentative definition of a continuum of *in-situ* development over the span of the entire Woodland period, with distinctive local variation as well as broad parallels to other regional developments. We have elsewhere reasoned that the Western Abenaki may well have an antiquity minimally spanning the entire Woodland period on the basis of this continuum of ceramic development (Petersen and Power, 1983; Petersen, n.d.b.). Likewise, a long span of *in-situ* ceramic development can be suggested for southwestern Maine (Hamilton and Yesner, 1981), which is broadly comparable to the Vermont sequence, but nonetheless distinctive. This span of development has less precise connection to the ethnographic record however, due to the smaller number of detailed analyses conducted in this portion of Maine.

Further substantiation of these continuities is afforded by an examination of the fiber perishables from both areas, including the Early Woodland materials mentioned here. It should be stressed that twist direction in cordage and weft (stitch) slant in twined fabrics are very highly sensitive, normally population specific attributes in fiber perishables, as well noted by Adovasio and other analysts of perishable industries (for example, Adovasio, 1977, 1979, 1983; Adovasio and Carlisle, 1982; Andrews and Adovasio, 1980; Fry and Adovasio, 1970; Maslowski, 1981; Weltfish, 1932).

> "Population" in this sense explicitly equates with an ethnic group in the sense that Pima or Paiute, Karok or Kwakiutl, Cheyenne or Shawnee are ethnic groups. While several linguistically related or unrelated groups may share the same stitch slant (as well as other aspects of production), rarely if ever does any one group regularly employ both of them *even* if some individuals *may* opt to use a non-customary pattern. Put another way, although a minor amount of idiosyncratic variation in twining weft manipulation preference may exist within a given population of weavers, rarely if ever will any group systematically exploit *both* possible stitch slants. Twining stitch slant (like work direction in the production of coiled baskets as well as initial spin or final twist in cordage manufacture) is not dependent on handedness. The preponderance of one or another twist direction or its apparent coexistence in some numbers cannot be explained on the basis of idiosyncratic terms alone. Indeed, there are virtually no ethnographic parallels for the coexistence of both twining twist directions in the same residence unit unless two different populations of weavers have been amalgamated, peacefully or otherwise. (Adovasio and Carlisle, 1982:848).

Numerous archaeological and ethnographic examples well substantiate the diagnostic nature of the attributes mentioned by Adovasio

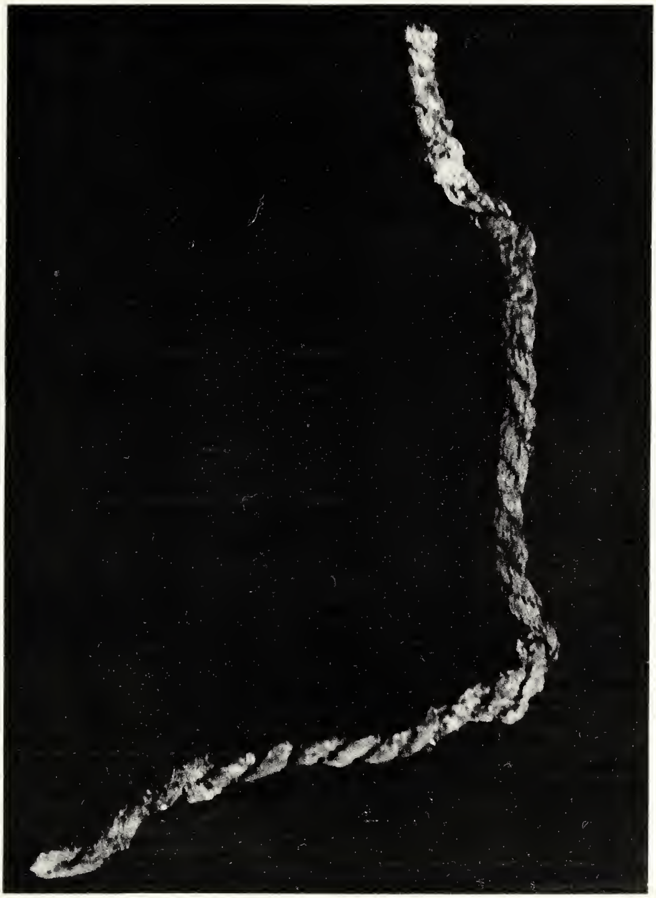

Fig. 2.—Rare example of actual 2-ply, Z-spin, S-twist cordage (S_z^z) from the Boucher site, feature 131. Total length is about 45.0 mm; diameter 1.35 mm.

and Carlisle here (for example, Adovasio, 1983; Andrews and Adovasio, 1980; Bower, 1980; Epstein, 1963). These and a host of other examples provide documentation of the distinctive patterning which characterizes technological learning networks, with preferred twist or weft slant ranging between 70–80% and often exceeding 90% in large samples of fiber perishables. Whether derived from the archaeological or ethnographic record, one or the other of the binary attribute states (S or Z) typically dominates a site-specific or regionally derived sample. Exceptions to this pattern are therefore worthy of hypothesis testing to account for such variability. Moreover, such preferences used in

Fig. 3.—Rare example of actual open simple twined basketry (fabric) from the Boucher site, feature 94A. Wefts and warps are composed of 2-ply, Z-spin, S-twist cordage (S_z^z). Total length of extant specimen (not visible) is 210.0 mm. Native copper bead in lower center section is about 6.80 mm in length.

conjunction with other attributes have enabled spatial differentiation of archaeological complexes in both synchronic and diachronic dimensions (for example, Adovasio, 1983; Andrews and Adovasio, 1980; Maslowski, 1981). The important point here is that once a population adopts a particular cordage twist or twined weft, they rarely if ever change it.

Although of small size in absolute terms, but not necessarily so in comparison with other samples, the Early Woodland fiber perishables from the Boucher site in the Lake Champlain drainage of Vermont (n = 9+) with sufficient detail to permit analysis reveal that S twist cordage and twined fabrics with S wefts account for at least 89% of the extant perishables (Figs. 2–3). More recent samples of fiber perishables (n = 31+) from the late and terminal Middle Woodland periods, ca. A.D. 600 to A.D. 1000 in the same drainage include at least 84% with S twist or S wefts (Petersen and Power, 1983), thereby paralleling the continuity reflected in the ceramics.

Conversely, the Early Woodland fiber perishables (n = 6+) from the Great Diamond Island site in Casco Bay on the coast of Maine indicate

Fig. 4.—Exterior/interior "corded" (Vinette I-like) ceramic vessels from the Great Diamond Island site.

a pattern of continuity where 66% of the specimens were Z twist cordage or twined fabrics with Z wefts (Figs. 4–5). Later samples of fiber perishables from Middle and Late Woodland occupations of the Great Diamond Island site (n = 11+), ca. A.D. 600 to A.D. 1200 include at least 64% with a Z twist or Z wefts (Hamilton and Yesner, 1981).

These samples demonstrate both local continuities in the manufacture of perishables as well as different preferences between the two areas of the interior Lake Champlain drainage and coastal Casco Bay over time. Of related interest, samples of Early Woodland perishables from 25 other sites in Maine indicate the overall presence of dominant S twist cordage and S wefts from 16 "interior" sites, with generally predominant Z twist cordage and fabrics with Z wefts at nine "coastal locales and one "interior" site (see Fig. 6, Table 2; Doyle et al., 1982; Petersen, n.d.a.; Spiess et al., 1983). While all of these latter samples are dreadfully small, it seems quite possible that these distinct differences in fiber perishable preferences are reflective of distinct interior and coastal groups in Maine during the Early Woodland period. Moreover, other samples from both coastal and interior settings in Maine, reveal that cordage twist preferences (S or Z) remain likewise constant at most sites under current investigation, often surpassing an 80%

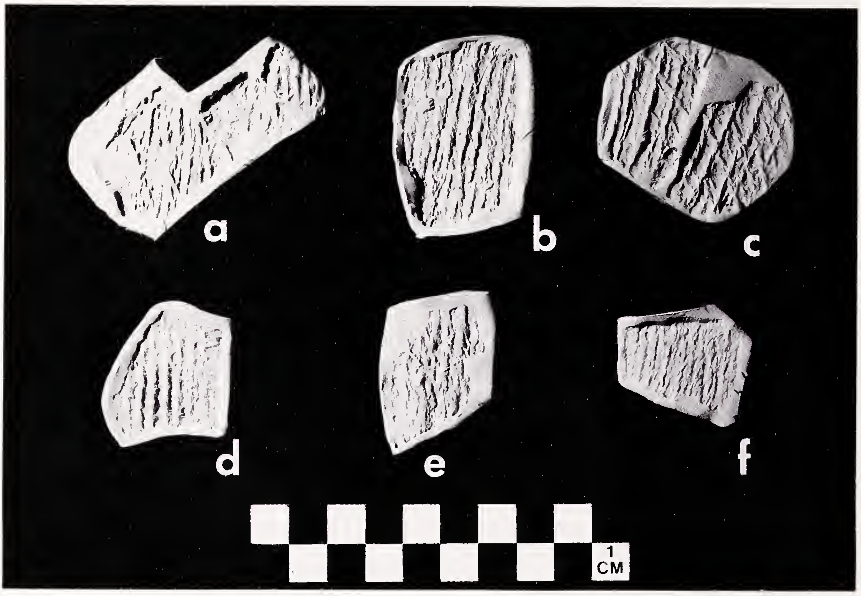

Fig. 5.—Fiber perishable positive casts from sites in Maine: a, stretched open simple twining with Z_s^s cordage wefts, Hamilton site; b, stretched open simple twining with S_z^z cordage wefts, Basin Island site; c, open simple twining with S_z^z cordage wefts (and warps), Great Diamond Island site; d, stretched open simple twining with S_z^z cordage wefts, Sebasticook I site; e, stretched open simple twining with S_z^z cordage wefts, Hamilton site; f, close twining with Z_s^s cordage wefts, Hamilton site.

preference over a 2000 year period (Petersen, n.d.a.). Again, we find here suggestive evidence of long term, *in-situ* continuities at both coastal and interior locales in Maine during the Woodland (Ceramic) period. Curiously, however, this dichotomy disappeared after A.D. 1000, a matter which is beyond the scope of this treatment, but which is addressed in some detail elsewhere (Petersen, n.d.a.; Petersen and Hamilton [with LaBar and Hedden], 1984).

The implications of this apparent coastal/interior difference in perishable twist preference are potentially complex, but it seems safe to suggest that distinct and different technological populations were present in coastal and interior environments over much of the span of the entire Woodland (Ceramic) period in Maine. We feel that the available data permit us to question previous models of seasonal movement between coastal and interior locales in Maine and the Maritimes, paralleling arguments recently presented by Sanger (1982) on the basis of subsistence data. The social implications of our observations are po-

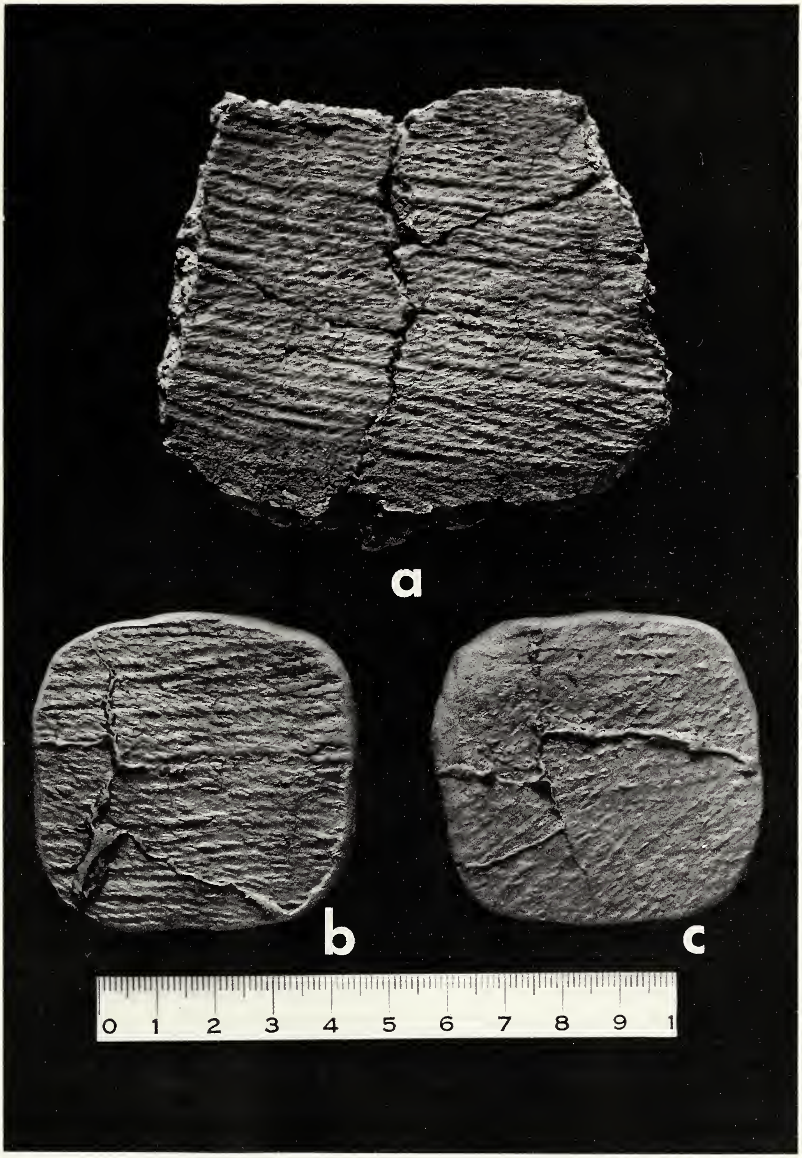

Fig. 6.—Exterior/interior "corded" (Vinette I-like) ceramic sherd and perishable positive casts from the Rhoda site in Maine: a, Vinette I-like ceramic sherd showing interior surface; b, positive cast of interior surface showing stretched open simple twining with Z_s^s cordage wefts; c, positive cast of exterior surface showing extensive smoothing over original impression.

tentially diverse: How do technological populations correlate with social groups? What factors best account for technological differentiation in the first place? and What does the identification of such technological populations mean in terms of regional culture history and previous behavioral reconstructions? We suggest that differentiation of technological populations can be minimally interpreted as being indicative of different social groups, whether local or regional bands, or in this case, that previously unrecognized differences in ethnic populations may be ultimately detailed in Maine (see Adovasio, 1983; Wiessner, 1983). This and a host of other questions bear further investigation.

SUMMARY AND CONCLUSIONS

Our current understanding of Early Woodland ceramic and perishable fiber industries in the Northeast is obviously uneven and incomplete. We have clearly managed a fair start in detailing the variety and significance of the earliest ceramics in the Northeast. Contemporaneous fiber perishables remain little known, however, in spite of their long tenure in the technological inventory of aboriginal populations within the broad region and common usage in the surface finishing of Early Woodland ceramics. The available sample nonetheless provides tentative definition of the relative diversity of structural forms, technological sophistication and widespread similarities of cordage, netting, plaiting and twining industries across the Northeast during the Early Woodland period, ca. 1200 B.C. to 200 B. C. The complexity in Early Woodland fiber perishables is anticipated in the very rare occurrences across eastern North America of even older samples.

An admittedly simplistic but suggestive example of the utility of detailed technical analyses of both ceramics and fiber perishables has been presented here for its summary descriptive value and to encourage further research along similar lines. We expect that the complexity of this reconstruction will be further elaborated, modified or rejected with subsequent investigation, as is the way of archaeological research.

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FLORAL VASCULAR ANATOMY OF *JAPONOLIRION OSENSE* NAKAI (LILIACEAE) AND ITS TRIBAL RELATIONSHIP

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Abstract

Japonolirion osense, a rare, serpentine endemic of Japan known from only two general areas, has been associated in the limited literature with the tribe Helonieae—*Helonias* in eastern North America, *Heloniopsis* in Japan and Korea, and *Ypsilandra* in western China. This is the first report on the floral vascular anatomy of "the lily of Japan." The pedicel to stigma vasculature of *J. osense* is a simple axial system with fusion dorsals and unbranched ventrals. The three septicidal carpels are loosely connected with only stigmatic tissue along their central floral axis. Each carpel terminates in a short free style. Three representative genera of the Helonieae have simple dorsals and highly branched ventrals, three fused septa, a massive basal receptacle that is fused along along the floral axis, a fusion style that is depressed into the upper ovary area, winged seeds, and they share loculicidal dehiscence. The tribal association of *Japonolirion* should be with the Tofieldieae and not the Helonieae.

Introduction

Japonolirion osense Nakai is among the rarest of flowering plants in the Japanese Islands (Hara and Kanai, 1959; Shimizu and Satomi, 1977). It is limited to serpentine areas in Honshu and Hokkaido. In Honshu the plants are found in the Ose region (Mount Shibutsu) which is the type locality and in the Mount Tanigawa region of Kodzuke Province (Gumma Prefecture). In Hokkaido the plant occurs only in

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the Teshio region (Toikanbetsu). The latter area is characterized by cold, high elevation, serpentine swamps.

Nakai (1930) first described this monotypic genus and its associated species from Ose in Honshu, hence its specific name. The type specimen is in the Herbarium of the University of Tokyo (TI). Makino and Tatewaki, in Tatewaki (1931), described another species from Hokkaido, that is *Japonolilion* (Japonolirion) *saitoi*, but this northern population has since been treated as a variety, that is *J. osense* var. *saitoi* (Makino & Tatew.) Ohwi. Hara and Kanai (1959) have presented a distribution map of the species, while only the northern var. *saitoi* was mapped for Hokkaido by Tatewaki (1954). The species has been illustrated in Ohwi's *Flora of Japan* (1965, fig. 2), Kitamura et al., *Illustrated Herbaceous Flora of Japan* (1964, vol. III, pl. 43, fig. 271), and Shimizu's *New Alpine Flora of Japan* (1983, vol. II, pl. 107, fig. 334), and Satake et al., *Wild Flowers of Japan* (1981, Vol. I, pl. 18, fig. 2).

The systematic relationship of this rare lily was first referred to the Helonieae by Nakai (1930) in his type description. This tribal association was again repeated in Kitamura et al. (1964) and Shimizu (1983). Both authors also repeated the reported $2n = 24$ chromosome count published by Sato (1942). Other than the type description and the limited floristic treatments previously cited, little direct evidence has been provided to substantiate a relationship to the Helonieae. This report presents the floral vascular anatomy of *J. osense* and is followed by an inference on a new tribal association.

MATERIALS AND METHODS

Collections fixed in FAA of both flowering and fruiting inflorescences of *Japonolirion osense* var. *saitoi* sampled near Toikanbetsu, Rumoi, Hokkaido, were presented by Gen Murata of Kyoto University. Standarized, paraffin, serial sections on 30 small flowers were prepared between 12–15 μ and stained in safranin-methylene blue (Johansen, 1940; Sass, 1958). As an additional check on these serial sections, whole flowers were cleared and the vasculature stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

The method of presenting the continuous floral vascular anatomy follows that used in our previous papers (Utech and Kawano, 1975, 1976, 1980, 1981; Utech, 1978*a*, 1978*b*, 1978*c*, 1978*d*, 1978*e*, 1979*a*, 1979*b*, 1980, 1982). Figs. 2–4 are composite photomicrographs presenting the vascular floral anatomy, whereas Figs. 5–7 are line-drawn summary diagrams. In Fig. 6, projected views of the vascular continuity are represented from along both the dorsal and ventral radii. No teleological implication is intended by the descriptive manner of vasculature presentation and discussion. The various bundles and traces are letter-coded for ease in comparison and imply no direct homology to previously presented species.

OBSERVATIONS

Pedicel Vascularization

The inflorescence of *Japonolirion osense* is a dense, simple, erect raceme with several to relatively many flowers. The inflorescence is

Fig. 1.—Close up of inflorescence and flowers of *Japonolirion osense.* Material from FAA collection. Scale indicated, bar = 1 cm.

normally 15–40 cm long, glabrous, weakly angled in cross-section or ridged in longitudinal section, and exceeds the leaves in height. There is a single flower per node, and each is subtended by a brownish, scarious bract which is 1.5–3.0 mm long, and one-nerved (Figs. 1, 2A). The bracts subtending each pedicel are similar to those lower on the inflorescence, but only reduced in size. The flowering pedicels are 1.5–3.0 (4.0) mm long and ascending.

For most of the flowering pedicel's length, there are three, large, equally spaced, vascular bundles in cross-section (Figs. 3A–B, 5A, 6A, A′). Near the base of each flower, the associated pedicel has a triangular shape in cross-section. At this lower receptacle level each of the three

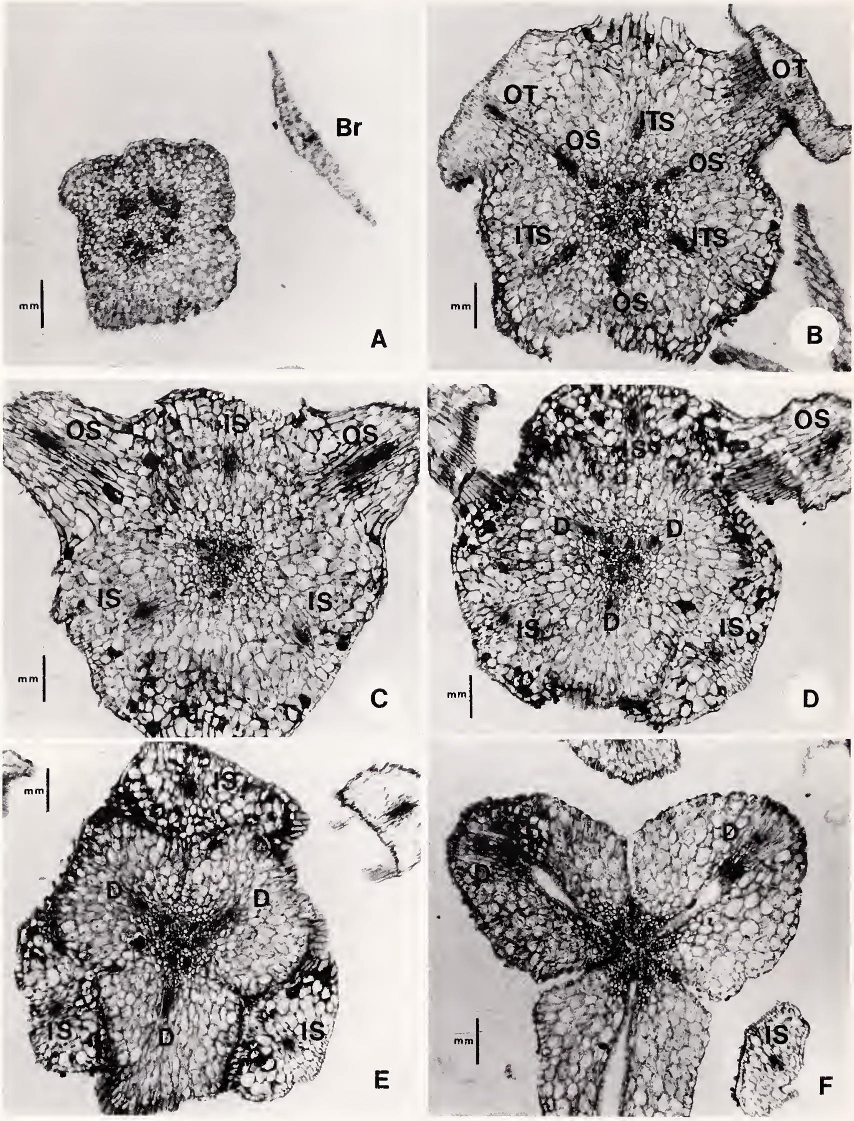

Fig. 2.—Pedicel, tepal and stamen vascularization in *J. osense*. Scale indicated, bar = 1 mm. (A) Pedicel and bract cross-section showing three clusters of bundles in the pedicel at the level of the tri-parted subdivision and a single vein (trace) in the subtending bract (Br). (B) Receptacle cross-section showing the vascularization of the outer tepals (OT), outer stamens (OS) and the common inner tepal-stamen area (ITS). The outer tepal bundles (OT; only 2 shown) shared a common origin with the three outer stamen (OS) bundles at a lower level in the common outer tepal-stamen bundles (OTS; not shown).

pedicel bundles undergoes a tri-parted radial division which results in three sets of three bundles each (Figs. 3C, 5B–C, 6B–C, 6B′–C′, 7).

Tepal and Stamen Vascularization

The six, greenish yellow tepals are free to their base and persist after anthesis (Fig. 1). There is a slight size difference between the three outer tepals and the three inner tepals. The tepals of the outer cycle are somewhat shorter in length (1.5–2.0 mm) than those of the inner cycle (2.0–2.5 mm) as well as somewhat narrower. Though small, the tepals of both cycles are broadly lanceolate. There are no glands or basal succate depression associated with the tepals of either cycle. The tepals of both cycles have only a single midrib vein, that is, an outer tepal (OT) bundle and an inner tepal (IT) bundle. There is no formation of tepal laterals in either cycle.

The six stamens, three outer and three inner, are equal in size, similar in shape, and equally spared in their respective cycles. All six stamens are as long as the inner perianth cycle. The white filaments are glabrous and subulate. The ovate anthers are bilocular, basifixed and introrse (Fig. 4F). Connective tips are not present on the anther sacs. There is a single bundle per stamen, that is, an outer stamen (OS) bundle in each of the three outer stamens and an inner stamen (IS) bundle in each of the three inner stamens.

Vascularization of the tepal and stamen cycles is simple and direct, and involves the subdivision of the three existing compound pedical bundles (Fig. 7). In the case of the vascularization of the outer tepals and outer stamens, subdivision of existing compound bundles is involved, whereas the vascularization of the inner tepals and inner stamens occurs via the subdivision of compound fusion bundles formed within the receptacle area (Figs. 2B–E, 3D–E, 5C–H, 6D–H).

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Three pairs of bundles are grouped in the central axial area along the ITS radii. Gaps are present in this central area along the OT-OS radii. (C) Receptacle cross-section above B showing the departure of the three outer stamen (OS) and the three inner stamen (IS). At this level the common ITS bundles have already divided and the blades of the inner tepals have been cut off. In the central axial area, the fusion dorsals are being formed. (D) Receptacle cross-section above C showing the formation of the fusion dorsals (D), the formation of the inner stamens with their bundles (IS) and the final departure of the outer stamens (OS). In the central axial area there are three pairs of bundles. The gaps along the OT-OS radii were closed with the formation of the dorsals, but there are now gaps along the IT-IS radii. (E) Receptacle cross-section above C showing the departure of the inner stamen with their bundles (IS) and the outward movement of the three dorsals (D) under the unopened locules. (F) Lower gynoecial cross-section showing the opened locules with the dorsals (D) in their outer carpellary position and the six ventrals in their central axial position.

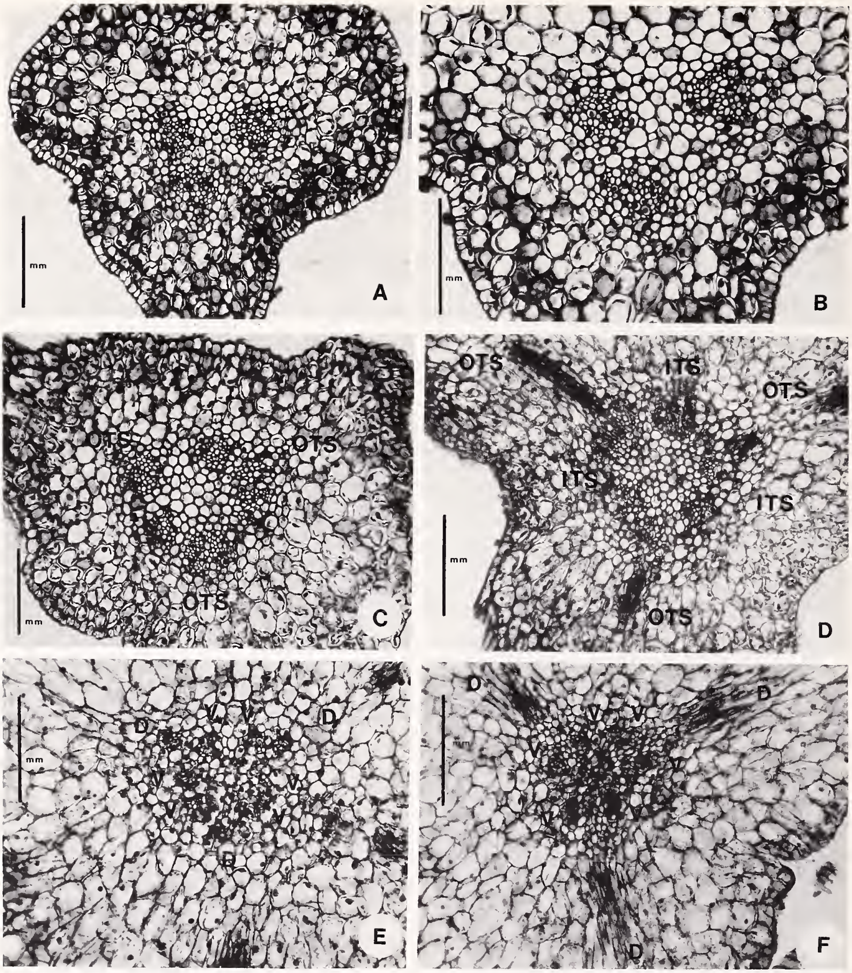

Fig. 3.—Vascularization of the pedicel, tepals and lower gynoecium in *J. osense*. Scale indicated, bar = 1 mm. (A) Pedicel cross-section showing the three compound bundles prior to the tri-parted division. (B) Enlargement of A showing the three compound bundles. (C) Pedicel cross-section showing the tri-parted division of the three pedicel bundles. The central product of each division is the common outer tepal-stamen (OTS) bundle. (D) Lower receptacle cross-section showing the departure of the three common OTS bundles and the formation of the common inner tepal-stamen bundles (ITS). (E) Lower gynoecial cross-section showing the three dorsals (D) and the six ventrals (V). (F) Lower gynoecial cross-section showing the departure of the three dorsals (D) and the six remaining ventrals (V).

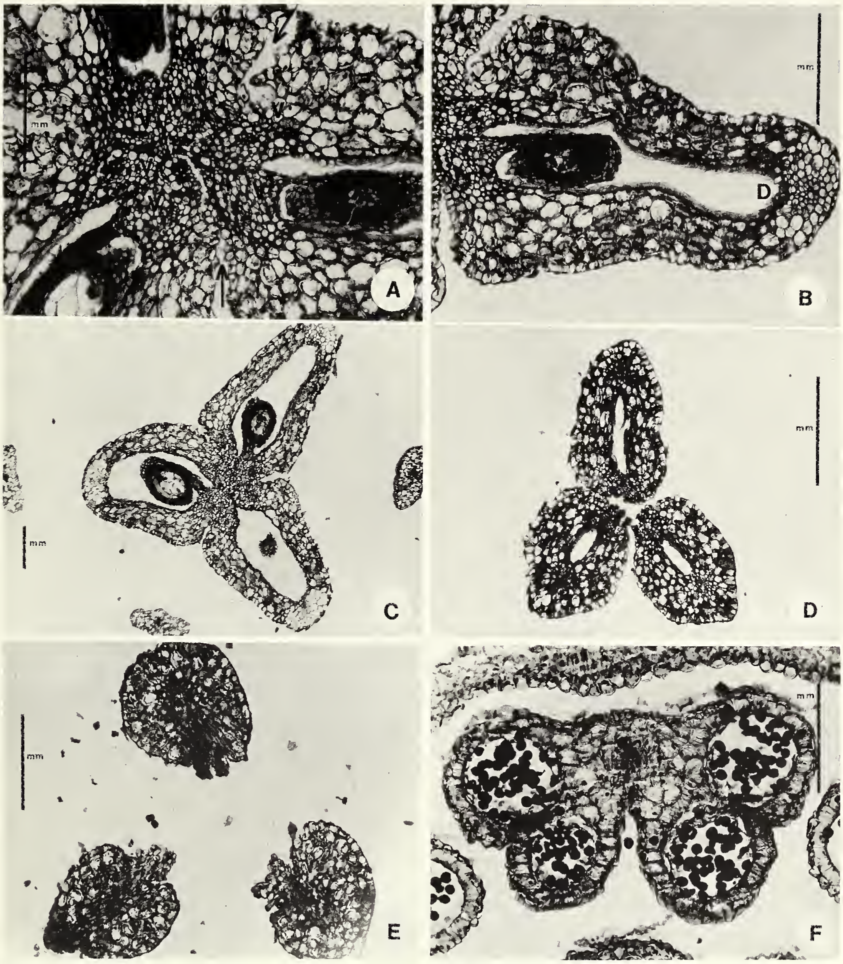

Fig. 4.—Gynoecial and stamen vascularization and morphology in *J. osense.* Scale indicated, bar = 1 mm. (A) Gynoecial cross-section showing the location of the six ventrals (V) and the weak zone of inter-digitating papillae (arrows) which separate the three carpels. (B) Gynoecial cross-section at the same level as A showing the dorsal (D) bundle surrounded by sheath cells. (C) Overall gynoecial cross-section showing the three carpels with ovules and the ventral and dorsal regions. (D) Upper gynoecial cross-section showing the three freed carpels. Dorsal and ventral bundles are still present at this level. (E) Stylar region cross-section showing the inner facing papillae of the stigmatic zone (arrows). The dorsals are still present at this level. (F) Mid-anthers cross-section showing the bilocular and introrse condition. All anthers are similar in size and shape, basifixed, and contain a single bundle.

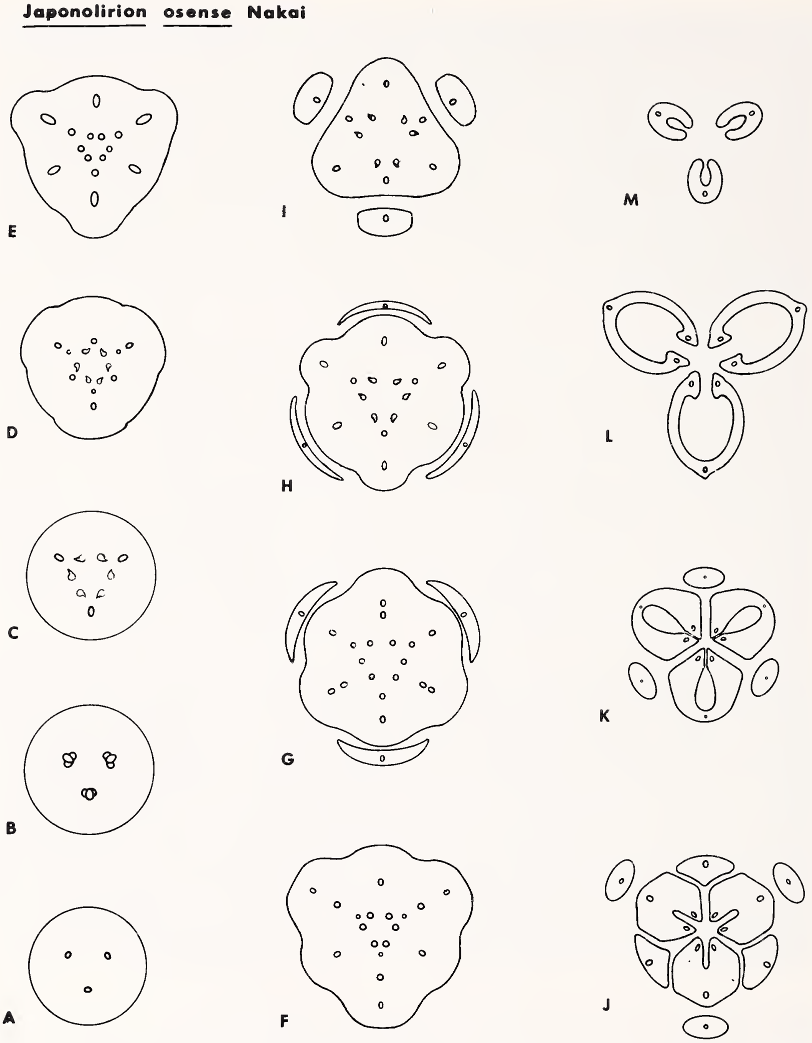

Fig. 5.—Selected summary floral cross-section of *J. osense.* (A) Lower pedicel level with three compound bundles each 120° apart. (B) Pedicel level showing the tri-parted subdivision of the three compound bundles. (C) Pedicel level following the tri-parted subdivision. The center bundle of each three which departs establishes the common outer tepal-stamen (OTS) bundle. (D) Lower receptacle level showing the formation of the three common inner tepal-stamen (ITS) bundles via fusion from the inner six remaining bundles. The ITS bundles are midway between the common outer tepal and stamen radii. The outer tepal (OT) and outer stamen (OS) bundles are also formed at this level from the division of their common bundle. (E) Lower receptacle level showing the departure of the three outer tepal traces (OT) and the common inner tepal-stamen traces.

Following the tri-parted radial division of the three large pedicel bundles in the lower receptacle area, the center bundle of each group of three establishes a radius along which the outer tepals and stamens form. These three radii are 120° apart. The three bundles which are along these radii are compound and have been designated as the common outer tepal and outer stamen bundles (OTS). Subsequent subdivision of these bundles results in the formation of the three outer tepal bundles (OT) and the three outer stamen (OS) bundles (Figs. 2B–D, 3D, 5C–H, 7). It should also be noted that the OS-OT-OTS radii are vertically co-planar with the radii of the three pedicel bundles.

Following the formation of the common OTS bundles via the tri-parted divisions, the two lateral bundles which flank each OTS bundle again undergo a radial division. The closest two product halves of these divisons but from different OTS bundles fuse. These three fusion products are 120° apart and mid-way between the OTS bundles. These fusion products have been designated as the common inner tepal-stamen (ITS) bundles (Figs. 2B, 5D, 6D, D′, 7). Further subdivision of these bundles results in the formation of the three inner tepal bundles (IT) and the three inner stamen (IS) bundles (Figs. 2C–E, 5F–J, 6F–J, F′–J′, 7). The patterns of subdivision of both the common OTS and the common ITS are similar but their origins are different. The OTS was a compound bundle continuous with the pedicel supply following the tri-parted division, whereas the ITS was a compound fusion bundle formed between products of the tri-parted division.

Mid-way between the OTS and ITS radii are the remaining product halves which did not fuse and were derived from the bundles involved

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The three outer stamen (OS) remain in the central area at this level. The cross-sectional shape is decidedly lobed at this level. (F) Lower receptacle level showing the formation of the three dorsals (D) along the common outer tepal and stamen radii from the inner six remaining bundles. There has been no division in the common inner tepal-stamen (ITS) bundles at this level. (G) Departure of the outer tepals with a single bundle (OT) and the division of the three common ITS bundles into inner tepal (IT) and inner stamen (OS) bundles. (H) Departure of the inner tepals with a single bundle (IT) and the outward departure of the OS and D bundles within the receptacle area. (I) Departure of the outer stamens with a single bundle (OS) and the outward departure of the IS bundles within the receptacle area. The three dorsals (D) are each associated with two of the six central bundles and will establish the ventral (V) supply. (J) Departure of the inner stamens (wedge shaped) with a single bundle (IS) and formation of the three weakly connate carpels. The dorsal (D) and ventral (V) supplies are established in each carpel. The three outer filaments have an elliptic cross-section. (K) Lower gynoecial level where the ventrals supply the ovules. The three inner filaments also have an elliptic cross-section. (L) Middle gynoecial level showing the carpellary supply and the relationships of the three carpels. (M) Upper stylar area with only the dorsal supply remaining.

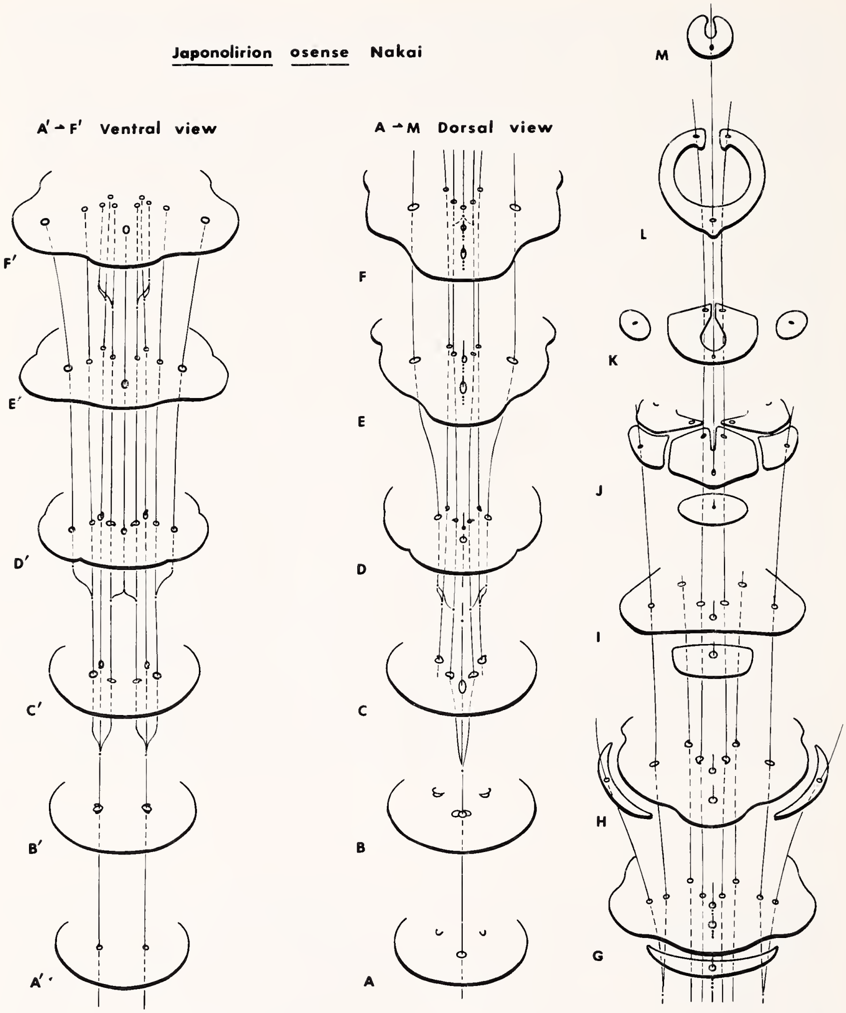

Fig. 6.—Projected cross-sections of *J. osense*. The lettered sections with connected bundles correspond to the same sections in Fig. 5. The series A to M are projected along a dorsal or an outer tepal-stamen radius, while the series A′ to F′ are projected along a ventral or an inner tepal-stamen radius. Both section A and A′ are the same section but viewed from two different radii.

in the formation of the fusion ITS bundles. These centrally located six bundles are arranged in three pairs and they will undergo further subdivision and fusion to establish the dorsal (D) and ventral (V) supplies (Fig. 7).

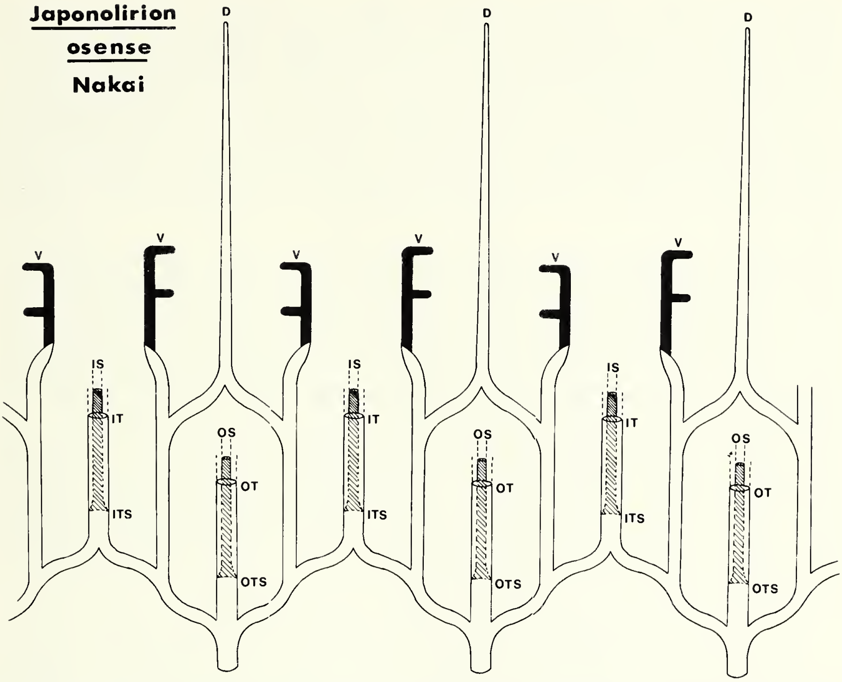

Fig. 7.—Summary longitudinal diagram for the floral vascular supply of *J. osense*. The various codes for the bundles are explained in the text: OTS = common outer tepal-stamen; ITS = common inner tepal-stamen; OT = outer tepal; OS = outer stamen; IT = inner tepal; IS = inner stamen; D = dorsal; V = ventral.

Gynoecial Vascularization

The superior gynoecium in *Japonolirion osense* consists of three weakly connate carpels except apically where the three short (0.5–0.75 mm), recurved styles diverge. The limited lateral carpel fusion is due chiefly to the inter-digitating of papillae along the septal faces. In cross-section, the gynoecium is three lobed (Figs. 2F, 4C–E, 5J, 6J, J′). There are no dorsal grooves to indicate a dehiscent zone. The greenish, glabrous, elliptic, fruiting gynoecium is between 2.5–3.0 mm long and separate septicidally through the weakly connate zone between the carpels. Neither raphides nor other intra-cellular inclusions were observed from the pedicel through the stylar-stigmatic zone.

Vascularization of the carpels is also simple and direct. At the level where the common OTS and ITS bundles are all present, the central gynoecial area has six bundles organized into three pairs. Each of these bundles divides and the two product halves closest to the OTS radii fuse to form the dorsals (D) (Figs. 2D–E, 3E–F, 5F, 6F, F′, 7). The three dorsals depart outward horizontally under the unopened locules. The locules open via a slit along the OTS radii, not perpendicular to it. When the dorsals are formed, a gap is closed. This gap resulted from the tri-parted division in lower pedicle area (Fig. 7). The dorsals are fusion products which do not undergo any further division. They follow a direct course into the small stylar arms and end (Figs. 4D–E, 5M, 6M).

The other remaining product halves that were not involved in the formation of the fusion dorsals (D), become the six ventrals (V). The two ventrals (V) which supply a given carpel (Figs. 3E–F, 5F–J, 6F–J, F′–J′, 7) are the two remaining and continuing products following the division and and fusion which formed the dorsals. There are neither septal axial bundles of any type nor any inter-connections between the dorsal and ventral supplies following their origins.

Two ovules are supplied from each ventral via simple, direct, horizontal funicular traces. On the average, each carpel has four ovules. One to two wingless seeds are usually observed in each mature carpel. Septicidal dehiscence or parting through the weakly connate septal zones is characteristic of this species.

DISCUSSION AND CONCLUDING REMARKS

The pedicel to style floral vascular anatomy of *Japonolirion osense* can be summarized as follows (see also Fig. 7). There are three, equally spaced, compound bundles in the pedicel. Each of these undergoes a tri-parted division in the lower receptacle area. The central element of each set of three directly establishes the common outer tepal-stamen (OTS) bundle. Following another subdivision of the isolated OTS bundles, the outer tepal (OT) and outer stamen (OS) bundles are formed. The paired lateral elements of the tri-parted division divide and the resulting products closest to each other, but from different sets, fuse to form the common inner tepal-stamen (ITS) bundles. These bundles, like the OTS, divide to form the inner tepal (IT) and inner stamen (IS) bundles. The remaining six elements of the lateral pairs continue and establish the dorsal and ventral supplies. Each of these six bundles divides and the resulting products closest to the OTS radii fuse to form the dorsals (D). Three such fusion dorsals are formed. The other six remaining products, that is those not involved in the formation of the dorsals, become the six simple ventrals (V). No septal axials are formed in this species. There is no interconnection between the dorsal and ventral supplies once the dorsals and ventrals are established. The dorsals follow a direct course into the distal portion of their associated carpels and terminate in the free styles.

The floral morphology of *Japonolirion osense* is characterized by three weakly connate carpels. Each has a free, slightly recurved style. The locules open along the OTS radii, not perpendicular to it. Septicidal dehiscence is the rule for the fruiting gynoecium. Neither septal glands nor nectaries associated with the tepals are present in the species. Raphides were not observed in any floral tissue. Furthermore, no raphides were reported in *Tofieldia* (Sterling, 1979) and *Pleea* (Utech, 1978*d*).

Three genera, which are commonly grouped in the Helonieae, are *Helonias, Heloniopsis,* and *Ypsilandra* (Engler, 1888; Krause, 1930). The monotypic *Helonias bullata* L. occurs locally in eastern North America (Utech, 1978*c*). Four species of *Heloniopsis* have been described from Korea, Japan, and Taiwan. *Heloniopsis orientalis* (Thunb.) C. Tanaka is the commonest and has the widest range—occurring throughout Japan (Utech and Kawano, 1981). Five species of *Ypsilandra* occurring in the higher Himalayan elevations of Burma, Nepal, Tibet, and western China are known. The Japanese endemic *Japonolirion osense* has been associated with this liliaceous tribe (Nakai, 1930; Kitamura et al., 1964; Shimizu, 1983).

The floral vascular anatomies and morphologies of three representative genera of the Helonieae have been previously investigated: *Helonias bullata* (Utech, 1978*c*), *Heloniopsis orientalis* (Utech and Kawano, 1981) and *Ypsilandra thibetica* (Utech, manuscript in preparation). Sterling (1980) has also reported a high degree of similarity in the carpel morphology of these three genera. The similarity in floral vascular anatomy and floral morphology between these three species from three different genera is extremely high and almost all of these shared characters are not observed in *Japonolirion.*

The following floral vascular and morphological characters are shared by *Helonias, Heloniopsis* and *Ypsilandra,* but do not occur in *Japonolirion*: 6-ridged pedicels, basal tepal nectaries, broad basal receptacle, fused floral axis, locules opening perpendicular to OTS radii, dorsal grooves, fused septa, sunken styles, winged seeds, loculicidal dehiscence, simple (unfused) dorsal bundles, complex (highly branched) ventrals, and septal axials (Utech, 1978*c*; Utech and Kawano, 1981; Sterling, 1980).

Furthermore, *Helonias bullata* (Utech, 1980) and *Heloniopsis orientalis* (Nakamura, 1967) share a similar $2n = 34$ chromosome number and karyology. Although a count is still lacking for any member of the genus *Ypsilandra,* a count of $2n = 24$ has been reported for *Japonolirion osense* (Sato, 1942).

If the floral and karyological similarity of *Japonolirion* is not with the Helonieae, then what tribal, liliaceous association would be better.

From the limited work on the floral vascular anatomy and floral morphology of the tribe Tofieldieae (Anderson, 1940; Ambrose, 1975; Utech, 1978*d*; Sterling, 1979), there is a high degree of similarity in *Tofieldia* sensu lato and that reported here for *Japonolirion*. The tribal association of *Japonolirion* should be with the Tofieldieae and not with the Helonieae.

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CATALOG OF THE RECENT SCANDENTIA AND PRIMATES IN THE CARNEGIE MUSEUM OF NATURAL HISTORY

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Abstract

The Section of Mammals, Carnegie Museum of Natural History, houses six specimens of Recent tree shrews and 611 specimens of Recent primates. The only family in the Order Scandentia is Tupaiidae. Primate families represented are Lemuridae, Lorisidae, Cebidae, Callitrichidae, Cercopithecidae, Pongidae, and Hominidae. For each specimen the following data are recorded: locality; date collected; catalog number; sex; age; nature of specimen; condition of specimen and comments. The latter category gives information on the condition of the skin and skeletal material, and gives information on the availability of the specimen.

Introduction

The Section of Mammals, Carnegie Museum of Natural History, currently holds six specimens of Recent tree shrews and 611 specimens of Recent primates. The majority of the collection of tree shrews and primates consists of specimens preserved as skins with skulls. However, the collection also contains fluid-preserved material and disarticulated

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skeletons as well as body mounts and mounted articulated skeletons. These specimens are housed primarily in the research collections of the Section of Mammals, but most of the mounted material is on display at this time in the public galleries of the Museum.

The primary purpose of this catalog is to make the availability of this material known to the scientific community. It is extremely difficult to obtain new primate specimens because most species are considered to be threatened with extinction (Berger et al., 1979; Kavanagh, 1983). All species are placed at least as Status II (Threatened) under the Convention on International Trade in Endangered Species. Therefore, it is necessary for researchers to make maximum use of material stored in museum collections. Because specimens stored in this collection are essentially irreplaceable, none is available for study on loan. However, all qualified researchers are welcome to study any of the specimens at the collection facilities of the Section of Mammals.

All collection data files of the Section of Mammals have been computerized. This catalog presents selected data categories of which some are available on the computer file, but others have been specifically generated for this publication. Other categories of data are also available on the computer file; this additional information is available upon request. The format of this catalog is patterned after Napier's (1976, 1981) *Catalogue of Primates in the British Museum (Natural History).*

CLASSIFICATION

The collection of the Section of Mammals and this catalog follow G. G. Simpson's (1945) classification in *The Principles of Classification and a Classification of Mammals* through the level of subfamily. However, we place the tree shrews into a separate order, Scandentia, as done by most recent authors (see Luckett, 1980; Honacki et al., 1982; Dawson and Krishtalka, 1984). Below the level of subfamily, specimens are arranged alphabetically by genus, species, and finally subspecies, if these levels of identification have been made. At the lowest identified taxonomic level, specimens are further arranged alphabetically by collecting locality, beginning with country and progressing through specific locality. Skeletal material with no accompanying study skin is arranged separately at the end of the collection. This material is arranged numerically by taxa. It is hoped that by arranging this catalog in the same order as the collection that work by researchers will be facilitated.

Tree shrews were identified using the key in Lekagul and McNeely (1977). There is no single source for the taxonomy or identification of members of the Order Primates. We have used standard summary references or the latest reviews or revisions for those groups for which they are available. References that have been studied and utilized are as follows: Berger et al. (1979); Dandelot (1971); Dorst and Dandelot

(1970); Fooden (1969); Hershkovitz (1977); Kavanagh (1983); Kingdon (1971); Napier and Napier (1967); Napier (1976, 1981); Nash (1983); Osman Hill (1953, 1957, 1960, 1962, 1966, 1970, 1974); Simpson (1945).

EXPLANATION OF HEADINGS

Locality.—Collecting localities appear as listed on the original skin tags. If spelling variations have been found, the spelling which appears in the most recent edition of the Standard Names Gazetteer for the appropriate country (printed by the United States Board of Geographic Names) will be shown in brackets following the place name in question.

Of the 617 tree shrew and primate specimens in the collection, 60 were zoo or laboratory specimens. In most cases, original localities are not known for these animals. To facilitate recognition of locality information pertaining to captive specimens, these data are followed by an asterisk. Further, the place of their captivity is named under comments.

The specific localities of some specimens collected by Childs Frick in Ethiopia and Kenya were obtained using Friedmann (1930).

Date of collection.—For wild taken specimens, this date refers to the day on which the animal was obtained. In nearly all cases for zoo and laboratory specimens, the only date which is available is the date on which the animal died in captivity. In rare cases when more information is known about a particular captive specimen, those data will be shown under the "Comments" category.

Sex.—Three symbols are used for denoting sex: F, M, ? (undetermined by original collector). Where not denoted on the original tag, sex has sometimes been inferred based on the examination of adult skulls. This practice has not been used for the preparation of the current catalog, but in instances where such conclusions have been drawn previously, the appropriate symbol will be enclosed in brackets.

Age.—Following Napier (1976, 1981) three age categories are used to indicate the age of specimens. The age classes are differentiated as follows:

Infant (Inf):	Any stage of dental development up to complete deciduous dentition;
Adult (Ad):	Complete permanent dentition;
Juvenile (Juv):	Any stage of dental development between the other two.

When skulls were not available, skins were judged to be Adult [Ad] or Immature [Imm] based on size, color, or other appropriate characters. This latter category includes both infant and juvenile specimens because they could not be separated using only characteristics of the skin. Specimens aged by using the skin only are enclosed in brackets under this category.

Nature of specimen.—This category describes the type of preservation used for each specimen and corresponds to the two letter abbreviation system used on our computer file. The following list describes each type of preservation used in the primate collection: SK = skull only; SO = skin only; SS = skin and skull; SB = skin, skull, and body skeleton; SN = complete skeleton; BM = body mount; AL = alcoholic (preserved in 70% ethyl alcohol); CO = cranium only. If pecularities exist regarding availability of a specimen, these are noted by an asterisk following the two letter code. There are two types of specimens that carry the asterisk: 1) a specimen for which some of its parts are missing; 2) specimens on exhibit. These latter specimens are available for examination but this work must be planned with the understanding that the specimens are in exhibit areas and are not housed with the remainder of the primate collection. For further explanations regarding the availability status of a specimen refer to the Comments category.

Condition of specimen and comments.—This category is designed to inform the reader of the usefulness of a specimen for systematics research. The term "Good" is used for all specimens and specimen parts which are in useable condition for study. Damage to the skull is described so that measurability can be evaluated. All skins which are not prepared as conventional study skins are described. Captive animals are noted. Missing parts and exhibit specimens are noted.

TAXONOMIC LIST

- Scandentia
  - Tupaiidae
    - Tupaiinae
      - *Tupaia glis wilkensoni*
      - *Tupaia glis*
- Primates
  - Lemuridae
    - Lemurinae
      - *Lemur rubiventer*
      - *Lemur variegata*
  - Lorisidae
    - Lorisinae
      - *Arctocebus calabarensis aureus*
      - *Nycticebus coucang*
      - *Perodicticus potto edwardsi*
      - *Perodicticus potto ibeanus*
      - *Perodicticus potto potto*
    - Galaginae
      - *Galago alleni*
      - *Galago crassicaudatus lönnbergi*
      - *Galago crassicaudatus monteiri*
      - *Galago demidovii anomurus*
      - *Galago demidovii demidovii*
      - *Galago demidovii murinus*
      - *Galago demidovii thomasi*
      - *Galago elegantulus pallidus*
      - *Galago garnettii lasiotus*
      - *Galago inustus*
      - *Galago senegalensis braccatus*
      - *Galago senegalensis gallarum*
      - *Galago senegalensis moholi*
      - *Galago senegalensis senegalensis*
      - *Galago zanzibaricus*
  - Cebidae
    - Aotinae
      - *Aotus azarae azarae*
      - *Aotus azarae boliviensis*
      - *Aotus lemurinus griseimembra*
      - *Aotus* species
      - *Callicebus moloch donacephilus*
    - Pitheciinae
      - *Chiropotes satanas chiropotes*
      - *Pithecia pithecia*
    - Alouattinae
      - *Alouatta caraya caraya*
      - *Alouatta guariba clamitans*
      - *Alouatta palliata aequatorialis*
      - *Alouatta palliata palliata*
      - *Alouatta seniculus sara*
      - *Alouatta seniculus seniculus*
      - *Alouatta seniculus straminae*
      - *Alouatta seniculus*
    - Cebinae
      - *Cebus albifrons hypoleucus*
      - *Cebus albifrons leucocephalus*
      - *Cebus albifrons versicolor*
      - *Cebus apella apella*
      - *Cebus apella pallidus*
      - *Cebus apella*
      - *Cebus capucinus capucinus*
      - *Cebus capucinus imitator*
      - *Cebus capucinus*
      - *Cebus olivaceus*
      - *Cebus* species
      - *Saimiri boliviensis*
      - *Saimiri oerstedii citrinellus*
      - *Saimiri oerstedii oerstedii*
      - *Saimiri sciureus albifrons*
      - *Saimiri sciureus nigriceps*
      - *Saimiri sciureus sciureus*
    - Atelinae
      - *Ateles belzebuth marginatus*
      - *Ateles fusciceps*
      - *Ateles geoffroyi ornatus*
      - *Ateles geoffroyi panamensis*
      - *Ateles geoffroyi vellerosus*
      - *Ateles paniscus chamek*
      - *Ateles paniscus paniscus*
      - *Ateles* species
  - Callitrichidae
      - *Callithrix argentata argentata*
      - *Callithrix argentata melanura*
      - *Callithrix jacchus jacchus*
      - *Callithrix jacchus*
      - *Saguinus midas midas*
      - *Saguinus oedipus geoffroyi*
      - *Saguinus oedipus oedipus*
      - *Saguinus oedipus*

Cercopithecidae
  Cercopithecinae
    Cercocebus albigena johnstoni
    Cercocebus albigena zenkeri
    Cercocebus galeritus agilis
    Cercocebus torquatus atys
    Cercocebus torquatus torquatus
    Cercocebus torquatus
    Cercopithecus aethiops
    Cercopithecus albogularis albotorquatus
    Cercopithecus albogularis erythrarchus
    Cercopithecus albogularis kibonotensis
    Cercopithecus albogularis kolbi
    Cercopithecus ascanius schmidti
    Cercopithecus campbelli
    Cercopithecus cephus cephus
    Cercopithecus cynosuros helvescens
    Cercopithecus diana diana
    Cercopithecus l'hoesti l'hoesti
    Cercopithecus l'hoesti preussi
    Cercopithecus mitis mitis
    Cercopithecus mitis stuhlmanni
    Cercopithecus mona
    Cercopithecus neglectus
    Cercopithecus nictitans nictitans
    Cercopithecus nigroviridis
    Cercopithecus patas
    Cercopithecus cf. *petaurista*
    Cercopithecus pogonias grayi
    Cercopithecus pogonias pogonias
    Cercopithecus pygerythrus arenarius
    Cercopithecus pygerythrus zavattarii
    Cercopithecus sabaeus
    Cercopithecus talapoin
    Cercopithecus tantalus budgetii
    Cercopithecus tantalus tantalus
    Cercopithecus species
    Macaca fascicularis
    Macaca maurus
    Macaca mulatta mulatta
    Macaca mulatta
    Macaca nemestrina nemestrina
    Macaca nigra
    Macaca sylvana
    Papio anubis anubis
    Papio anubis doguera
    Papio anubis furax
    Papio anubis neumanni
    Papio anubis
    Papio cynocephalus cynocephalus
    Papio cynocephalus
    Papio hamadryas
    Papio leucophaeus leucophaeus
    Papio leucophaeus
    Papio papio
    Papio sphinx madarogaster
    Papio sphinx
    Papio ursinus griseipus
    Papio ursinus ruacana
    Papio ursinus
    Papio species
    Theropithecus gelada
  Colobinae
    Colobus angolensis palliatus
    Colobus guereza guereza
    Colobus guereza kikuyensis
    Colobus guereza matschiei
    Colobus guereza occidentalis
    Colobus guereza
    Colobus pennanti
    Colobus rufomitratus tephrosceles
    Presbytis aygula
    Presbytis entellus
Pongidae
  Hylobatinae
    Hylobates lar
    Hylobates pileatus
    Hylobates syndactylus
  Ponginae
    Gorilla gorilla gorilla
    Gorilla gorilla
    Pan troglodytes schweinfurthi
    Pan troglodytes troglodytes
    Pan troglodytes
    Pongo pygmaeus
Hominidae
    Homo sapiens

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CATALOG OF THE ORDER SCANDENTIA

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
TUPAIIDAE						
TUPAIINAE						
Tupaia glis wilkensoni						
Thailand: Surat Thani Prov.; Muang Sarat Thani Dist., Khao Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06′N, 99°01′E	6 Aug 1983	CM 87903	F	Ad	SB	Good
Thailand: Surat Thani Prov.; Muang Sarat Thani Dist., Khao Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06′N, 99°01′E	6 Aug 1983	CM 87904	M	Ad	SB	Good
Thailand: Surat Thani Prov.; Muang Sarat Thani Dist., Khao Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06′N, 99°01′E	7 Aug 1983	CM 87905	M	Ad	SS	Good
Thailand: Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18′N, 98°58′E	5 Aug 1983	CM 87906	F	Ad	SB	Good
Thailand: Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18′N, 98°58′E	9 Aug 1983	CM 87907	F	Ad	SS	Good
Tupaia glis						
Locality unknown*	21 Sep 1967	CM 59514	F	Juv	SB	Good; Pittsburgh Aviary

CATALOG OF THE ORDER PRIMATES

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
LEMURIDAE						
LEMURINAE						
Lemur rubiventer						
Madagascar	unknown	CM 20984	?	Ad	SK	Good
Lemur variegata						
Madagascar*	unknown	CM 1671	?	Ad	SN*	Good; Pittsburgh Zoological Garden specimen; on exhibit
Madagascar*	unknown	CM 1721	?	Ad	SK*	Good; Pittsburgh Zoological Garden specimen; on exhibit
Madagascar*	29 Sep 1908	CM 1807	M	Ad	SS	Good; Pittsburgh Zoological Garden specimen; on exhibit
Madagascar*	30 Dec 1912	CM 2374	M	Ad	SN	Good; Pittsburgh Zoological Garden specimen

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
LORISIDAE						
LORISINAE						
Arctocebus calabarensis aureus						
Cameroon: Lolodorf	27 May 1936	CM 13188	M	Ad	SS	Frontal-nasal area broken
Cameroon: Sangmelima	18 May 1932	CM 9570	M	Ad	SS	Occipital region damaged
Nycticebus coucang						
Locality unknown*	22 Jan 1968	CM 59517	?	Ad	SN	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	22 Jan 1968	CM 59518	?	Ad	SN	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	22 Jan 1968	CM 59519	?	Ad	SN	Good; Pittsburgh Zoological Garden specimen
Indonesia: Sumatra	unknown	CM 1766	?	Ad	SN*	Good; on exhibit
Perodicticus potto edwardsi						
Cameroon: 15 km W Eseka	24 Apr 1974	CM 41117	F	Ad	SS	Skull damaged but measurable
Cameroon: Ebolowa	9 Jun 1942	CM 42330	M	Ad	SS	Good
Cameroon: Elat	5 Dec 1913	CM 3895	F	Ad	SS	Occipital area, left bulla, and part of parietal missing
Cameroon: Lolodorf	24 Oct 1914	CM 3913	M	Inf	SS	Good
Cameroon: Lolodorf	24 Oct 1914	CM 3926	F	Ad	SS	Good
Cameroon: Lolodorf	6 Mar 1918	CM 4557	M	Ad	SS	Good

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: Lolodorf	29 Mar 1918	CM 4628	M	Ad	SS	Good
Cameroon: Lolodorf	19 Oct 1937	CM 16085	F	Ad	SS	Skull: broken in half, toothrow intact
Cameroon: Lolodorf	11 Apr 1938	CM 16086	M	Ad	SS	Good
Cameroon: Lolodorf	19 May 1938	CM 16087	M	Ad	SS	Good
Cameroon: Melan, 25 mi S Lolodorf	19 Jun 1936	CM 13187	M	Ad	SS	Good
Cameroon: Metet	22 Apr 1919	CM 4663	M	Ad	SS	Good
Cameroon: Metet	15 Mar 1919	CM 5100	M	Ad	SS	Good
Cameroon: Sangmelima	23 Apr 1934	CM 10321	M	Ad	SS	Occipital region damaged
Cameroon: Sangmelima	24 Apr 1934	CM 10322	M	Ad	SS	Occipital region damaged
Perodicticus potto ibeanus						
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Jul 1960	CM 57885	F	[Ad]	SB*	Skull missing
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Jul 1960	CM 57886	M	Ad	SB	Good
Uganda: Kigezi District, Kayonza Forest	9 Aug 1960	CM 57887	M	Ad	SB	Good
Perodicticus potto potto						
Ivory Coast: 15 km N Lakota, 06°00′N, 04°53′W	21 Oct 1971	CM 69182	M	Inf	SS	Good
Ivory Coast: 15 km N Lakota, 06°00′N, 04°53′W	23 Oct 1971	CM 69183	M	Ad	SS	Good
Ivory Coast: 15 km N Lakota, 06°00′N, 04°53′W	24 Oct 1971	CM 69184	F	Ad	SS	Good
Ivory Coast: 23 km E Toumodi, 06°33′N, 04°49′W	14 Oct 1971	CM 69185	M	Ad	SS	Nasals missing, frontal region damaged
Ivory Coast: 23 km E Toumodi, 06°33′N, 04°49′W	15 Oct 1971	CM 69186	M	Ad	SS	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
GALAGINAE						
Galago alleni						
Cameroon: 15 km W Eseka	10 Feb 1974	CM 41118	F	Ad	SS	Good
Cameroon: 15 km W Eseka	10 Feb 1974	CM 41119	F	Ad	SB	Measurable
Cameroon: Ebolowa	12 Jul 1937	CM 14920	M	Ad	SS	Good
Cameroon: Efulen	28 Jul 1911	CM 2205	M	Ad	SS	Skull fragmentary, toothrow intact
Cameroon: Lolodorf	2 Mar 1911	CM 2204	M	Ad	SS	Good
Cameroon: Lolodorf	8 Dec 1913	CM 2875	M	[Ad]	SS*	Skull missing
Cameroon: Lolodorf	15 April 1914	CM 2927	F	Ad	SS	Good
Cameroon: Lolodorf	26 Aug 1914	CM 3898	M	Ad	SS	Nasals missing
Cameroon: Lolodorf	30 Mar 1918	CM 4559	M	Ad	SS	Occipital condyles damaged
Cameroon: Lolodorf	30 Mar 1920	CM 5129	M	[Ad]	SS*	Skull missing
Cameroon: Lolodorf	30 Oct 1937	CM 16089	M	Juv	SS	Occipital region damaged
Cameroon: Lolodorf	6 Jun 1938	CM 16090	M	Ad	SS	Good
Cameroon: Lolodorf	13 Jun 1938	CM 16091	M	Ad	SS	Good
Cameroon: Mengale	18 Jul 1943	CM 42331	F	[Ad]	SS*	Skull: only braincase present; skin: good
Cameroon: Sangmelima	10 Jan 1933	CM 9574	M	Juv	SS	Nasals, maxillaries, pre-maxillaries and occipital regions damaged; zygomatic arches broken
Galago crassicaudatus lönnbergi						
Zimbabwe: Melsetter District, Mount Selinda	27 Nov 1929	CM 6301	M	Ad	SS	Good
Zimbabwe: Melsetter District, Mount Selinda	27 Nov 1929	CM 6302	M	Inf	SS	Good

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Zimbabwe: Melsetter District, Mount Selinda	27 Nov 1929	CM 6303	M	Inf	SS	Skull fragmentary
Zimbabwe: Melsetter District, Mount Selinda	27 Nov 1929	CM 6304	F	Ad	SS	Right orbit and zygomatic arch broken
Galago crassicaudatus monteiri						
Angola: Malange District, Chitau	12 Jan 1931	CM 6974	M	Juv	SK	Skull fragmentary
Angola: Malange District, Chitau	13 Jan 1931	CM 6977	M	Ad	SS	Good
Angola: Malange District, Chitau	13 Jan 1931	CM 6978	F	Ad	SK	Palate damaged; right orbit and zygomatic arch broken
Angola: Gauca River	5 Jan 1931	CM 6950	M	Ad	SK	Good
Angola: Gauca River	7 Jan 1931	CM 6965	M	Ad	SK	Occipital region and orbits damaged
Galago demidovii anomurus						
Central African Republic: Bangassou	31 Dec 1974	CM 41121	M	Ad	SS	Skull fragmentary
Galago demidovii demidovii						
Ghana: Eastern Region, 9 mi NE Accra	21 Sep 1971	CM 69187	M	[Ad]	SO	Good
Ghana: Eastern Region, 9 mi NE Accra	21 Sep 1971	CM 69188	M	[Ad]	SO	Good
Galago demidovii murinus						
Cameroon: Campo	14 May 1931	CM 7437	F	Ad	SS	Occipital region damaged
Cameroon: Eboje	12 May 1931	CM 7436	M	[Ad]	SO	Good
Cameroon: Eseka	6 Nov 1973	CM 41120	F	Ad	SS	Good
Cameroon: Lolodorf	22 Apr 1914	CM 2929	M	Ad	SS	Good
Cameroon: Lolodorf	27 Apr 1914	CM 2942	M	Ad	SS	Good
Cameroon: Lolodorf	30 Apr 1914	CM 2950	M	Ad	SS	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: Lolodorf	25 Apr 1914	CM 3683	M	Ad	SS	Good
Cameroon: Lolodorf	21 May 1914	CM 3687	?	Ad	SS	Occipital region damaged
Cameroon: Lolodorf	19 Jan 1915	CM 3690	M	Ad	SS	Occipital and premaxillary regions damaged
Cameroon: Lolodorf	19 Nov 1914	CM 3911	M	Ad	SS	Good
Cameroon: Lolodorf	30 Mar 1918	CM 4563	M	Ad	SS	Good
Cameroon: Lolodorf	30 May 1918	CM 4604	M	Ad	SS	Good
Cameroon: Lolodorf	2 May 1919	CM 4872	M	Ad	SS	Occipital region damaged
Cameroon: Lolodorf	2 May 1919	CM 4873	F	Ad	SS	Occipital region damaged
Cameroon: Lolodorf	14 Apr 1936	CM 13189	M	Ad	SS	Skull fragmentary
Cameroon: Lolodorf	29 Apr 1937	CM 14919	M	Inf	SS	Bones of skull crushed together
Cameroon: Lolodorf	12 Jul 1938	CM 16088	M	Ad	SS	Occipital region damaged
Cameroon: Metet	2 Jul 1919	CM 4670	M	Ad	SS	Right orbit and zygomatic arch smashed
Cameroon: Sangmelima	17 May 1932	CM 9571	M	Ad	SS	Occipital region damaged
Cameroon: Sangmelima	13 Apr 1933	CM 9572	M	Inf	SS	Nasals, premaxillary and occipital regions damaged
Galago demidovii thomasi						
Uganda: Toro District, Mpanga Forest, 5000 ft, 00°33′N, 30°24′E	17 Jul 1960	CM 57702	M	Ad	SS	Braincase and occipital condyles damaged

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Galago elegantulus pallidus						
Cameroon: Ebolowa	5 May 1937	CM 14922	M	Ad	SS	Nasals missing; occipital region damaged
Cameroon: Efulen	28 Jul 1911	CM 2207	F	Ad	SS	Occipital region damaged
Cameroon: Efulen	29 Jul 1911	CM 2208	M	Ad	SS	Occipital region damaged
Cameroon: Eseka, 03°38′N, 10°47′E	8 May 1974	CM 41122	M	Ad	SS	Good
Cameroon: 15 km W Eseka	1 Feb 1974	CM 42292	M	Ad	SB	Braincase broken; occipital region damaged
Cameroon: Lolodorf	2 Nov 1923	CM 5628	F	[Ad]	SS*	Skull missing
Cameroon: Lolodorf	20 Sep 1924	CM 5678	M	Inf	SS	Palate broken; orbits, zygomatic arches, and occipital region damaged
Cameroon: Lolodorf	1 Mar 1937	CM 14921	M	Ad	SS	Good
Cameroon: Mengale	15 May 1942	CM 42333	F	Ad	SS	Good
Cameroon: Mengale	16 Apr 1942	CM 42334	M	Ad	SS	Good
Cameroon: Mengale	18 Jul 1943	CM 42335	F	Ad	SS	Good
Cameroon: Metet	1 Jul 1919	CM 5104	M	[Ad]	SS*	Skull missing
Cameroon: Mbalmayo, Metet	20 Aug 1941	CM 42332	M	Ad	SS	Basioccipital region missing
Cameroon: Mbalmayo, Metet	6 Aug 1941	CM 42336	F	Ad	SS	Basioccipital region missing
Cameroon: Mbalmayo, Metet	20 Aug 1941	CM 42337	M	Ad	SS	Basioccipital region missing

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: Olama	19 May 1914	CM 3688	F	Ad	SS	Occipital region damaged
Cameroon: Sangmelima	29 Dec 1932	CM 9573	F	Ad	SS	Occipital region damaged
Cameroon: Sangmelima	14 Apr 1933	CM 9575	M	Ad	SS	Occipital region damaged
Cameroon: Sangmelima	14 Apr 1933	CM 9576	M	Ad	SS	Occipital region damaged
Galago garnettii lasiotis						
Kenya: Coast Region, Sokoke Forest	2 Aug 1964	CM 57944	M	Ad	SS	Good
Kenya: Coast Region, Sokoke Forest	9 Aug 1964	CM 57945	M	Ad	SS	Good
Kenya: Coast Region, Sokoke Forest	9 Aug 1964	CM 57946	M	Ad	SS	Good
Galago inustus						
Uganda: Toro District, Mpanga Forest, 5000 ft, 00°33′N, 30°24′E	18 Jul 1960	CM 57703	F	Ad	SS	Good
Galago senegalensis braccatus						
Kenya: Coast Region, Maungu, near Voi	28 Jul 1963	CM 61525	F	Ad	SS	Good
Kenya: Eastern Region, Tana River at mouth of Thika River	25 Aug 1912	CM 4407	M	Ad	SS	Occipital region damaged
Kenya: Eastern Region, Tana River at mouth of Thika River	25 Aug 1912	CM 4408	M	Ad	SS	Good
Kenya: Rift Valley Region, Uasonyiro River, [Ewaso Ngiro (northern)] Nanyuki	3 Sep 1964	CM 57950	F	Ad	SS	Good
Tanzania: Northern Province, 30 mi W Loliondo	31 Aug 1960	CM 57704	?	Ad	SS	Skull fragmentary
Tanzania: Northern Province, 30 mi W Loliondo	29 Aug 1960	CM 57706	M	Ad	SS	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Galago senegalensis gallarum						
Kenya: Eastern Region, Malca Muda area [Melka Mude]	8 Feb 1956	CM 39927	?	Ad	SS	Good
Kenya: Eastern Region, Malca Muda area [Melka Mude]	8 Feb 1956	CM 39928	?	Ad	SS	Good
Kenya: Eastern Region, Malca Muda area [Melka Mude]	8 Feb 1956	CM 39929	?	Ad	SS	Nasals incomplete; premaxillaries and maxillaries damaged; left orbit and zygomatic arch broken
Kenya: Eastern Region, Malca Muda area [Melka Mude]	8 Feb 1956	CM 39936	?	Ad	SK	Good
Galago senegalensis moholi						
Angola: Malange District, Chitau	14 Jan 1931	CM 6982	M	Ad	SS	Good
Angola: Malange District, Chitau	14 Jan 1931	CM 6983	M	Ad	SK	Occipitial and premaxillary region damaged
Angola: Malange District, Chitau	14 Jan 1931	CM 6984	M	Ad	SK	Occipital region damaged
Angola: Malange District, Gauca River, 20 mi E Donde	5 Jan 1931	CM 6946	F	[Ad]	SO	Good
Angola: Gauca River	5 Jan 1931	CM 6941	F	Ad	SK	Occipital region damaged
Angola: Gauca River	5 Jan 1931	CM 6943	M	Ad	SK	Good
Angola: Gauca River	5 Jan 1931	CM 6944	F	Ad	SK	Good
Angola: Gauca River	5 Jan 1931	CM 6945	F	Juv	SK	Occipital region damaged
Angola: Gauca River	6 Jan 1931	CM 6952	F	Ad	SK	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Angola: Gauca River	6 Jan 1931	CM 6953	M	Ad	SK	Good
Angola: Gauca River	6 Jan 1931	CM 6954	M	Ad	SK	Good
Angola: Gauca River	6 Jan 1931	CM 6955	M	Juv	SK	Good
Angola: Gauca River	6 Jan 1931	CM 6958	M	Juv	SK	Good
Angola: Gauca River	6 Jan 1931	CM 6959	F	Ad	SK	Good
Angola: Gauca River	6 Jan 1931	CM 6960	M	Ad	SK	Good
Angola: Gauca River	7 Jan 1931	CM 6963	?	Ad	SN	Skull fragmentary, toothrow intact
Angola: Gauca River	7 Jan 1931	CM 6964	?	Juv	SN	Skull fragmentary, toothrow intact
Botswana: Kwae River, 75 mi N Maun	30 Jun 1964	CM 57949	M	[Imm]	SO	Skin: tanned, fair condition
Tanzania: Central Province, 50 mi N Dodoma, 3500 ft	12 Sep 1960	CM 57705	M	Ad	SS	Good
Galago senegalensis senegalensis						
Ghana: specific locality unknown	unknown	CM 1672	?	Ad	SN*	Good; on exhibit
Ivory Coast: 25 km W Bouake, 07°55′N, 05°00′W	29 Oct 1971	CM 69189	M	Ad	SS	Good
Ivory Coast: 25 km W Bouake, 07°55′N, 05°00′W	29 Oct 1971	CM 69190	F	Ad	SS	Left upper toothrow and right zygomatic damaged; skin: good
Ivory Coast: 25 km W Bouake, 07°55′N, 05°00′W	31 Oct 1971	CM 69191	F	Ad	SS	Left upper toothrow and right zygomatic damaged; skin: good
Kenya: Rift Valley Region, Lokitanyala Escarpment, 70 mi W (by road) Lodwar	19 Jun 1960	CM 61552	F	Ad	SS	Good

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Galago zanzibaricus						
Kenya: Coast Region, Sokoke Forest	5 Aug 1964	CM 57947	M	Ad	SS	Skull broken, severe damage to braincase
Kenya: Coast Region, Sokoke Forest	9 Aug 1964	CM 57948	M	Ad	SS	Good
CEBIDAE						
AOTINAE						
Aotus azarae azarae						
Bolivia: Dept Santa Cruz, Province Cordillera, Rio Grande	3 Sep 1909	CM 1980	M	Ad	SS	Upper incisors broken
Bolivia: Dept Santa Cruz, Province Cordillera, Rio Grande	3 Sep 1909	CM 1981	F	Ad	SS	Occipital and parietals broken
Bolivia: Dept Santa Cruz, Province Cordillera, Rio Grande	3 Sep 1909	CM 1982	M	Ad	SB	Good
Bolivia: Dept Santa Cruz, Province Cordillera, Rio Grande	3 Sep 1909	CM 1983	M	Ad	SS	Braincase damaged
Bolivia: Dept Santa Cruz, Province Cordillera, Rio Grande	4 Sep 1909	CM 1984	M	Ad	SS	Good
Aotus azarae boliviensis						
Bolivia: Dept Santa Cruz, Rio Quiser, north of Chiquitos	14 Jun 1918	CM 5020	M	Ad	SS	Premaxillaries broken
Bolivia: Dept Santa Cruz, Rio Quiser, north of Chiquitos	14 Jun 1918	CM 5021	F	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Surutu	8 Sep 1910	CM 2189	F	Ad	SS	Nasals broken
Bolivia: Dept Santa Cruz, specific locality unknown	1910	CM 20939	?	Ad	SK	Good
Aotus lemurinus griseimembra						
Colombia: Dept Magdalena, Bonda	3 Jun 1899	CM 1003	M	Ad	SB	Skull: good; skin: fragmentary

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Colombia: Dept Magdalena, Bonda	3 Jun 1899	CM 1004	F	Ad	SB	Braincase damaged; skin: fragmentary
Aotus species						
Locality unknown	unknown	CM 1996	?	Ad	SK	Orbits and zygomatic arches destroyed, nasal and maxillary region damaged
Callicebus moloch donacephilus						
Bolivia: Dept Santa Cruz, Buenavista	Nov 1911	CM 2740	M	Ad	SS	No lower jaw; skin: fragmentary
Bolivia: Dept Santa Cruz, Buenavista	Nov 1911	CM 2741	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Puerto Suarez	8 Jan 1904	CM 21065	?	Ad	SS	Orbits and zygomatic arches broken; skin: fragmentary
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	28 Jun 1909	CM 1926	F	Ad	SS	Good
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	30 Jul 1909	CM 1953	M	Juv	SS	Good
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	30 Jul 1909	CM 1954	F	Juv	SS	Good
PITHECIINAE						
Chiropotes satanas chiropotes						
Suriname: specific locality unknown	1966	CM 51862	?	Ad	SK	Occipital region damaged
Suriname: Nickerie, Sipaliwini airstrip	12 Nov 1981	CM 76820	?	Ad	SK	Good
Suriname: Nickerie, Sipaliwini airstrip	14 Nov 1981	CM 76821	F	Juv	SB	Good

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Pithecia pithecia						
Suriname: specific locality unknown	1966	CM 51863	?	Ad	SK	Skull fragment
Locality unknown*	18 Aug 1950	CM 61340	F	Juv	SB*	Skull: good; skin: missing; Pittsburgh Zoological Garden specimen
ALOUATTINAE						
Alouatta caraya caraya						
Brazil: Mato Grosso, Fazenda San Martin, about 150 km S, Corumba	1967	CM 61430	M	Ad	SK	Good
Brazil: Mato Grosso, Fazenda San Martin, about 150 km S, Corumba	1967	CM 61431	F	Ad	SK	Upper incisors broken
Alouatta guariba clamitans						
Brazil: Santa Catarina	unknown	CM 1719	M	Ad	SK*	Good; on exhibit
Brazil: Santa Catarina	unknown	CM 1765	M	Ad	SN*	Good; on exhibit
Alouatta palliata aequatorialis						
Colombia: Dept Bolivar, Lorica	23 Feb 1916	CM 3601	M	Ad	SS	Digit bones exposed in study skin; nasals and upper incisors damaged
Alouatta palliata palliata						
Costa Rica: Guacimo	12 Dec 1903	CM 1363	F	[Ad]	SS*	Skull: missing; study skin folded at waist, bones of digits intact and exposed

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Costa Rica: Guacimo	12 Dec 1903	CM 1364	F	[Ad]	SS*	Skull: missing; study skin folded at waist, bones of digits intact and exposed
Alouatta seniculus sara						
Bolivia: Dept Santa Cruz, Rio Surutu	10 Aug 1910	CM 2185	F	Ad	SS	Skull: good; some postcranial bones; skin: tanned
Bolivia: Dept Santa Cruz, Rio Surutu	unknown	CM 2191	?	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Surutu	10 Aug 1910	CM 2726	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Yapacani	26 Aug 1913	CM 2776	M	Ad	SS	Skull: good; skin: tanned
Bolivia: Dept Santa Cruz, Province del Sara, specific locality unknown	1910	CM 20940	?	Ad	SK	Good
Bolivia: specific locality unknown	unknown	CM 2190	?	Ad	SS	Good
Alouatta seniculus seniculus						
Colombia: Dept Bolivar, Lorica	17 Feb 1916	CM 3598	F	Ad	SS	Skull: good; skin: poor
Colombia: Dept Bolivar, Turbaco	9 Jan 1916	CM 3586	M	Ad	SS	Skull: good; digit bones exposed on study skin; dental anomaly
Colombia: Dept Magdalena, Bonda	18 Mar 1899	CM 708	F	Juv	SS	Good
Colombia: Dept Magdalena, Cacaqualito	23 Jun 1898	CM 644	M	Juv	SS	Good
Colombia: Dept Magdalena, Santa Marta, Don Diego	6 Feb 1913	CM 3153	?	Ad	SS	Damage to right orbit, zygomatic arch and left mandible

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	5 Oct 1913	CM 2709	F	Ad	SS	Good
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	5 Oct 1913	CM 2710	M	Inf	SS	Skull fragmentary
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	6 Oct 1913	CM 2711	F	Ad	SB	Skull: good; skin: tail torn from study skin
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	6 Oct 1913	CM 2712	F	Ad	SS*	Skull: good; some postcranial bones found; skin missing
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	7 Oct 1913	CM 2714	M	Ad	SS	Good
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	14 Oct 1913	CM 2716	M	Ad	SS	Good
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	14 Oct 1913	CM 2717	M	Ad	SS	Damage to left side of skull and lower jaw
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	14 Oct 1913	CM 2718	M	Ad	SS	Frontal and parietals missing, braincase damaged; digit bones exposed on study skin
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	14 Oct 1913	CM 2719	F	Ad	SS	Nasals broken
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	14 Oct 1913	CM 2720	F	Juv	SS*	Lower jaw missing
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	7 Oct 1913	CM 2722	M	Ad	SN*	Skull only found; good
Colombia: Dept Magdalena, specific locality unknown	1898	CM 651	?	Juv	SS	Good; some postcranial bones

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Colombia: Dept Magdalena, specific locality unknown	1898	CM 652	?	[Ad]	SS*	Skull missing
Colombia: Dept Magdalena, specific locality unknown	unknown	CM 702	[F]	Ad	SS*	Skull: good; body mounted
Alouatta seniculus straminea						
Suriname: Nickerie, Kayserberg airstrip, 03°06′N, 56°27′W	30 Apr 1980	CM 68447	M	Ad	SK	Good
Suriname: Nickerie, Kayserberg airstrip, 03°06′N, 56°27′W	3 May 1980	CM 68448	M	Ad	SK	Good
Suriname: specific locality unknown	1966	CM 51860	M	Ad	SK	Good
Suriname: specific locality unknown	1966	CM 51861	M	Ad	SK	Good
Alouatta seniculus						
Colombia: specific locality unknown	unknown	CM 680	M	Ad	SN*	Good; on exhibit
Locality unknown	unknown	CM 6393	?	Ad	SK*	Good; on exhibit
CEBINAE						
Cebus albifrons hypoleucus						
Colombia: Dept Magdalena, Bonda	27 Oct 1898	CM 658	?	Inf	SS	Braincase broken; some postcranial bones
Colombia: Dept Magdalena, Bonda	9 Dec 1898	CM 664	?	Ad	SS	Skull: good; some postcranial bones
Colombia: Dept Magdalena, Bonda	Oct 1899	CM 1021	F	Ad	SS	Upper incisors broken; lower jaw broken
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	6 Oct 1913	CM 2713	F	Ad	SS	Skull: good; skin: poor
Colombia: Dept Magdalena, Santa Marta, Trojas de Cataca	7 Oct 1913	CM 2715	F	Ad	SB	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cebus albifrons leucocephalus						
Colombia: Dept Santander, El Tamber	17 Dec 1916	CM 3947	M	Ad	SS	Good
Colombia: Dept Santander, El Tamber	29 Dec 1916	CM 3949	M	Ad	SS	Good
Colombia: Dept Santander, El Tamber	8 Jan 1917	CM 3952	F	Inf	SS	Braincase broken
Cebus albifrons versicolor						
Colombia: Dept Magdalena, Gamarra	11 Jul 1916	CM 3873	F	Ad	SS	Braincase damaged; upper and lower right canines broken
Colombia: Dept Magdalena, Gamarra	11 Jul 1916	CM 3874	F	Ad	SS	Good
Colombia: Dept Magdalena, Gamarra	11 Jul 1916	CM 3875	F	Ad	SB	Good
Colombia: Dept Magdalena, Gamarra	13 Jul 1916	CM 3876	M	Ad	SB	Left upper canine and right zygomatic arch broken, left temporal region and lower jaw damaged
Cebus albifrons						
Colombia: Dept Magdalena, specific locality unknown	unknown	CM 1050	M	Ad	SB	Skull: good; skin: dried, in poor condition
Cebus apella apella						
Suriname: Brokopondo, Rudi Kappelvliegveld, 03°47′N, 56°08′W, 320 m	6 Nov 1981	CM 76822	?	Ad	SK	Braincase broken, numerous teeth missing
Suriname: Nickerie, Kayserberg airstrip, 03°06′N, 56°27′W	30 Apr 1980	CM 68449	?	Ad	SK	Braincase cracked, occipital region damaged

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Suriname: Nickerie, Sipaliwini airstrip, 02°02′N, 56°07′W	13 Nov 1981	CM 76823	M	Ad	SB	Good
Suriname: specific locality unknown	1966	CM 51864	?	Ad	CO	Teeth missing, only molars present
Cebus apella pallidus						
Bolivia: Dept Santa Cruz, Buenavista	12 Aug 1910	CM 2187	F	Ad	SS	Skull: good, some postcranial bones present; skin: flat preparation in poor condition
Bolivia: Dept Santa Cruz, Rio Surutu	24 Jul 1910	CM 2175	F	[Ad]	SS*	Skull missing
Bolivia: Dept Santa Cruz, Rio Surutu	24 Jul 1910	CM 2176	F	[Ad]	SS*	Skull missing
Bolivia: Dept Santa Cruz, Rio Surutu	24 Jul 1910	CM 2737	?	Ad	SS	Nasals broken
Bolivia: Dept Santa Cruz, Rio Surutu	2 May 1919	CM 5038	F	Ad	SS	Toothrow damaged on left side—upper and lower; braincase cracked; lower jaw damaged
Bolivia: Dept Santa Cruz, Rio Surutu	2 May 1919	CM 5039	F	Ad	SS	Some teeth missing
Bolivia: Dept Santa Cruz, Rio Surutu	12 May 1919	CM 5041	M	Ad	SS	Left zygomatic arch and left mandible broken
Bolivia: Dept Santa Cruz, Rio Surutu	12 May 1919	CM 5044	F	Ad	SS	Left zygomatic arch broken, most lower teeth missing
Bolivia: Dept Santa Cruz, Rio Yapacani	18 Aug 1913	CM 2765	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Yapacani	18 Aug 1913	CM 2766	F	Ad	SS	Skull: good; skin: tanned with digit bones intact

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Bolivia: Dept Santa Cruz, Rio Yapacani	20 Aug 1913	CM 2768	F	Juv	SS	Good
Bolivia: Dept Santa Cruz, Rio Yapacani	20 Aug 1913	CM 2769	F	Juv	SS	Skull: good; skin: dried flat with digit bones intact
Bolivia: Dept Santa Cruz, Province del Sara, specific locality unknown	10 Aug 1910	CM 2186	?	Juv	SS	Good
Cebus apella						
Bolivia: specific locality unknown	unknown	CM 6394	?	Ad	SK	Good
Bolivia: specific locality unknown	unknown	CM 6395	?	Ad	SK	Good
Bolivia: specific locality unknown	unknown	CM 6396	?	Ad	SK	Braincase and right zygomatic arch broken; dental anomaly
Brazil: Santa Catarina	unknown	CM 1669	?	Ad	SN*	Good; on exhibit
Locality unknown	unknown	CM 6397	?	Ad	SK	Good
Cebus capucinus capucinus						
Colombia: Rio Atrato, Santata	13 Jan 1918	CM 4450	M	Juv	SS	Good
Cebus capucinus imitator						
Costa Rica: Pozo Azul	5 Jun 1902	CM 1250	F	Ad	SS	Measurable but shot damaged, several teeth missing
Costa Rica: Pozo Azul	4 Jul 1902	CM 1322	F	Juv	SS	Good
Costa Rica: Volcano Turrialba	20 Apr 1903	CM 1336	M	[Ad]	SS*	Skull involved with mix-up with CM 1337, and CM 1338
Costa Rica: Volcano Turrialba	20 Apr 1903	CM 1337	F	[Ad]	SS*	See above (CM 1336)

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Costa Rica: Volcano Turrialba	20 Apr 1903	CM 1338	M	[Ad]	SS*	See above (CM 1336)
Cebus capucinus						
Locality unknown*	unknown	CM 943	M	[Ad]	SS*	Skull missing; Pittsburgh Zoological Garden specimen
Locality unknown	1902	CM 1321	?	[Imm]	SS*	Skull missing
Cebus olivaceus						
Suriname: Nickerie, Sipaliwini airstrip, 02°02′N, 56°07′W	12 Nov 1981	CM 76824	M	Ad	SB	Good
Cebus species						
Locality unknown*	1940	CM 19590	?	[Imm]	AL	Newborn; Pittsburgh Zoological Garden specimen
Saimiri boliviensis						
Bolivia: Dept Santa Cruz, Rio Talometa	4 Jun 1917	CM 4933	M	[Ad]	SO	Good
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	16 Jun 1909	CM 1921	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	17 Jun 1909	CM 1925	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	21 Jul 1909	CM 1946	M	Juv	SS	Right zygomatic arch broken
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	23 Jul 1909	CM 1947	M	Juv	SS	Braincase damaged
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	18 Sep 1909	CM 1992	M	Ad	SS	Braincase damaged, right bulla missing
Bolivia: Dept Santa Cruz, Santa Cruz de la Sierra	9 Sep 1909	CM 2143	M	Juv	SS	Good

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Saimiri oerstedii citrinellus						
Costa Rica: Pozo Azul	31 May 1902	CM 1248	F	Ad	SS	Braincase damaged, right bulla and lower jaw missing; study skin with digit bones intact and exposed
Costa Rica: Pozo Azul	31 May 1902	CM 1249	M	[Imm]	SS*	Skull missing; study skin with digit bones intact and exposed
Costa Rica: Pozo Azul	3 Jul 1902	CM 1323	F	[Ad]	SS*	Skull missing; study skin with digit bones intact and exposed
Saimiri oerstedii oerstedii						
Costa Rica: El Pozo de Terraba	14 Jun 1907	CM 1572	M	Ad	SS	Skull fragmentary, toothrow intact
Costa Rica: El Pozo de Terraba	14 Jun 1907	CM 1573	M	Ad	SS	Good
Costa Rica: El Pozo de Terraba	14 Jun 1907	CM 1574	F	Ad	SS	Left temporal region broken and left bulla missing
Costa Rica: El Pozo de Terraba	14 Jun 1907	CM 1575	M	Ad	SS	Braincase damaged but measurable
Costa Rica: El Pozo de Terraba	19 Jun 1907	CM 1577	M	Ad	SS	Good
Costa Rica: El Pozo de Terraba	14 Jun 1907	CM 1578	F	Ad	SS	Good
Costa Rica: El Pozo de Terraba	19 Jun 1907	CM 1579	M	Ad	SS	Good
Costa Rica: El Pozo de Terraba	27 Jun 1907	CM 1581	F	Juv	SS	Good
Costa Rica: El Pozo de Terraba	27 Jun 1907	CM 1582	F	Ad	SS	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Costa Rica: El Pozo de Terraba	27 Jun 1907	CM 1583	F	Ad	SS	Occipital region damaged
Costa Rica: El Pozo de Terraba	27 Jun 1907	CM 1584	F	Ad	SS	Upper incisors broken
Costa Rica: El Pozo de Terraba	28 Jun 1907	CM 1585	F	Ad	SS	Good
Costa Rica: El Pozo de Terraba	28 Jun 1907	CM 1586	F	Ad	SS	Occipital region and palate damaged
Costa Rica: El Pozo de Terraba	2 Jul 1907	CM 1588	M	Ad	SS	Good
Costa Rica: El Pozo de Terraba	2 Jul 1907	CM 1589	M	Ad	SS	Good
Costa Rica: El Pozo de Terraba	2 Jul 1907	CM 1590	M	Ad	SS	Good
Costa Rica: El Pozo de Terraba	2 Jul 1907	CM 1591	F	Juv	SS	Good
Costa Rica: El Pozo de Terraba	2 Jul 1907	CM 1593	F	Ad	SS	Good
Costa Rica: El Pozo de Terraba	2 Jul 1907	CM 1594	F	Ad	SS	Incisors damaged
Saimiri sciureus albifrons						
Colombia: Meta, Rio Yerly, La Macarena, 1500 ft	26 Feb 1967	CM 87902	M	Ad	SS	Skull: good; skin: tanned
Saimiri sciureus nigriceps						
Peru: Rio Huallaga, Tingo Maria	18 Oct 1922	CM 12175	M	Ad	SS	Good
Saimiri sciureus sciureus						
Suriname: Nickerie, Sipaliwini airstrip, 02°02′N, 56°07′W	13 Nov 1981	CM 76825	F	Ad	SB	Braincase damaged
Suriname: Paramaribo, Charlesburg	17 Aug 1966	CM 51865	F	Ad	SB	Braincase, maxillary region, nasals, left bulla, and right toothrow (upper and lower) damaged
Suriname: specific locality unknown	1966	CM 51866	?	[Imm]	SO	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
ATELINAE						
Ateles belzebuth marginatus						
Locality unknown*	Dec 1907	CM 1559	F	Ad	SS	Skull: good; tanned skin in pieces; Pittsburgh Zoological Garden specimen
Ateles fusciceps						
Locality unknown*	10 Jul 1939	CM 17455	M	Ad	SS	Palate damaged, skull glued in several places
Ateles geoffroyi ornatus						
Costa Rica: Bebedero	5 May 1906	CM 1511	F	[Ad]	BM*	Good; on exhibit
Costa Rica: Bebedero	9 May 1906	CM 1512	M	[Ad]	BM*	Good; on exhibit
Costa Rica: Guapiles	15 May 1903	CM 1328	?	Ad	SS	Skull: good; skin: feet damaged
Ateles geoffroyi panamensis						
Costa Rica: Pozo Azul	13 Jun 1902	CM 1252	F	Ad	SS	Skull: good; skin: limbs torn, and digit bones are exposed
Costa Rica: Pozo Azul	5 Jul 1902	CM 1254	F	Ad	SS	Skull: numerous teeth missing, other teeth have been glued; skin: tail and legs badly torn, digit bones exposed

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Costa Rica: El Pozo de Terraba	17 Jun 1907	CM 1576	F	Ad	SS	Good
Ateles geoffroyi vellerosus						
Honduras: specific locality unknown	1948	CM 63110	?	Ad	SK	Good
Honduras: specific locality unknown	1948	CM 63111	?	Ad	SK	Good
Ateles paniscus chamek						
Bolivia: Dept Santa Cruz, Rio Yapacani	22 Aug 1913	CM 2772	F	Ad	SS	Braincase, left orbit and zygomatic arch damaged; skin: tanned
Bolivia: Dept Santa Cruz, Rio Yapacani	23 Aug 1913	CM 2773	F	Ad	SB	Skull: good; skin: tanned with limb bones intact
Bolivia: Dept Santa Cruz, Rio Yapacani	23 Aug 1913	CM 2774	F	Ad	SS	Some teeth glued
Bolivia: Dept Santa Cruz, Rio Yapacani	26 Aug 1913	CM 2775	F	Ad	SB	Good
Ateles paniscus paniscus						
Suriname: Nickerie, Kayserberg airstrip, 03°06′N, 56°27′W	3 May 1980	CM 68450	F	Ad	SK	Good
Suriname: Nickerie, Kayserberg airstrip, 03°06′N, 56°27′W	3 May 1980	CM 68451	M	Ad	SK	Good; dental anomaly
Suriname: Nickerie, Sipaliwini airstrip, 02°02′N, 56°07′W	17 Nov 1981	CM 76826	F	Ad	SB	Good
Suriname: specific locality unknown	1966	CM 51867	?	Ad	SK	Good
***Ateles* species**						
Locality unknown*	17 Jul 1938	CM 17454	M	Juv	SB	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	17 Feb 1941	CM 19360	F	Juv	SB	Good; Pittsburgh Zoological Garden specimen

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Locality unknown*	22 Aug 1949	CM 30363	F	Ad	SS*	Skull: good; skin: missing; Pittsburgh Zoological Garden specimen
CALLITRICHIDAE						
Callithrix argentata argentata						
Brazil: Rio Tapajos, Tauary	25 Aug 1932	CM 12187	F	Ad	SS	Good
Callithrix argentata melanura						
Bolivia: Dept Santa Cruz, Chiquitos, Rio Quiser	14 Jun 1918	CM 5011	F	Ad	SS	Left side of lower jaw broken
Bolivia: Dept Santa Cruz, Chiquitos, Rio Quiser	14 Jun 1918	CM 5012	M	Juv	SS	Good
Bolivia: Dept Santa Cruz, Chiquitos, Rio Quiser	14 Jun 1918	CM 5013	F	Ad	SS	Premaxillaries and palate damaged
Bolivia: Dept Santa Cruz, Chiquitos, Rio Quiser	14 Jun 1918	CM 5016	F	Ad	SB	Skull fragmentary
Bolivia: Dept Santa Cruz, Chiquitos, Rio San Julian, Palmarito	25 May 1918	CM 4978	F	[Ad]	SO	Good
Bolivia: Dept Santa Cruz, Chiquitos, Rio San Julian, Palmarito	27 May 1918	CM 4985	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Grande, Rio Mapaiso, 400 ft	12 Aug 1909	CM 1963	M	Ad	SS	Upper incisors missing
Bolivia: Dept Santa Cruz, Rio Grande, Rio Mapaiso, 400 ft	12 Aug 1909	CM 1964	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Grande, Rio Mapaiso, 400 ft	12 Aug 1909	CM 1965	M	Ad	SS	Good
Bolivia: Dept Santa Cruz, Rio Grande, Rio Mapaiso, 400 ft	12 Aug 1909	CM 1966	F	Ad	SB	Skull shot damaged but measurable

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Callithrix jacchus jacchus						
Brazil: Pernambuco [Recife]	unknown	CM 1244	F	Ad	SK	Measurable
Brazil: Piauhy, Deserto	5 Apr 1925	CM 12174	F	Ad	SS	Good
Callithrix jacchus						
Brazil: Bahia	unknown	CM 1670	?	Ad	SN*	Good; on exhibit
Brazil: Bahia	unknown	CM 1720	?	Ad	SK*	Good; on exhibit
Locality unknown	unknown	CM 1480	?	Ad	SN	Only skull found
Locality unknown	Nov 1910	CM 2864	M	Ad	SN	Many teeth missing
Saguinus midas midas						
Suriname: Saramacca, 5 km N, 23 km W Kwakoegron, 05°17′N, 55°33′W	2 Sep 1979	CM 64462	M	Ad	SB	Lower jaw broken
Suriname: Suriname, Powaka	23 Sep 1966	CM 51868	M	Ad	SB	Good
Saguinus oedipus geoffroyi						
Colombia: Rio Atrato, Santata	23 Jan 1918	CM 4441	F	Ad	SS	Skull: lower jaw broken, right maxillary region damaged; skin: digit bones intact and exposed
Colombia: Rio Atrato, Santata	25 Jan 1918	CM 4442	M	Ad	SS	Good
Colombia: Rio Atrato, Santata	25 Jan 1918	CM 4443	M	Ad	SS	Study skin with digit bones intact and exposed
Colombia: Rio Atrato, Santata	25 Jan 1918	CM 4444	M	Ad	SS	Skull: good; skin: unstuffed in poor condition
Colombia: Rio Atrato, Santata	25 Jan 1918	CM 4445	M	Ad	SS	Skull: good; skin: digit bones intact and exposed

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Colombia: Rio Atrato, Santata	26 Jan 1918	CM 4446	M	Juv	SB	Good
Colombia: Rio Atrato, Santata	26 Jan 1918	CM 4447	M	Ad	SS	Skull: good; skin: digit bones intact and exposed
Colombia: Rio Atrato, Santata	30 Jan 1918	CM 4448	M	Ad	SS	Good
Colombia: Rio Atrato, Santata	1 Feb 1918	CM 4449	F	Ad	SS	Skull: good; skin: digit bones intact and exposed
Saguinus oedipus oedipus						
Colombia: Dept Bolivar, Jaraquiel	4 Mar 1916	CM 3609	M	Ad	SB	Good
Colombia: Dept Bolivar, Jaraquiel	6 Mar 1916	CM 3611	F	Juv	SB	Good
Colombia: Dept Bolivar, Jaraquiel	6 Mar 1916	CM 3612	M	Ad	SS	Braincase damaged, bullar region and basioccipital missing
Colombia: Dept Bolivar, Jaraquiel	6 Mar 1916	CM 3614	M	Ad	SS	Good
Colombia: Dept Bolivar, Jaraquiel	6 Mar 1916	CM 3615	M	Ad	SS	Good
Colombia: Dept Bolivar, Jaraquiel	7 Mar 1916	CM 3619	M	Ad	SS	Damage to numerous upper teeth
Colombia: Dept Bolivar, Jaraquiel	7 Mar 1916	CM 3620	M	Ad	SS	Good
Colombia: Dept Bolivar, Jaraquiel	7 Mar 1916	CM 3621	M	Ad	SS	Good
Saguinus oedipus						
Locality unknown	Sep 1913	CM 6360	M	Ad	SN	Braincase and left zygomatic arch damaged, left bulla missing

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
CERCOPITHECIDAE						
CERCOPITHECINAE						
Cercocebus albigena johnstoni						
Uganda: Toro District, Mongiro, Bwamba Forest, 2200 ft	26 Jul 1960	CM 57926	F	Ad	SB	Skull: good; skin: tanned
Cercocebus albigena zenkeri						
Cameroon: Lolodorf	5 Jun 1925	CM 5671	F	Juv	SS	Occipital region damaged
Cercocebus galeritus agilis						
Zaire: Gemena Zone, Tandala	19 Jul 1979	CM 86712	F	Ad	SS	Skull: good; skin: salted and folded
Cercocebus torquatus atys						
Liberia: specific locality unknown	unknown	CM 1717	F	Juv	SK*	Good; on exhibit
Locality unknown*	18 Mar 1937	CM 10764	M	Juv	SB	Right orbit and zygomatic arch damaged, nasals missing; skeleton in poor condition; Pittsburgh Zoological Garden specimen
Locality unknown*	16 Feb 1938	CM 14908	F	Juv	SB	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	20 Feb 1945	CM 22574	M	Ad	SB	Good; Pittsburgh Zoological Garden specimen

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cercocebus torquatus torquatus						
Cameroon: Edea	6 Jun 1922	CM 20902	F	Ad	SS	Good
Cameroon: Edea	17 Aug 1922	CM 20903	M	Ad	SS	Skull: good; skin: torn in numerous places
Cercocebus torquatus						
Locality unknown*	4 Oct 1946	CM 30375	M	Juv	SB	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	21 Dec 1965	CM 40612	M	Ad	SB	Good; Pittsburgh Zoological Garden specimen
Cercopithecus aethiops						
Kenya: Athi River, near Juja Farm(?)	31 Aug 1912	CM 5871	?	[Ad]	SS*	Skull: missing; skin: tanned; locality questionable
Locality unknown*	2 Aug 1940	CM 18772	F	Ad	SB	Good; Pittsburgh Zoological Garden specimen
Cercopithecus albogularis albotorquatus						
Kenya: Northeastern Region, Tana River, Kolokoko [Korokora], Garrissa	27 Jun 1960	CM 57834	M	Ad	SS	Skull: good; skin: tanned
Kenya: Northeastern Region, Tana River, 40 mi N Kolokoko [Korokora]	26 Jun 1960	CM 57835	F	Ad	SS	Skull: good; skin: tanned
Kenya: Northeastern Region, Tana River, Kolokoko [Korokora], Garrissa	30 Jun 1960	CM 57836	M	Ad	SS	Skull: good; skin: tanned
Kenya: Northeastern Region, Tana River, Kolokoko [Korokora], Garrissa	30 Jun 1960	CM 57837	M	Ad	SS	Skull: good; skin: tanned

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Kenya: Northeastern Region, Tana River, Kolokoko [Korokora], Garrissa	30 Jun 1960	CM 57838	F	Ad	SS	Skull: good; skin: tanned
Cercopithecus albogularis erythrarchus						
Zimbabwe: Melsetter District, Mount Selinda	10 Dec 1929	CM 6310	F	Juv	SS	Good
Zimbabwe: Melsetter District, Mount Selinda	23 Dec 1929	CM 6314	M	Inf	SS	Good, with limb bones
Cercopithecus albogularis kibonotensis						
Kenya: Coast Region, Shimoni	14 Aug 1964	CM 57953	F	Juv	SS	Skull: good; skin: salted and folded
Kenya: Coast Region, Sokoke Forest	7 Aug 1964	CM 57951	M	Ad	SS	Skull: good; skin: salted and folded
Kenya: Coast Region, Sokoke Forest	10 Aug 1964	CM 57952	M	Ad	SS	Skull: good; skin: salted and folded
Tanzania: Tanga Province, Usambara Mts, near Amani, 3000 ft	21 Oct 1960	CM 57846	F	Ad	SB	Tooth loss due to decay; skin: dried but not stuffed, brittle
Cercopithecus albogularis kolbi						
Kenya: Central Region, Nyeri	16 Feb 1910	CM 20856	?	Juv	SS	Skull: good, with some postcranial bones; skin: dried and partially stuffed with excelsior
Kenya: Central Region, Nyeri	16 Feb 1910	CM 20857	?	Ad	SS	Skull: good, with some postcranial bones; skin: dried and partially stuffed with excelsior

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Kenya: Central Region, Nyeri	16 Feb 1910	CM 20858	?	Juv	SS	Skull: good, with some postcranial bones; skin: dried and partially stuffed with excelsior
Kenya: Central Region, Nyeri	16 Feb 1910	CM 20859	?	Ad	SS	Skull: damage to parietal region, some postcranial bones; skin: dried and partially stuffed with excelsior
Kenya: Eastern Region, Meru Forest	9 Aug 1912	CM 20862	M	Juv	PS	Good
Locality unknown	unknown	CM 5887	?	[Ad]	SS*	Skull: missing; skin: tanned
Locality unknown	unknown	CM 5888	?	[Ad]	SS*	Skull: missing; skin: tanned
Cercopithecus ascanius schmidti						
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Jul 1960	CM 57839	M	Ad	SS	Skull: good, with some postcranial bones; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Jul 1960	CM 57840	M	Ad	SS	Skull: good, with some postcranial bones; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Jul 1960	CM 57841	M	Ad	SS	Skull: good, with some postcranial bones; skin: tanned

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Uganda: Kigezi District, Kayonza Forest	1960	CM 57844	F	[Ad]	SB*	Skeletal parts missing
Uganda: Kigezi District, Kayonza Forest	8 Aug 1960	CM 57845	F	Ad	SS	Skull: good; skin: tanned
Uganda: Toro District, Mongiro, Bwamba Forest, 2000 ft	23 Jul 1960	CM 57842	M	Ad	SS	Skull: good; skin: tanned
Uganda: Toro District, Mongiro, Bwamba Forest, 2000 ft	28 Jul 1960	CM 57843	M	Ad	SB	Skull: good; skin: tanned
Zaire: Bumba Zone, Yalosemba	9 Jun 1979	CM 86705	F	Ad	SS	Skull: good; skin: salted and folded
Zaire: Gemena Zone, Tandala	5 Jul 1979	CM 86706	M	Ad	SS	Skull: good; skin: salted and folded
Cercopithecus campbelli						
Locality unknown*	12 May 1937	CM 13057	F	Ad	SB	Good; Pittsburgh Zoological Garden specimen
Cercopithecus cephus cephus						
Cameroon: Bafia	28 Jan 1928	CM 6146	M	Ad	SS	Occipital region damaged; some postcranial bones
Cameroon: Bafia	27 Jan 1928	CM 6147	M	Juv	SS	Occipital region damaged; some postcranial bones
Cameroon: Bafia	23 May 1944	CM 42339	M	[Ad]	SS*	Skull: missing; skin: dried with limb bones still attached
Cameroon: Lolodorf	28 Dec 1923	CM 5372	M	Juv	SS	Good
Cameroon: Lolodorf	28 Dec 1923	CM 5377	F	Ad	SS	Good
Cameroon: Lolodorf	13 Oct 1926	CM 5763	F	Ad	SS	Occipital region damaged; some postcranial bones

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: Lolodorf	27 Feb 1936	CM 13190	M	Ad	SS	Occipital region damaged; some postcranial bones
Cameroon: Lolodorf	27 Feb 1936	CM 13191	F	Ad	SS	Occipital region damaged; some postcranial bones
Cameroon: Lolodorf	27 Mar 1936	CM 13192	F	Juv	SS	Occipital region damaged; some postcranial bones
Cameroon: Metet	28 Dec 1918	CM 5096	F	Juv	SS	Braincase wired together; some postcranial bones
Cameroon: specific locality unknown	12 Feb 1914	CM 17515	?	Ad	SK	Good
Cercopithecus cynosuros helvescens						
Angola: Cuando River, Luiana Camp, 3478 ft, 23°00'S, 17°30'E	23 Sep 1964	CM 40479	F	Ad	SK	Left orbit and both bullae damaged
Cercopithecus diana diana						
Locality unknown*	28 Jan 1947	CM 30408	F	Juv	SB	Pittsburgh Zoological Garden specimen
Cercopithecus l'hoesti l'hoesti						
Uganda: Kigezi District, Impenetrable Forest	8 Feb 1960	CM 57847	M	Ad	SB	Good
Uganda: Kigezi District, Impenetrable Forest	8 Feb 1960	CM 57848	F	Ad	SS	Skull: good; skin: tanned
Uganda: Kigezi District, Kayonza Forest	1960	CM 57849	?	Ad	SB	Both first upper incisors broken off; skin: tanned

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cercopithecus l'hoesti preussi						
Cameroon: Edea	6 Jul 1922	CM 20907	F	Ad	SS	Good
Cameroon: Edea	14 Aug 1922	CM 20908	M	Ad	SS	Good
Cameroon: Lolodorf	12 Feb 1914	CM 20917	M	Ad	SK	Some postcranial bones
Cercopithecus mitis mitis						
Angola: Ngara	11 Mar 1931	CM 7035	M	[Ad]	SS*	Skull: missing
Cercopithecus mitis stuhlmanni						
Kenya: Rift Valley Region, West Pokot District, North Cherengani Mts, 7000 ft	9 Jun 1960	CM 61553	F	Ad	SS	Good
Kenya: Rift Valley Region, West Pokot District, North Cherengani Mts, 7000 ft	9 Jun 1960	CM 61554	M	Juv	SS	Occipital region damaged
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Aug 1960	CM 57850	F	Ad	SS	Skull: good, some postcranial bones; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Aug 1960	CM 57851	M	Ad	SB	Skull: good; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	9 Aug 1960	CM 57852	M	Ad	SB	Skull: good; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	1960	CM 57853	M	Ad	SB	Skull: fragmentary, toothrow intact; skin: tanned
Uganda: Kigezi District, Impenetrable Forest	2 Aug 1960	CM 57857	M	Ad	SB	Skull broken into two parts
Uganda: Kigezi District, Impenetrable Forest	3 Aug 1960	CM 57858	M	Ad	SB	Good
Uganda: Kigezi District, Impenetrable Forest	1960	CM 57859	F	Ad	SS	Skull: good, with some postcranial bones

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Uganda: Kigezi District, Mafuga Forest, near Kabale, 8000 ft	1 Aug 1960	CM 57856	M	Ad	SB	Good
Uganda: Kigezi District, Kayonza Forest	1960	CM 57860	M	Ad	SN*	Lower jaw missing, damage to braincase
Uganda: Toro District, Mpanga Forest	21 Jul 1960	CM 57854	M	Ad	SB	Good
Uganda: Toro District, Mpanga Forest	21 Jul 1960	CM 57855	M	Ad	SB	Good
Cercopithecus mona						
Cameroon: Edea	20 Aug 1922	CM 20910	M	Ad	SS	Good
Cameroon: Yanfeben, Bafia	25 May 1944	CM 42340	M	Ad	SS	Occipital region damaged; skin dried with limb bones intact
Cameroon: Yanfeben, Bafia	26 May 1944	CM 42341	M	Ad	SS	Occipital region damaged; skin dried with limb bones intact
Cercopithecus neglectus						
Cameroon: Sangmelima	11 Mar 1932	CM 9567	M	Juv	SS	Occipital region damaged, some postcranial bones
Cameroon: Sangmelima	16 Feb 1934	CM 10323	M	Ad	SS	Occipital region damaged, some postcranial bones
Cameroon: Sangmelima	6 Jul 1934	CM 10324	M	Ad	SS	Left premaxillary and maxillary region damaged, some postcranial bones

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Kenya: Rift Valley Region, West Pokot District, North Cherengani Mts, 7000 ft	9 Jun 1960	CM 61555	M	Ad	SS	Good
Kenya: Rift Valley Region, West Pokot District, North Cherengani Mts, 7000 ft	9 Jun 1960	CM 61556	M	Juv	SS	Good
Uganda: Toro District, Mongiro, Bwamba Forest	28 Jul 1960	CM 57861	F	Ad	SB	Good
Zaire: Bumba Zone, Yalosemba	18 Jun 1979	CM 86711	M	Ad	SS	Cranium severely damaged by shot, left side gone; skin: salted and folded
Cercopithecus nictitans nictitans						
Cameroon: Edea	31 Jul 1922	CM 20906	F	Ad	SS	Good
Cameroon: Edea	17 Aug 1922	CM 20909	M	Ad	SS	Skull: good; skin: tanned, torn into several pieces
Cameroon: Lolodorf	20 Nov 1920	CM 5138	M	Ad	SS	Good with some post-cranial bones
Cameroon: Lolodorf	6 Nov 1920	CM 5143	M	Ad	SS	Good, with some postcranial bones
Cameroon: Lolodorf	29 Dec 1923	CM 5373	F	Ad	SS	Good with some postcranial bones
Cameroon: Lolodorf	27 Dec 1923	CM 5374	M	Ad	SS	Good with some postcranial bones
Cameroon: Lolodorf	26 Dec 1923	CM 5375	M	Ad	SS	Good with some postcranial bones
Cameroon: Lolodorf	4 Jun 1925	CM 5674	M	Ad	SS	Occipital region and left bulla damaged, left zygomatic arch broken
Cameroon: Lolodorf	8 Nov 1928	CM 6148	M	Ad	SS	Occipital region damaged

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: Lolodorf	28 Feb 1936	CM 13193	F	Ad	SS	Occipital region damaged, lower jaw broken; measurable but damaged by shot; some postcranial bones
Cameroon: Lolodorf	29 Feb 1936	CM 13194	M	Ad	SS	Occipital region damaged
Cameroon: Lolodorf	9 Mar 1936	CM 13195	M	Ad	SS	Occipital region damaged
Cameroon: Nsola	21 Jun 1924	CM 5663	F	Ad	SS	Good with some postcranial bones
Zaire: Bumba Zone, Yalosemba	15 Jun 1979	CM 86707	M	Ad	SS	Skull: good, some shot damage; skin: salted and folded
Zaire: Bumba Zone, Yalosemba	12 Jun 1979	CM 86708	F	Ad	SS	Skull: good, right side of jaw broken at site of old injury
Cercopithecus nigroviridis						
Zaire: Bumba Zone, Yalosemba	9 Jun 1979	CM 86704	F	Ad	SS	Skull: good; skin: salted and folded
Cercopithecus patas						
Locality unknown*	28 Jan 1947	CM 30409	M	Juv	SS	Occipital region damaged, some postcranial bones; Pittsburgh Zoological Garden specimen

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Locality unknown*	25 Feb 1947	CM 30410	M	Juv	SS	Basioccipital region damaged, some postcranial bones; Pittsburgh Zoological Garden specimen
Sudan: Kordofan District, specific locality unknown	unknown	CM 1665	?	Juv	SN	Good
Cercopithecus* cf. *petaurista						
Locality unknown*	21 Dec 1965	CM 40611	F	Inf	SB	Good; Pittsburgh Zoological Garden specimen
Cercopithecus pogonias grayi						
Cameroon: Lolodorf	26 Oct 1920	CM 5140	M	Ad	SS	Good
Cameroon: Lolodorf	5 Jun 1925	CM 5670	F	Juv	SS	Occipital region damaged, some postcranial bones
Cameroon: Lolodorf	6 Apr 1936	CM 13196	M	Ad	SS	Occipital region damaged
Cameroon: Lolodorf	6 Apr 1936	CM 13197	F	Ad	SS	Occipital region damaged, some postcranial bones
Cameroon: Lolodorf	20 Apr 1936	CM 13198	F	Juv	SS	Good, with some postcranial bones
Cameroon: Sangmelima	21 Mar 1932	CM 9568	F	Juv	SS	Occipital region and braincase damaged, some postcranial bones

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Zaire: Bumba Zone, Yalosemba	13 Jun 1979	CM 86709	F	Ad	SS	Skull: cranium damaged by shot; skin: salted and folded
Zaire: Bumba Zone, Yalosemba	14 Jun 1979	CM 86710	M	Ad	SS	Skull: good, slight shot damage; skin: salted and folded
Cercopithecus pogonias pogonias						
Cameroon: Edea	4 Jul 1922	CM 20904	F	Ad	SS	Good
Cameroon: Edea	24 Jul 1922	CM 20905	M	Ad	SS	Good
Cercopithecus pygerythruus arenarius						
Kenya: Guaso Nyiro [Ewaso Ngiro]	23 Jan 1910	CM 20855	F	Ad	SS*	Lower jaw missing, damage to palate; skin: dried and folded, limb bones intact
Kenya: Eastern Region, Ithanga Hills	29 Dec 1909	CM 20854	M	Juv	SS*	Lower jaw missing; skin: dried and folded
Kenya: Eastern Region, Meru Forest	9 Aug 1912	CM 20861	F	Ad	SK	Good with some postcranial bones
Cercopithecus pygerythrus zavattarii						
Ethiopia: Bodessa-Sagon River area	6 Jun 1912	CM 5846	M	Inf	SS*	Only skull found, basioccipital missing
Ethiopia: Lake Abaya	23 Mar 1912	CM 20860	M	Ad	SK*	Cranium only with slight damage to palate, some postcranial bones

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Ethiopia: Sagon River	6 Jun 1912	CM 5844	M	Ad	SS	Skull: good; skin: stuffed with excelsior, right leg and inguinal region torn and brittle
Ethiopia: Sagon River	6 Jun 1912	CM 5845	F	Ad	SS*	Cranium only, in good condition; skin: dried, not stuffed, head missing
Ethiopia: Sagon River	6 Jun 1912	CM 5847	F	Ad	SS	Good with some postcranial bones
Ethiopia: specific locality unknown	31 Aug 1912	CM 5872	?	[Ad]	SS*	Skull: missing; skin: dried and turned inside out
Locality unknown	Jun 1940	CM 18695	M	Inf	SB	Basioccipital missing
Cercopithecus sabaeus						
Locality unknown*	4 Jan 1938	CM 14749	M	Juv	SS	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	22 Nov 1944	CM 22302	F	Ad	SS	Good; Pittsburgh Zoological Garden specimen
Cercopithecus talapoin						
Cameroon: Lolodorf	4 Jun 1925	CM 5672	F	Ad	SS	Good
Cameroon: Lolodorf	4 Jun 1925	CM 5673	M	Juv	SS	Basioccipital damaged
Cameroon: 7 mi S Lolodorf	27 Jan 1936	CM 13199	F	Ad	SS	Good with postcranial bones

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: 7 mi S Lolodorf	27 Jan 1936	CM 13200	M	Ad	SS	Good with postcranial bones
Cameroon: 7 mi S Lolodorf	27 Jan 1936	CM 13201	M	Ad	SS	Occipital region damaged
Cameroon: Nyabessam	19 Jan 1942	CM 42342	M	Ad	SS	Skull: good; skin: dried with limbs everted, not stuffed
Cercopithecus tantalus budgetti						
Kenya: Rift Valley Region, Narok District, Uaso Nyiro [Ewaso Ngiro], near Narok	25 Aug 1960	CM 57865	M	Juv	SB	Skull: good; skin: dried with head everted
Uganda: Ankole District, Lake Lutoto	31 Aug 1960	CM 57863	M	Ad	SB	Skull: good; skin: tanned
Uganda: Ankole District, Lake Lutoto	31 Aug 1960	CM 57864	M	Ad	SB	Skull: good; skin: tanned
Uganda: Toro District, Mongiro, Bwamba Forest	28 Jul 1960	CM 57862	M	Ad	SB	Good
Cercopithecus tantalus tantalus						
Cameroon: Sangmelima	21 Apr 1933	CM 9569	M	Ad	SS	Occipital region damaged
Cameroon: Yangeben, Bafia	24 May 1944	CM 42338	F	Ad	SS	Basioccipital region damaged; skin: dried flat with limb bones everted
***Cercopithecus* species**						
Ethiopia: specific locality unknown	2 Dec 1910	CM 2865	M	Ad	SN	Some teeth missing, others glued

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Ethiopia: specific locality unknown	1911–1912	CM 20863	?	Juv	SK	Some postcranial bones present
Ethiopia: specific locality unknown	1911–1912	CM 20864	?	Juv	SK	Some postcranial bones present
Locality unknown*	4 Oct 1940	CM 18773	M	Juv	SN	Skull good but postcranial skeleton very chalky; Pittsburgh Zoological Garden specimen
Macaca fascicularis						
Indonesia: Java	unknown	CM 1661	?	Juv	SN*	Good; on exhibit
Indonesia: Java	unknown	CM 1718	F	Juv	SK*	Good; on exhibit
Macaca maurus						
Indonesia: Moluccas, Halmahera(?)	unknown	CM 1663	?	Juv	SN*	Good; on exhibit; locality doubtful
Macaca mulatta						
Locality unknown*	5 Dec 1937	CM 14750	F	Juv	SS	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	1938	CM 20803	F	[Imm]	AL	Infant; Pittsburgh Zoological Garden specimen
Macaca mulatta mulatta						
India: Madras	unknown	CM 1662	?	Ad	SN*	Good; on exhibit
Macaca nemestrina nemestrina						
Indonesia: Sumatra	unknown	CM 1660	M	Ad	SN*	Good; on exhibit

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Macaca nigra						
Indonesia: Sulawesi	unknown	CM 1664	?	Ad	SN*	Good; on exhibit
Macaca sylvanus						
Morocco: Meknes Province, 18 km S Azrou, 33°16′N, 05°12′W	1969–1970	CM 45290	?	Ad	SK	Good
Papio anubis anubis						
Cameroon: Yoko	23 Jan 1937	CM 16092	M	Ad	SS	Good, with some postcranial bones; skin: tanned
Papio anubis doguera						
Ethiopia: Gidabo River	16 Mar 1912	CM 5828	F	Juv	SS	Good, with some postcranial bones
Ethiopia: specific locality unknown	1912	CM 5829	?	Juv	SS	Shot damage to braincase; skin: dried with head everted
Papio anubis furax						
Kenya: specific locality unknown	23 Jan 1910	CM 2055	M	Ad	SS	Good with some postcranial bones
Papio anubis neumanni						
Kenya: Keri Camp	18 Mar 1910	CM 2095	M	Juv	SS	Good with some postcranial bones; skin: tanned
Kenya: Eastern Region, Narok District, Uaso Nyiro [Ewaso Ngiro], near Narok	26 Aug 1960	CM 57866	M	Ad	SS	Skull: good; skin: tanned

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Papio anubis						
Sudan: Sennaar	unknown	CM 1666	M	Ad	SN*	Good; on exhibit
Sudan: Sennaar	unknown	CM 1667	M	Ad	SN*	Good; on exhibit
Sudan: Sennaar	unknown	CM 1715	F	Juv	SK*	Good; on exhibit
Papio cynocephalus cynocephalus						
Kenya: 160 mi from Uganda railroad	1 Apr 1910	CM 2103	M	Juv	SS	Good, with some postcranial bones; skin: tanned
Papio cynocephalus						
Locality unknown*	about 1900	CM 472	?	[Imm]	SO	Skin: good; Pittsburgh Zoological Garden specimen
Locality unknown*	about 1900	CM 473	?	[Imm]	SO	Skin: good; Pittsburgh Zoological Garden specimen
Locality unknown*	about 1900	CM 1214	M	[Ad]	SO	Skin: good; Pittsburgh Zoological Garden specimen
Locality unknown*	12 Aug 1938	CM 17484	F	Ad	SB	Occipital region damaged; skin: tanned; Pittsburgh Zoo through University of Pittsburgh
Papio hamadryas						
Ethiopia: Dire Daoua	11 Dec 1911	CM 20865	?	Juv	CO	Appears to be pick-up

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Ethiopia: specific locality unknown	unknown	CM 5765	?	Juv	SS	Skull: bullae damaged; skin: dried inside out
Ethiopia: specific locality unknown	unknown	CM 5766	?	Ad	SS	Skull: good with some postcranial bones; skin: tanned
Ethiopia: specific locality unknown	unknown	CM 5767	?	Ad	SS	Skull: left front damaged, only small part of lower jaw present; skin: tanned
Ethiopia: specific locality unknown	unknown	CM 5768	?	Juv	SS	Skull: good with some postcranial bones; skin: tanned
Papio leucophaeus leucophaeus						
Cameroon: Edea	26 Jun 1922	CM 20911	M	[Ad]	SO	Skin: good
Papio leucophaeus						
Locality unknown*	unknown	CM 1215	M	Juv	SS	Good; Pittsburgh Zoological Garden specimen
Papio papio						
Locality unknown*	unknown	CM 787	M	[Imm]	SS*	Skull: missing; skin: tanned; Pittsburgh Zoological Garden specimen

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Papio sphinx madarogaster						
Cameroon: Lolodorf	1926	CM 6153	?	Ad	SK	Occipital region damaged
Papio sphinx						
Locality unknown*	unknown	CM 1847	M	Ad	SB*	Skull: good; skin: mounted, on exhibit; Pittsburgh Zoological Garden specimen
Papio ursinus griseipes						
Zimbabwe: Mashonaland, Hartley Hills, Tchingas	24 Sep 1892	CM 294	M	Ad	SK	Good
Zimbabwe: Mashonaland, Hartley Hills, Tchingas	24 Sep 1892	CM 295	M	Ad	SK	Good
Papio ursinus ruacana						
Angola: Mucungu	25 Oct 1930	CM 6847	M	Ad	SB	Braincase missing, teeth extremely worn or missing; skin: tanned
Papio ursinus						
Locality unknown	12 Aug 1938	CM 17485	F	Ad	SB	Autopsied; postcranial bones overcleaned; skin: tanned
Locality unknown*	28 Apr 1949	CM 30423	M	Juv	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
***Papio* species**						
Locality unknown*	unknown	CM 516	M	Ad	SS*	Skull: good; skin: missing; Pittsburgh Zoological Garden specimen
Locality unknown*	unknown	CM 1081	M	Juv	SK	Skull: good; skin: missing; Pittsburgh Zoological Garden specimen
Locality unknown	unknown	CM 1399	?	Ad	SK	Good
Locality unknown*	unknown	CM 1464	M	Juv	SN	Measurable but damaged during cleaning; Pittsburgh Zoological Garden specimen
Locality unknown*	Dec 1907	CM 1560	F	Ad	SN	Good; Pittsburgh Zoological Garden specimen
Theropithecus gelada						
Ethiopia: specific locality unknown	Dec 1907	CM 1668	?	Ad	SN*	Good; on exhibit
COLOBINAE						
Colobus angolensis palliatus						
Kenya: Coast Region, Diani	15 Aug 1964	CM 57955	M	Ad	SS	Skull: good; skin: salted and folded
Kenya: Coast Region, Diani	15 Aug 1964	CM 57956	M	Juv	SS	Skull: good; skin: salted and folded
Kenya: Coast Region, Shimba Hills	13 Aug 1964	CM 57954	F	Juv	SS	Skull: good; skin: salted and folded
Tanzania: Southern Highlands Province, Mount Rungwe	1929	CM 6423	?	Ad	SK	Right zygomatic arch broken

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Tanzania: Southern Highlands Province, Mount Rungwe	1929	CM 6424	?	Ad	CO	Good
Tanzania: specific locality unknown	1960	CM 57878	M	Ad	SB	Skull: good; skin: tanned
Colobus guereza guereza						
Ethiopia: Arussi Plateau-Cofali area	1 Mar 1912	CM 5804	M	Ad	SS	Skull: good with some postcranial bones; skin: tanned
Ethiopia: Arussi Plateau-Cofali area	1 Mar 1912	CM 5807	M	Juv	SS	Skull: good with some postcranial bones; skin: tanned
Ethiopia: southwest Arussi Plateau	1 Mar 1912	CM 5805	M	Ad	SS	Skull: good with some postcranial bones; skin: tanned
Ethiopia: southwest Arussi Plateau	1 Mar 1912	CM 5806	F	Ad	SS	Skull: good with some postcranial bones; skin: tanned
Ethiopia: Cofali-Malke area	3 Mar 1912	CM 5810	M	[Imm]	SS*	Skull: missing
Ethiopia: Cofali-Malke area	3 Mar 1912	CM 5811	F	[Imm]	SS*	Skull: missing
Colobus guereza kikuyensis						
Kenya: Mount Kenya	1949	CM 59570	?	[Ad]	SO	Skin: tanned
Kenya: Mount Kenya	1949	CM 59571	?	[Ad]	SO	Skin: tanned
Kenya: Mount Kenya	1949	CM 59572	?	[Ad]	SO	Skin: tanned
Kenya: Mount Kenya	1949	CM 59573	?	[Ad]	SO	Skin: tanned

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Kenya: Mount Kenya	1949	CM 59574	?	[Ad]	SO	Skin: tanned
Kenya: Mount Kenya	1949	CM 59575	?	[Ad]	SO	Skin: tanned
Colobus guereza matschiei						
Kenya: Western Region, Kakamega Forest, near Kakamega	10 Jul 1960	CM 57867	F	Ad	SS	Skull: good with some postcranial bones; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	11 Jul 1960	CM 57868	M	Ad	SS	Skull: good with some postcranial bones; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	12 Jul 1960	CM 57869	M	Ad	SB	Skull: good; skin: tanned
Kenya: Western Region, Kakamega Forest, near Kakamega	12 Jul 1960	CM 57870	F	Ad	SB	On left side of skull, orbit, toothrow, palate, and maxillary damaged
Tanzania: Northern Province, 10 mi N Loliondo	28 Aug 1960	CM 57877	F	Ad	SS	Good
Colobus guereza occidentalis						
Cameroon: Efufup	30 Aug 1919	CM 5114	F	Ad	SS	Skull: good with some postcranial bones
Uganda: Kigezi District, Kayonza Forest	1960	CM 57874	M	Ad	SB	Skull: good; skin: tanned
Uganda: Kigezi District, Kayonza Forest	1960	CM 57875	M	Ad	SB	Skull: good; skin: tanned
Uganda: Kigezi District, Kayonza Forest	1960	CM 57876	F	Ad	SB	Braincase damaged, lower jaw broken; skin: tanned

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Uganda: Toro District, Fort Portal, Mpanga Forest	18 Jul 1960	CM 57871	M	Juv	SB	Good
Uganda: Toro District, Fort Portal, Mpanga Forest	16 Jul 1960	CM 57872	F	Ad	SB	Good
Uganda: Toro District, Fort Portal, Mpanga Forest	1960	CM 57879	F	Ad	SB	Good
Uganda: Toro District, Fort Portal, Mpanga Forest	1960	CM 57880	M	Ad	SB	Good
Uganda: Toro District, Mongiro, Bwamba Forest	27 Jul 1960	CM 57873	M	Ad	SB	Skull: good; skin: tanned
Colobus guereza						
Locality unknown	unknown	CM 20866	?	Ad	SK	Bullae damaged, left zygomatic arch broken
Colobus pennanti						
Zaire: Bumba Zone, Yalosemba	29 Jun 1979	CM 86713	F	Juv	SS	Skull: good; skin: salted and folded
Colobus rufomitratus tephrosceles						
Uganda: Toro District, Fort Portal, Mpanga Forest	16 Jul 1960	CM 57881	F	Ad	SB	Skull: good; skin: tanned
Uganda: Toro District, Fort Portal, Mpanga Forest	16 Jul 1960	CM 57882	M	Ad	SB	Skull: good; skin: tanned
Uganda: Toro District, Fort Portal, Mpanga Forest	17 Jul 1960	CM 57883	M	Ad	SB	Braincase damaged; skin: tanned
Uganda: Toro District, Fort Portal, Mpanga Forest	17 Jul 1960	CM 57884	M	Ad	SB	Skull: good; skin: tanned
Presbytis aygula						
Indonesia: Java	unknown	CM 1716	F	Juv	SK*	Good; on exhibit

Catalog of the Order Primates—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Presbytis entellus						
Sri Lanka	unknown	CM 1659	?	Ad	SN*	Good; on exhibit
Pongidae						
Hylobatinae						
Locality unknown	unknown	CM 155	?	Juv	SK*	Biological supply house specimen dissected for exhibit
Hylobates lar						
Locality unknown*	11 Feb 1948	CM 30391	?	Juv	SB	Good; Pittsburgh Zoological Garden specimen
Locality unknown*	22 Sep 1948	CM 30392	M	Ad	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	23 Sep 1948	CM 30393	M	Juv	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	7 Oct 1948	CM 30394	M	Juv	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	7 Oct 1948	CM 30395	M	Ad	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Hylobates pileatus						
Locality unknown*	29 Mar 1944	CM 22199	F	Juv	SB	Good; Pittsburgh Zoological Garden specimen
Hylobates syndactylus						
Indonesia: Sumatra	unknown	CM 1658	?	Ad	SN*	Good; on exhibit
PONGINAE						
Gorilla gorilla gorilla						
Cameroon: possibly vicinity of Butanga	23 Jul 1908	CM 1786	F	Ad	SB	Skull: good; skin: tanned
Cameroon: Ebolowa	7 Feb 1921	CM 20985	M	Ad	SN	Facial region heavily damaged; some skull measurements available
Cameroon: Mindini, Ebolowa	10 May 1921	CM 20986	F	Ad	SN	Good
Cameroon: Mindini, Ebolowa	9 Oct 1921	CM 20987	F	Juv	SN	Left side of skull damaged, some measurements possible
Cameroon: 25 mi SW Ebolowa	1941	CM 42753	[M]	Ad	SK	Left side of skull damaged, some measurements possible
Cameroon: 25 mi SW Ebolowa	10 Jun 1941	CM 42754	M	Ad	SK	Some teeth missing
Cameroon: Mekom, 25 mi SE Ebolowa	1941	CM 42755	M	Ad	SK	Good
Cameroon: Mekom, 25 mi SE Ebolowa	1941	CM 42756	M	Ad	SK	Basisphenoid damaged

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: near Efulen	1910	CM 5359	?	Inf	AL	Foetus and uterus (Schultz, 1927; Wislocki, 1929)
Cameroon: Metet	25 Apr 1919	CM 5103	M	Ad	SB	Good
Cameroon: specific locality unknown	27 Apr 1935	CM 5360	M	Ad	SK	Good but teeth glued
Cameroon: specific locality unknown	unknown	CM 92137	M	Ad	SN*	Mounted on exhibit
Gabon*	28 Dec 1978	CM 60283	M	Ad	PS*	Postcranial skeleton; skin: mounted; Pittsburgh Zoological Garden specimen
Gabon: Valley of Ogoue River	15 Oct 1897	CM 145	M	[Ad]	BM*	On exhibit
Gorilla gorilla						
Locality unknown*	21 Dec 1965	CM 40596	?	Juv	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	unknown	CM 59606	F	[Imm]	SO	Skin: tanned; Pittsburgh Zoological Garden specimen
Pan troglodytes schweinfurthi						
Uganda: Toro District, Mpanga Forest	20 Jul 1960	CM 57888	M	Ad	SB	Skull: good; skin: tanned
Pan troglodytes troglodytes						
Cameroon: Mekom, 25 mi SE Ebolowa	1941	CM 42757	F	Ad	SK	Good but some teeth missing
Cameroon: Mekom, 25 mi SE Ebolowa	1941	CM 42758	F	Juv	SK	Good

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Cameroon: 35 mi SW Ebolowa	1941	CM 42759	?	Ad	SK	Good
Cameroon: 35 mi SW Ebolowa	1941	CM 42760	?	Ad	SK	Good
Cameroon: 25 mi SW Ebolowa	1941	CM 42761	?	Juv	SK	Good
Cameroon: Lolodorf	13 Feb 1914	CM 2886	F	Juv	SS	Skull: good with some postcranial bones; skin: tanned
Cameroon: Lolodorf	30 Aug 1927	CM 6149	M	Ad	SS	Skull: good; skin: tanned
Cameroon: Lolodorf	17 Jan 1914	CM 20918	F	Ad	SK	Good
Cameroon: Metet	18 Jan 1919	CM 5099	F	Juv	SS	Good
Cameroon: specific locality unknown	unknown	CM 10325	?	Ad	SN	Good but some teeth missing
Pan troglodytes						
Locality unknown	unknown	CM 1479	M	Inf	SK*	Good, on exhibit
Locality unknown*	30 Mar 1914	CM 2866	M	[Imm]	SS*	Skull: missing, limb bones present; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	23 May 1949	CM 30422	M	Juv	SS	Skull: good with some postcranial bones; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	1952	CM 61360	?	Juv	SN	Good; University of Pittsburgh Virus Laboratory

CATALOG OF THE ORDER PRIMATES—*Continued.*

Locality	Date collected	Catalog number	Sex	Age	Nature of specimen	Condition of specimen and comments
Uganda: specific locality unknown	unknown	CM 1657	M	Juv	SN*	Mounted skeleton, on exhibit
Pongo pygmaeus						
Locality unknown*	9 Sep 1915	CM 3211	M	Inf	SS	Skull: fragmentary; Pittsburgh Zoological Garden specimen
Locality unknown*	24 Apr 1944	CM 22292	M	Ad	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	15 Jul 1968	CM 59526	F	Ad	SB	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
Locality unknown*	28 Mar 1950	CM 61335	?	Juv	SS	Skull: good; skin: tanned; Pittsburgh Zoological Garden specimen
HOMINIDAE						
Homo sapiens						
Canada: Quebec, Smith Island, Cape Smith, 60°40′N, 78°30′W	12 Jun 1945	CM 23782	?	Ad	CO	Pick-up, extremely weathered, no teeth
India: specific locality unknown*	Sep 1934	CM 10037	F	Ad	SN	Good, biological supply house specimen

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GROWTH PATTERNS AND SEASONAL THERMOGENESIS OF *PEROMYSCUS MANICULATUS* INHABITING THE APPALACHIAN AND ROCKY MOUNTAINS OF NORTH AMERICA

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Abstract

Deer mice (*Peromyscus maniculatus*) were live-trapped at two-week intervals from January 1974 to September 1975 in a subalpine forest (3120 m) of the Front Range of Colorado and from September 1979 to June 1981 in a mixed deciduous forest (450 m) of the Appalachian Mountains of Pennsylvania. On the Rocky Mountain Site (RMS), snow covered the ground for 7½ months, reaching a maximum depth of 270 cm; on the Appalachian Mountain Site (AMS), snowcover was intermittent reaching a maximum depth of 30 cm. The minimum temperature on both sites was −28°C. Subnivean activity of deer mice was monitored by use of live-traps located within trapping chimneys.

Growth dynamics of mice were analyzed year-round by plotting body weight distributions, tracing growth of individuals over consecutive trapping periods, and plotting instantaneous growth rates of the population through time. Deer mice on the RMS and AMS showed a gradual increase in weight from October to May. The overwintering cohort consisted principally of "immature" individuals—those animals born during late summer and autumn that have not reached sexual maturity. Seasonal metabolic shifts were determined in the laboratory by employing oxygen consumption techniques. Resting metabolic rates were significantly lower in winter-captured mice than in summer-captured mice on the AMS. *P. maniculatus* showed a decreased body temperature upon capture indicating winter torpor. Deer mice have evolved a diverse repertoire of mechanisms by which they conserve energy during periods of cold. Their ability to undergo torpor coupled with communal nesting, food hoarding, and construction of elaborate nests aids considerably in energy conservation during winter and in part accounts for the success and wide geographical and ecological distribution of the deer mouse in North America.

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INTRODUCTION

Field studies dealing with the year-round population ecology of small mammals in seasonal environments have reported a general retardation in body growth for many species during mid-winter. In general, a decrease in body weight is seen during autumn and winter with a weight gain in spring concomitant with reproductive activity. This loss of weight or slowed growth during winter confers the advantage of reducing caloric needs during this period when food is scarce (Fuller, 1969; Tast, 1972; Stebbins, 1976). In North America, seasonal weight changes are reported for microtine rodents such as *Microtus pennsylvanicus* (Brown, 1973; Iverson and Turner, 1974), *Microtus oeconomus* (Whitney, 1976), *Microtus xanthognathus* (Wolff and Lidicker, 1980), *Clethrionomys rutilus* (Sealander, 1966; Sealander and Bickerstaff, 1967; Fuller, 1969; Fuller et al., 1969; Whitney, 1976), and *Clethrionomys gapperi* (Fuller, 1969, 1977; Stebbins, 1976; Stinson, 1977; Merritt and Merritt, 1978*a*; Perrin, 1979). Seasonal weight declines are also reported for European microtine rodents—*M. oeconomus* (Tast, 1972), *Microtus agrestis* (Chitty, 1952), *Clethrionomys glareolus* (Bergstedt, 1965; Zejda, 1967, 1971; Bujlaska and Gliwicz, 1968; Hyvarinen and Heikura, 1971; Wiger, 1979) and *Clethrionomys rufocanus* (Kalela, 1957; Hyvarinen and Heikura, 1971).

In addition to microtine rodents, shrews (*Sorex* spp.) in Eurasia have been found to show body weight decreases during winter, the minimum weight occurring during the coldest months (January, February) (Dehnel, 1949; Mezhzherhin, 1964; Mezhzherin and Melnikova, 1966). In North America, no published work documents growth trends of shrews in northern latitudes on a year-round basis. However, data (Merritt, unpublished data) on year-round growth derived from live-trapping studies of *Blarina brevicauda* from the Appalachian Mountains of Pennsylvania indicate that a mid-winter reduction in weight does not occur for this shrew.

It is noteworthy that certain northern microtine rodents do not undergo winter weight declines. For instance, the collared lemming (*Dicrostonyx groenlandicus*) does not conform to the above trends of winter weight decline, but rather shows an accelerated growth under short-day photoperiods (Hasler et al., 1976; Mallory et al., 1981). This trend for microtine winter weight loss is also complicated by the fact that geographic variation may occur within a certain species. For instance, Merritt and Merritt (1978*a*) found retardation in growth of *C. gapperi* from the Rocky Mountains, but the same species live-trapped year-round from the Appalachian Mountains showed no significant decline in weight during winter months (Merritt, 1984*a*).

Research efforts monitoring year-round growth dynamics of cricetid rodents inhabiting seasonal environments are few. Sealander (1951) live-trapped *Peromyscus leucopus* in central Illinois during summer and winter and found winter animals averaged 3.66% heavier than summer caught animals. Fuller et al. (1969) found *P. maniculatus* to show a mid-winter weight loss followed by a spring gain in the vicinity of Great Slave Lake, northern Canada. In the Rocky Mountains of Colorado, Stinson (1977) and Merritt and Merritt (1978*b*) examined growth trends of *P. maniculatus* year-round in deciduous and coniferous forests, respectively. Stinson (1977) found deer mice to undergo a slight weight decline, whereas Merritt and Merritt (1978*b*) reported a gradual trend toward increasing weight through winter, peaking in summer. As indicated above, field studies on growth dynamics of *Peromyscus* tend to show contrasting results. This is due in part to poor trappability of deer mice in northern latitudes attributable to periodic bouts of torpor (Hill, 1975; Lynch et al., 1978; Vogt and Lynch, 1982) and to their largely unstudied communal nesting habits (Nicholson, 1941; Wolff and Hurlbutt, 1982).

It is the intent of the present study to examine the patterns of body growth and seasonal thermoregulatory and energetic needs of *P. maniculatus* in the Rocky Mountains and Appalachian Mountains of North America. Does this cricetid rodent show mid-winter growth declines as do many microtine rodents? Further, if growth changes are non-existent as a survival "tactic" during mid-winter, then what other anatomical, behavioral, or physiological mechanisms are employed that permit survival of this common North American rodent in seasonal environments?

METHODS AND MATERIALS

Study Areas

Two study sites were chosen to examine the population dynamics of *P. maniculatus.* Mice were live-trapped in a Colorado subalpine forest from January 1974 to September 1975 and from September 1979 to June 1981 in a mixed deciduous forest of the Appalachian Mountains of Pennsylvania. Both study sites were located at ca. 40°N latitude.

The Rocky Mountain Site (RMS) was located in Roosevelt National Forest, adjacent to the University of Colorado Mountain Research Station, NW¼ sec. 22, T1N, R73W, at an elevation of 3120 m. The study plot was dominated by Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) and was bisected by a creek. A lower synusia was dominated by myrtle blueberry (*Vaccinium myrtillus*) and abundant herbaceous growth such as *Lupinus argenteus, Pedicularis racemosa, Arnica cordifolia,* and *Epilobium angustifolium.* Streamside habitat supported a more diverse flora. The study area was characterized by a profuse debris of dead herbs and trees, stumps and fallen logs. A more detailed account of the flora of the RMS is given by Merritt and Merritt (1978*a*). This site was characterized by a continental climate with frequent strong winds due to Pacific air masses. Warm, dry winds (Chinook) are common and a "crestcloud" commonly occurred over the continental divide near the study area. Most of the precipitation on the Eastern Slope of the Front Range is attributable to Gulf air masses, that frequently occur in spring and autumn. These air masses are responsible for a rapid build-up of snow on the study area in spring. Snow covered the ground for about 7½ months of the year. Precipitation is usually greater than 75 cm per year, much of it in the form of frequent late winter snow storms and summer convectional storms. During my study, the temperatures for the area ranged from −25.6 to 23.9°C (mean annual temperature, 1.1°C). The growing season lasted for about 87 days at the elevation of the study site.

The Appalachian Mountain Site (AMS) was located in southeastern Westmoreland County, Pennsylvania (Powdermill Nature Reserve, Carnegie Museum of Natural History), at an elevation of 450 m. The study area occupied a northeast exposure and also was bisected by a creek. The upper canopy was formed principally by beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), cucumber tree (*Magnolia acuminata*), and red oak (*Quercus borealis*). The middle canopy was formed by striped maple (*Acer pennsylvanicum*), spice bush (*Lindera benzoin*), witch-hazel (*Hamamelis virginiana*), and rhododendron (*Rhododendron maximum*). During spring a lush lower synusia consisted of many herbs such as *Trillium* spp., *Viola* spp., mayapple (*Podophyllum peltatum*), white clintonia (*Clintonia umbellulata*), dwarf ginseng (*Panax trifolium*), partridgeberry (*Mitchella repens*), Indian cucumber-root (*Medeola virginiana*), and Virginia creeper (*Parthenocissus quinquefolia*) among others. By mid-summer, ferns (that is, *Polystichum acrostichoides, Dryopteris* spp.) constituted most of the groundcover. The forest floor was mesic and well drained and characterized by its deposits of residual sandstone boulders with an accumulation of humus and leaf litter between the rocks. Selective logging in early 1900 occurred throughout the study area.

The AMS is located within the physiographic division referred to as the Allegheny Mountains Section of the Appalachian Plateau Province of Pennsylvania (Grimm and Roberts, 1950:6). The area experiences a humid, continental climate marked by warm summers and cold winters. Prevailing winds are from the west. Local weather patterns show strong topographic influence due to the location of the study area between Chestnut and Laurel ridges (maximum elevation 606 m and 848 m, respectively). Annual precipitation in the vicinity of the study area ranges from 102 to 148 cm (mean, 122 cm). Temperatures range from a low of −31°C (usually occurring in January) to a high of about 36°C (occurring in July or August). Average annual temperature for the vicinity is about 7°C. Snowfalls are frequent and may be heavy from December through March. Snow may occur from October to April, however, a permanent snowcover normally persists for only about two months of the year. Snowfall amounts in the study region range from 66 to 225 cm (mean snowfall, 139 cm). The growing season lasts from 110 to 120 days in the vicinity of the study area.

Field Procedures

The RMS contained a 12 by 12 live-trapping quadrat with stations located at 10 m (1.2 ha). Two Sherman live-traps containing synthetic fiber nesting material and sunflower seeds as bait were placed at each station. Trapping chimneys were used to monitor subnivean activity (Merritt and Merritt, 1978*a*, 1978*b*, 1982). A similar methodology was employed on the AMS except that this study site was a 10 by 10 quadrat (1.0 ha) and trapping chimneys were of a different design. Two trapping periods per month, each consisting of 4 days, were employed to monitor the population year-round on both study sites.

Upon initial capture, voles were toe clipped for identification, at which time toe number, location on grid, weight, sex and reproductive status were recorded. Animals were weighed to the nearest 0.5 g using a Pesola scale and classified as adult, subadult or juvenile according to body weight and sexual maturity. Position of the testes (either abdominal or scrotal) was used to describe reproductive condition of males. Reproductive status of females was assessed by noting condition of the vulva (whether perforate or

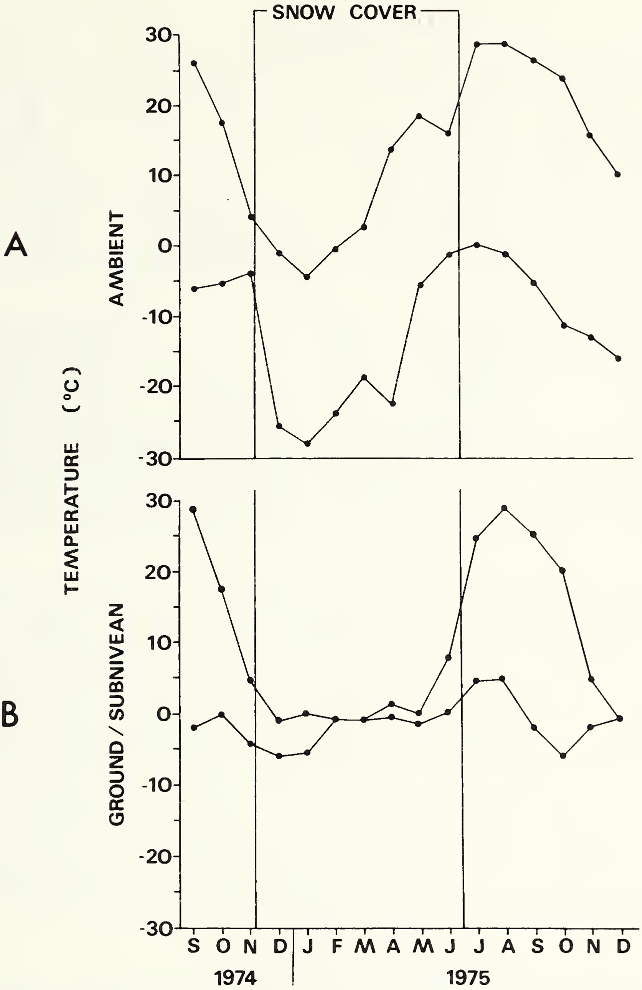

Fig. 1.—Temperatures recorded on the Rocky Mountain Site from September 1974 to December 1975. Maximum and minimum ambient temperatures recorded at 30cm above ground or snow (A). Maximum and minimum temperatures recorded on bare ground surface or in subnivean runway (B).

not perforate) and nipples (whether small, medium or lactating). Upon recapture during the same period, the toe number, location, and weight were recorded and the mouse released.

Daily temperatures were recorded on both study sites. On the RMS, ambient temperature was measured continuously by a Bendix hygrothermograph maintained at 30 cm from the ground/snow surface. Subnivean temperatures were recorded by a Dixon thermograph probe which was located in a subnivean runway (Fig. 1). On the AMS a

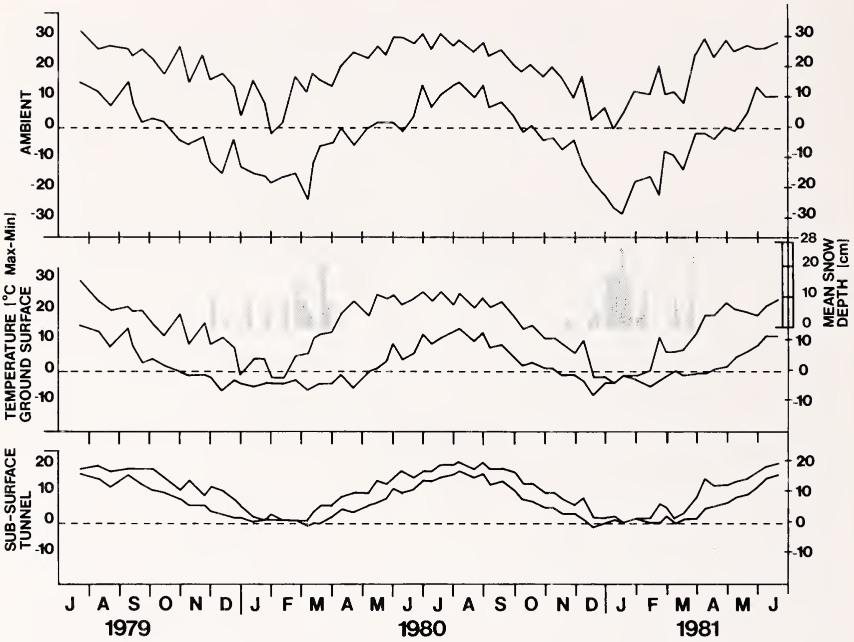

Fig. 2.—Maximum and minimum temperatures recorded on the Appalachian Mountain Site from July 1979 to June 1981. Temperatures were recorded in three zones: ambient (1.5 m above ground surface), on ground surface beneath leaf litter and within a subsurface tunnel located 30 cm below ground. Snow depths on study grid are shown by stippled bars.

three-point thermograph recorded temperatures below ground surface (sub-surface tunnel within a talus deposit), on ground surface/subnivean level, and at the ambient level (Fig. 2). On the AMS daily precipitation and snowfall also were recorded. Snow depths were recorded for both study sites at selected points.

Laboratory Procedures

Resting metabolic rate (RMR) for *P. maniculatus* was determined in the laboratory for animals from the RMS (winter only) and AMS using oxygen consumption techniques. Animals were collected in the field during summer (late August) and late winter (mid-March) and used in metabolic tests within 48 hrs after capture. Mice were maintained in the laboratory and given food (sunflower seeds) and water *ad libitum*. Oxygen consumption was measured at a temperature within the thermoneutral zone of *P. maniculatus*—29°C. Oxygen consumption was monitored using a positive pressure "push through" assembly with a Beckman G2 (RMS) and a Beckman 755 (AMS) paramagnetic oxygen analyzer. Mice were tested in a 380 ml glass jar equipped with air inlet and outlet. Before and after testing, each mouse was weighed to the nearest 0.1 g and their body temperature recorded by inserting a "YSI small animal probe" a distance of 15 mm into the rectum. The probe was held in place for 45 sec and body temperature recorded on a YSI 42SC

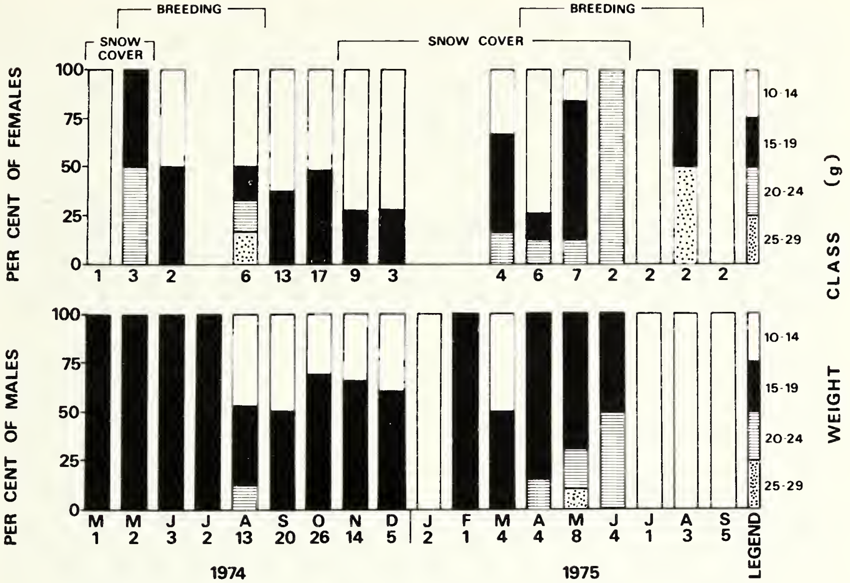

Fig. 3.—Histograms showing body weight distributions of male and female *Peromyscus maniculatus* on the Rocky Mountain Site from March 1974 to September 1975. Numbers on horizontal axis are monthly sample size.

tele-thermometer. RMR was computed according to the method of Depocas and Hart (1957), expressed in milliliters of oxygen consumed per gram per hour ($mlO_2/g/hr$) and corrected for standard temperature and pressure conditions. Differences in mean oxygen consumption of summer and winter animals were tested for significance at the 0.05 confidence level by Student's *t*-tests. See Merritt (1976) for specific details on methodology.

RESULTS

Growth

Growth dynamics of *P. maniculatus* were evaluted for 18 months on the RMS and for 22 months on the AMS by employing three different methods: 1) plotting body weight distributions of the entire marked population through time; 2) tracing growth of selected individuals over consecutive trapping periods; 3) plotting instantaneous growth rates (% growth per day) of the population through time.

Rocky Mountain site.—Body weight distributions for deer mice from the RMS were depicted as percent of males and females in four age-weight classes over time (Fig. 3). No mice were caught weighing less than 10 g nor more than 29 g. In March 1974, one male was in the 15 to 19 g weight class and a female in the 10 to 14 g class. When the

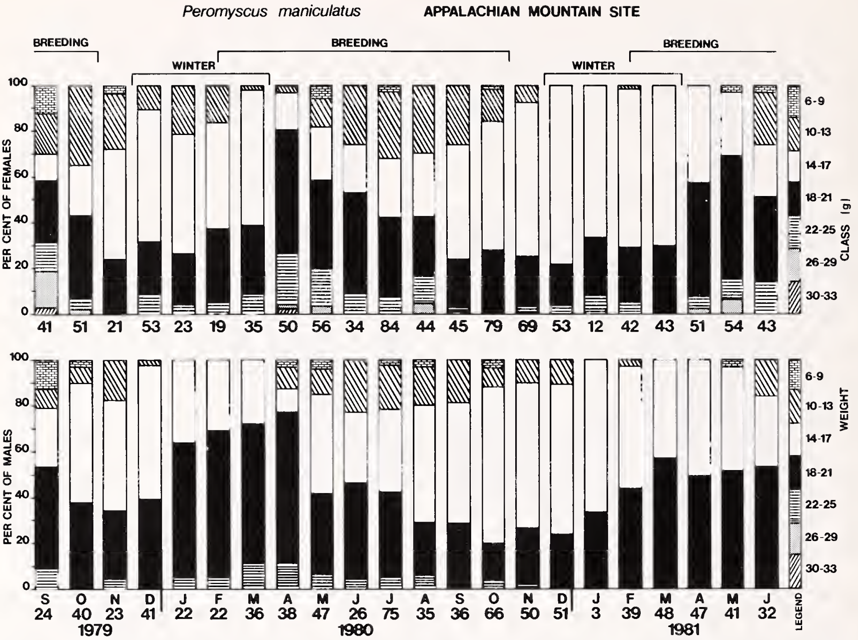

Fig. 4.—Histogram showing body weight distribution of male and female *Peromyscus maniculatus* on the Appalachian Mountain Site from September 1979 to June 1981. Numbers on horizontal axis are monthly sample size.

breeding season commenced, females weighed more than males. Approximately 20% of August-trapped females weighed 25 to 29 g, indicating pregnancy. About 50% of the population consisted of 10 to 14 g juveniles at this time. For the most part, overwintering mice were distributed in the 10 to 14 g and 15 to 19 g weight classes. In March 1975, a gradual increase in the number of animals in the 20 to 24 g class began, reaching 100% for females and 50% for males in June. This weight class was in breeding condition during spring snowmelt. Males were confined to the 10 to 14 g weight class for the remainder of the summer. Only two females were captured in August, one in the 15 to 19 g weight class and the other in the 25 to 29 g class (pregnant). The mean annual body weight for the population of *P. maniculatus* on the RMS for the 18-month study period was 15.8 g.

Appalachian Mountain site.—The same procedure was employed to analyze body weight distributions on the AMS as for the RMS above. Unlike the RMS, seven age-weight classes were defined and monitored for 22 months (September 1979 to June 1981) (Fig. 4). Mean annual body weight for deer mice on the RMS was similar to that calculated for mice on the AMS (15.8 g and 16.7 g, respectively). As shown in Fig. 4, during autumn 1979 the majority of deer mice were distributed in the heavier weight classes. At this time of year the population consisted principally of the spring-born cohort and juveniles born in late summer and early autumn. In addition, about 10% of females were visibly pregnant in September thus contributing to the 26 to 29 g and 30 to 33 g weight classes. During October and November, the autumn-born cohort moved into the 14 to 17 g "subadult" weight class which would ultimately contribute to the bulk of the overwintering cohort. This trend was also apparent on the RMS, although deer mice making up the overwintering cohort on the AMS were slightly larger. For example, 10% of females on the AMS in December were in the 22 to 25 g weight class, whereas this class was only found during summer months on the RMS. Most males overwintered in the 18 to 21 g class, whereas females were more evenly distributed in the 14 to 17 g and 18 to 21 g classes during winter.

No major changes occurred in weight class distribution during March 1980; however, in early April, pregnant deer mice appeared and by late April and early May juveniles began to appear. This trend was observed one month later on the RMS (Fig. 3). During summer, each month showed representatives in all age classes except the 30 to 33 g class. The transition from autumn to winter 1980 was similar to that of 1979 with the exception that the juvenile age class (6 to 9 g) was not represented in September and November. On the RMS this cohort comprised 100% of the September 1975 sample. Growth of the 10 to 13 g weight class during autumn and early winter culminated in an overwintering cohort of principally 14 to 17 g and 18 to 21 g subadults, although a small percentage of adult females (born in spring 1980) overwintered.

Reproductive effort commenced about one month later in 1981—pregnancy and juvenile recruitment occurred in April and May. A similar instance of delayed reproductive activity occurred on the RMS between 1974 and 1975 attributable to a longer period of snowcover during 1975 compared to 1974. On the AMS, neither ambient temperature nor snow depth seemed to be related to the difference in seasonal reproductive effort.

Rocky Mountain site.—Selected individual growth records are shown for *P. maniculatus* from the RMS in Fig. 5. The average weight in September 1974 for males was 14.6 g (SE = 1.23) and 13.5 g (SE = 0.50) for females. Fifty percent of these mice showed a slight weight gain in November, followed by a period of 3½ months in which most mice were not captured. No deermice were captured during January and February 1975. As a result, no interpretation of body weight changes

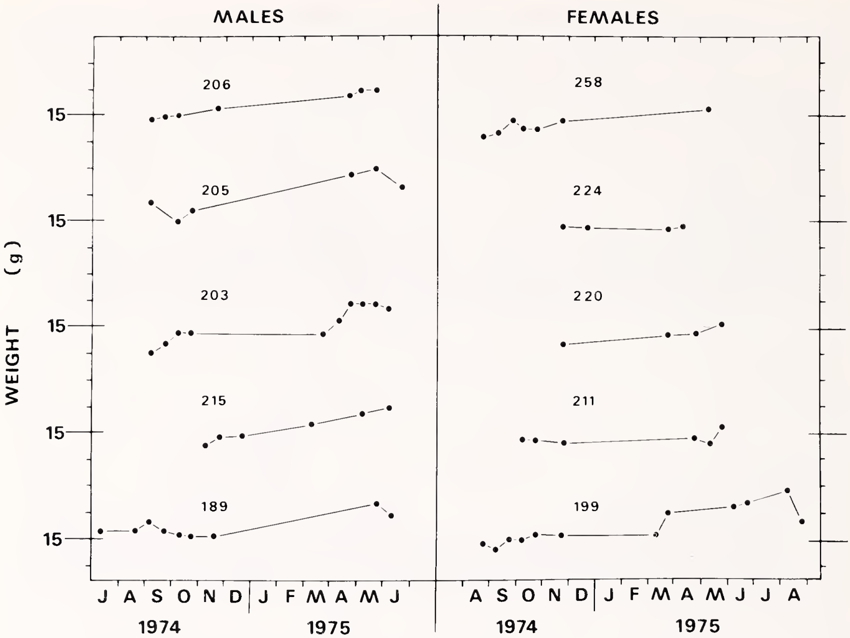

Fig. 5.—Weight records of selected male and female *Peromyscus maniculatus* (n = 10) from the Rocky Mountain Site. Divisions on the vertical axis are increments of 5 g. The number of the mouse is given above each weight record.

was possible during this period. When recaptured in March 1975, deer mice had increased in weight. Males caught in May averaged 20.3 g (SE = 1.24), whereas females weighed 16.3 g (SE = 0.62). Growth records for *P. maniculatus* show a gradual trend toward increasing weight through the winter, and peaking in summer. Mid-winter weights were not available due to poor trappability attributable to periodic torpor of *P. maniculatus* during winter months.

Appalachian Mountain site.—Individual growth rates are presented in Fig. 6. Mean body weight for October 1979 was 15.8 g (SE = 1.47) for males and 14.4 g (SE = 1.39) for females. These weights increased to an average of 18.9 g (SE = 0.66) for males and 15.2 g (SE = 0.79) for females during winter (February 1980). Weight of male deer mice remained stable in May 1980, averaging 18.9 g (SE = 0.77), but increased in females to 19.2 g (SE = 0.32). The increased weights of deer mice in May were attributable to reproductive activity which commenced in late March. As in *P. maniculatus* from the RMS (Fig. 5), a gradual increase in weight was seen in individuals traced from October 1979

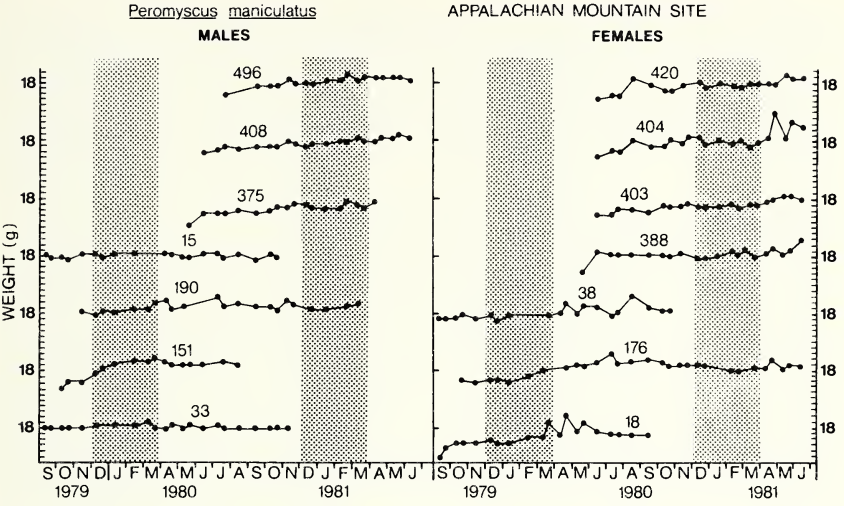

Fig. 6.—Weight records of selected individual male and female *Peromyscus maniculatus* (n = 14) from the Appalachian Mountain Site. Divisions on the vertical axis are increments of 2 g. The number of the mouse is given above each weight record. Length of calendar winter is shown by stippled area.

to May 1980. On the AMS, a gradual increase in average body weight (sexes combined) occurred from October 1979 to May 1980. Average weights were significantly different ($P < 0.05$) between October and February and May.

The following winter (1980–1981) mice showed a similar increase in weight from October 1980 to May 1981. Unlike the previous year, average weights were significantly different ($P < 0.05$) when compared seasonally. Mean body weight for October 1980 was 16.5 g (SE = 0.89) for males and slightly greater for females, 17.4 g (SE = 1.98). During February 1981 an increase was observed in both males (17.7 g, SE = 1.10) and females (17.5 g, SE = 0.95). This culminated in maximum average weights for males, 18.7 g (SE = 0.25) and for females, 19.6 g (SE = 0.20) during May 1981. Again, the increase from autumn to spring for *P. maniculatus* on the AMS compared similarly to that trend seen for deer mice on the RMS (Fig. 5).

Rocky Mountain and Appalachian Mountain sites.—Fig. 7 shows the instantaneous growth rate (% growth per day) of *P. maniculatus* on the RMS and AMS from 1974 to 1975 and 1979 to 1981, respectively. Data for each 4-week period were condensed by use of linear regression between mean body weight and growth rate for each time period. A single representative growth rate was calculated for each regression by

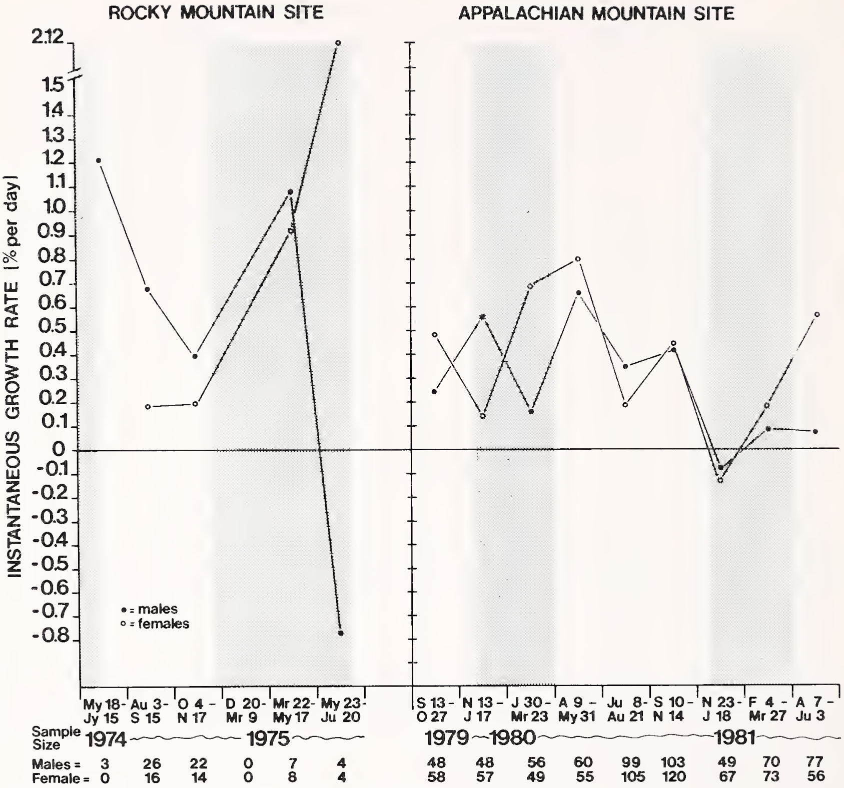

Fig. 7.—Instantaneous growth rate (% growth per day) of *Peromyscus maniculatus* on the Rocky Mountain Site (May 1974 to June 1975) and the Appalachian Mountain Site (September 1979 to June 1981). Sample sizes for males and females are given below dates on the horizontal axis. Period of snowcover is shown by stippled area on the Rocky Mountain Site. Length of calendar winter is shown by stipple for the Appalachian Mountain Site.

adjusting the growth rate to a hypothetical 14 g deer mouse for the RMS and an 18 g deer mouse for the AMS. These weights are the median weight of mice from each study site.

As evidenced in Fig. 7, growth rates were highest in spring on both study sites. This correlates well with individual growth records for both sites (Figs. 5, 6). Growth rates were lowest during late autumn and early winter on both sites. Negative growth was seen in males on the RMS during late spring and early summer, but growth was rapid for females during this same time. This discrepancy may be due to low sample sizes. On the AMS growth was negative in early winter 1980, but positive during February and March 1981. On both sites, slowed growth occurred during autumn. As seen in Figs. 3 and 4, the autumn population consisted principally of mice born either in late summer or early autumn. This group tended to show a slowed growth during a short period in mid-winter with an increase concomitant with reproductive effort in late March.

Metabolism

Table 1 summarizes metabolic studies of *P. maniculatus* collected during summer and winter on the RMS and AMS. Metabolic data derived from oxygen consumption techniques is expressed in two ways: 1) metabolism per unit weight of animal (ml O_2/g/hr) and referred to as RMR and 2) total caloric needs of an animal per unit time (cal/animal/hr) and referred to caloric requirement. On the RMS, sample size was very small due to poor trappability attributable to torpidity and communal nesting habits during cold winter months. No deer mice were tested during summer on the RMS.

On the AMS, resting metabolic rate (RMR) for winter-captured mice was about 31% lower than RMR for summer-captured mice. This energy savings was slightly increased (35%) when expressed as total caloric requirement. A significant difference ($P < 0.05$) was found in RMR and caloric requirement of deer mice when compared between seasons on the AMS. No significant differences were found between body temperatures and body weights of mice between seasons on the AMS.

It is noteworthy that deer mice showed depressed body temperatures upon and shortly after their capture. Rectal temperatures of five winter-captured deer mice from the AMS ranged from 27 to 35°C (mean = 30.2°C), twenty minutes following capture. Once housed in the laboratory (temperature = 15°C) mice quickly resumed normal body temperatures (36°C) and their activity levels increased.

DISCUSSION

Survival of small mammals inhabiting seasonal environments is strongly influenced by cold temperatures encountered in microhabitats in which they forage and nest. Two periods of the year are reported to impose hardships for small mammals inhabiting seasonal environments—autumn and mid-winter. Formozov (1946) and Pruitt (1957, 1970) referred to the "autumnal thermal overturn" as that time of the year when ambient temperatures fall below ground temperatures. When snow thickness is sufficient to insulate soil against fluctuating ambient temperatures a "hiemal threshold" is established at which time small mammals restrict foraging to the stable thermal regime of the subnivean environment.

Table 1.—*Seasonal energy requirements of* Peromyscus maniculatus *from Rocky Mountain and Appalachian Mountain sites. Resting metabolic rates (RMR) measured at 29°C. Summer sample late August; winter samples mid-February (RMS) and mid-March (AMS).*

Location	Season	Body weight (g)	Body temperature (°C)	Sample size	RMR (ml O_2/g/hr)	Caloric requirement[1] (cal/animal/hr)
Rocky Mountain site	Winter	21.5 ± 3.04	36.0 ± 0.49	2	2.49 ± 0.61	252.7 ± 27.2
	Summer	—	—	—	—	—
Appalachian Mountain site	Winter	17.4 ± 2.22	35.9 ± 0.14	5	2.08 ± 0.44	173.8 ± 38.12
	Summer	18.4 ± 1.81	35.4 ± 0.54	6	3.02 ± 0.35	265.9 ± 12.11

[1] Caloric requirement based on RMR. Values given are means ± 1 SD.

Pruitt (1957:134) indicated that the period of autumn freeze is ". . . undoubtedly the most crucial interval in the bioclimate of the forest floor mammals because during this period occur the greatest fluctations in bioclimate temperatures." The severity of the autumn freeze was indicated by Vaughan (1969) studying small mammals in a subalpine meadow near Rabbit Ears Pass, Colorado. Intensive sampling yielded no *Microtus montanus* during November 1965, when temperatures of −20°C were recorded with no protective snowcover. He attributed low densities the following summer to high mortality the preceding autumn. Further, Stinson (1977:64) indicated that ". . . the fall freeze was a time of severe hardship and several species went extinct locally." This local extinction was due to late establishment of the hiemal threshold.

A second critical period to survival of small mammals is mid-winter (Pruitt, 1957; Beer, 1961). Beer (1961) found poor survival for *C. gapperi* and *P. leucopus* in a Minnesota deciduous forest. He attributed this trend to a sparse snowcover beneath which mice could not burrow to escape cold temperatures. Fuller et al. (1969) suggested that cold temperatures in "full winter" caused high mortality in *C. rutilus.* See Merritt (1984*b*) for a review of the role of winter in the ecology of small mammals.

Small mammals residing in seasonal environments have evolved mechanisms to cope with periods of hardship such as those described above. Such "survival attributes" are not evenly distributed among all taxonomic groups, but where present may act synergistically to optimize survival. Some important mechanisms employed by small mammals when faced with periods of cold include the following: 1) decrease in body weight during autumn and winter with weight gain in spring (Iverson and Turner, 1974; Fuller, 1977; Stebbins, 1976; Merritt and Merritt, 1978*a*; Perrin, 1979); 2) lower total rate of metabolism during winter, in order to reduce caloric needs (Wunder et al., 1977; Merritt and Merritt, 1978*a*; Merritt, 1984*a*; Petterborg, 1978); 3) minimize thermal conductance by increasing hair density and length in winter (Borowski, 1958; Sealander, 1951, 1972; Khateeb and Johnson, 1971); 4) behavioral thermoregulation, for example, construction of elaborate nests and huddling (Pearson, 1947; Sealander, 1952; King et al., 1964; Layne, 1969; Hart, 1971; West, 1977; Wolff and Lidicker, 1981; Wolff and Hurlbutt, 1982); 5) abandon homeothermy for torpor (Morhardt and Hudson, 1966; Hudson, 1973; Hill, 1975; Wang and Hudson, 1978; Lynch et al., 1980; Vogt and Lynch, 1982); 6) food hoarding and availability of energy rich food during winter (Eisenberg, 1968; Tast, 1966, 1972; Wolff and Lidicker, 1981); 7) winter foraging confined to stable thermal regime within subnivean or subterranean microhabitat (Pruitt, 1957; Hayward, 1965; Sealander, 1966; Kucera and Fuller, 1978; Merritt and Merritt, 1978*a*; Merritt, 1984*a*; Webster and Brooks, 1981); 8) increase thermogenic capabilities in order to meet cold stress by activation of non-shivering thermogenesis (Jansky, 1973; Lynch, 1973; Heldmaier et al., 1981; Feist, 1984; Wunder, 1984).

The following discussion will address only two of the above mechanisms influencing the overwinter survival of *P. maniculatus.* Seasonal growth patterns and metabolic requirements are compared in two contrasting montane environments in light of their role in the survival of this common, widespread small mammal.

Growth Dynamics

A voluminous literature supports the fact that many northern small mammals (mostly microtines) tend to be smaller in winter than in summer. There is reportedly strong selection favoring small size in winter because it permits a decrease in caloric needs during this period when food availability is low (Mezhzherin and Melnikova, 1966; Fuller, 1969; Stebbins, 1976, 1978). Tast (1972) found that weight of overwintering *M. oeconomus* in Finnish Lapland was correlated with the amount of food available—if the nutrient-rich first-year rhizomes of *Eriophorum angustifolium* were plentiful, voles weighed more during winter, but if rhizomes were sparse, voles were smaller. Kalela (1957) and Mezhzherin (1964) indicated that weight loss during winter would tend to reduce energy requirements of small mammals. Further, Whitney (1973, 1976), Iverson and Turner (1974), Stinson (1977), Merritt and Merritt (1978*a*) contended that the decline in weight of individual *Microtus* and *Clethrionomys* began in late summer and early autumn when food was still abundant. Factors controlling seasonal changes in body weight are not fully known; however, Turcěk (1954) and more recently Petterborg (1978) suggested that weight gain in small mammals is under hormonal control—the endocrine system acting via an environmental cue such as photoperiod. Perhaps this may explain why body weight fluctuations are out of phase with food availability as shown in studies above.

Weight dynamics reported for *P. maniculatus* show contrasting patterns. Merritt and Merritt (1978*b*) indicated that growth records for deer mice on their Rocky Mountain site showed a gradual trend toward increasing weight through winter, and peaking in summer. In contrast, Fuller (1969) and Fuller et al. (1969) noted that weights of *P. maniculatus* declined during winter in their study area near Great Slave Lake, N.W.T. Stinson (1977) also noted a slight decline in weight of deer mice during mid-winter in a deciduous forest located in the Front Range of the Rocky Mountains of Colorado. In the present study, a gradual increase in weight was seen from October to May in *P. maniculatus* on the AMS for a two-year sample period. A similar trend was observed for deer mice on the RMS during the one-year sample period. Both the AMS and RMS populations possessed an overwintering cohort consisting principally of "immature" individuals—those animals born during late summer and autumn that have not reached sexual maturity. The growth trends from the RMS should be interpreted with caution due to the lack of captures during mid-winter attributable to periodic torpor in deer mice. Although torpidity did reduce trappability on the AMS in the present study, data are sufficient to accurately assess weight trends on this site with a good degree of certainty. The contrasting viewpoints on weight dynamics of *P. maniculatus* may in part be due to different techniques in analysis. Many investigators measure mean population weight which necessarily incorporates all cohorts trapped at a given time into the sample. It seems logical to follow individuals through many trapping periods in order to secure an accurate measure of growth changes (see Merritt, 1984*a*, for additional comments on growth analysis).

Results of the present study indicate that retardation in growth during winter is not an important energy-saving mechanism for *P. maniculatus*. Unlike microtine species (Merritt, 1984*a*), deer mice appear to have evolved a greater number of anatomical, physiological, and behavioral "mechanisms" which are employed to conserve energy during mid-winter. Some of their physiological options will be discussed at this time.

Energy Relationships

Of the many metabolic studies of *P. maniculatus*, only one has addressed winter metabolic requirements of the deer mouse (see Hart, 1972, for review). Once again, this lack of winter data may be due to an inability to capture deer mice during winter in north temperate areas due to their periodic bouts of torpor and communal nesting habits. Pearson (1947) measured the oxygen consumption (within thermoneutrality) of summer-caught *P. maniculatus*. Minimum BMR was 2.6 ml O_2/g/hr with an average 24-hr value of 3.6 ml/g/hr. Brower and Cade (1966) measured metabolic patterns of *P. maniculatus* and other woodland small mammals from the northern Adirondack Mountains of New York. Minimum metabolism for summer-captured deer mice employing oxygen consumption techniques within thermoneutrality was 1.8 ml O_2/g/hr ($n = 7$). These results compare closely with those derived by McNab and Morrison (1963) for two western subspecies of *P. maniculatus* live-trapped during summer (*P. m. gambeli* = 2.04 ml O_2/g/hr, *P. m. sonoriensis* = 1.67 ml O_2/g/hr). RMR values from my study were similar to those of Pearson (1947:138), but slightly higher than those of Brower and Cade (1966) and McNab and Morrison (1963).

To my knowledge, the only winter study of metabolism of *P. maniculatus* is the work of Stebbins et al. (1980). They measured average daily metabolic rate (ADMR) and RMR of four adult deer mice maintained in outdoor cages in a seminatural environment near Lethbridge, Alberta, Canada. Deer mice (born in captivity from stock captured the previous summer) showed an ADMR 46% higher in January than in July and a RMR 43% higher in January than in July. Stebbins et al. (1980) concluded that the higher metabolic rates recorded in winter presumably reflect increased thermoregulatory demands. They reported also that no torpor was observed during winter in their experimental animals.

Results of my study contrast with those of Stebbins et al. (1980)—specifically, RMR was significantly lower in winter-captured *P. maniculatus* than in summer-captured mice on the AMS. The disparity between results of the present study and those of Stebbins et al. (1980) may be due to different methodologies. Deer mice tested by Stebbins et al. (1980) were subjected to temperatures ranging from −22° to 32°C, food and water were provided *ad libitum,* activity was unrestricted and four animals were run together while provided with a nest and nesting material. I used metabolic trials at thermoneutrality, and animals were tested singly in a post-absorptive state while confined in a 380 ml glass jar. These widely divergent techniques make a comparison of results tenuous at best, and each study must be viewed in the context of its unique methodology.

In the present study, *P. maniculatus* showed a decreased body temperature upon capture, although each animal quickly resumed normal body temperature when placed in the laboratory. Winter torpidity is common in *P. maniculatus* from the AMS and RMS and this decreased body temperature reduces energy expenditure and reduces food requirement during periods of cold. It is possible that the lower metabolic rate during winter on the AMS may be a physiological response to a winter increase in hair density and length (Sealander, 1951, 1972; Khateeb and Johnson, 1971; B. A. Wunder, personal communication), although this was not tested in the present study.

CONCLUSIONS

Small mammals are able to survive rigorous variations in their microclimates only by appropriate physiological, anatomical, and behavioral responses. These responses in turn reduce the physiological stress of cold to the individual thus optimizing survival. Small mammals show great variation and plasticity in their physiological constitutions both geographically and phylogenetically.

The objective of my study was to assess the role of seasonal growth changes in the energy budget of the deer mouse (*P. maniculatus*). The results of this research indicate that, unlike most microtine rodents which tend to undergo weight declines in winter, this seasonal reduction of weight does not occur in deer mice examined from the Rocky and Appalachian Mountains of North America. My research demonstrates that *P. maniculatus* maintains a lower metabolic rate during winter whereby reducing its caloric requirements during this period of the year when food is scarce. Lower metabolic rate and lower energy requirements probably contribute to the favorable energy budgets that permit deer mice to grow, if only slightly, during the winter months.

Deer mice have evolved a diverse repertoire of mechanisms by which they conserve energy during periods of cold. Notable among these is their ability to abandon homeothermy for torpor—this facility has never been shown in voles, which must continue to forage in coldest conditions and thus are strongly regulated by the quality and quantity of food. The ability for torpor coupled with communal nesting, food hoarding, and construction of elaborate nests aid considerably in energy conservation. These survival attributes and others mentioned earlier, account in part for the success and resultant wide geographical and ecological distribution of the deer mouse in North America.

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KARYOTYPES OF SOUTHERN AFRICAN GERBILS, GENUS *GERBILLURUS* SHORTRIDGE, 1942 (RODENTIA: CRICETIDAE)

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Abstract

Standard karyotypic data are presented for the species of the southern African rodent genus *Gerbillurus*. *Gerbillurus paeba* and *G. tytonis* have a diploid number of 36 and 68 autosomal arms. The karyotypes are morphologically similar to each other. *G. vallinus* and *G. setzeri* have a diploid number equaling 60, but the karyotypes differ in chromosome morphology. The autosomal arm number is 80 for the former and 76 for the latter species. Speculations on phylogenetic relationships are presented.

Introduction

Among the gerbilline rodents of Africa, the genus *Gerbillurus* Shortridge, 1942, is endemic to the more arid and semi-arid regions of southern Africa. It ranges through southwestern Angola, South West Africa/Namibia, Botswana, southwestern and southern Zimbabwe, southcentral Moçambique, northern Transvaal, western Orange Free State, as well as the western, central, and southeastern Cape Province (De Graaff, 1981).

The generic status of *Gerbillurus* Shortridge, 1942, with type species

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G. vallinus, has been unclear. *Gerbillurus* has been regarded as a synonym of *Gerbillus* Desmarest, 1804, by Ellerman et al. (1953). Shortridge (1942), Bauer and Niethammer (1960), Herold and Niethammer (1963), and Schlitter (1973) regarded it as a subgenus of *Gerbillus.* Roberts (1951), Lundholm (1955), Lay (1972), Davis (1975), Schlitter (1976), Pavlinov (1982), Honacki et al. (1982), and Petter (1983) considered *Gerbillurus* as a distinct genus. Pavlinov (1982:30) described a new subgenus, *Progerbillurus* to include *Gerbillus paeba* A. Smith, 1836 (cited by Pavlinov as 1834) and Petter (1983:266) proposed a new subgenus, *Paratatera,* to include *Gerbillurus tytonis* (Bauer and Niethammer, 1960).

The karyological study reported upon here was undertaken to supplement a morphometric analysis of species parameters, in an attempt to acquire a wider perception of species limits and relationships. The taxonomic treatment of Davis (1975) was used as the basis for examining the karyological relationships of the species of *Gerbillurus.* Davis (1975) recognized four species—*G. paeba* (A. Smith, 1836); *G. vallinus* (Thomas, 1918); *G. tytonis* (Bauer and Niethammer, 1960); and *G. setzeri* (Schlitter, 1973). Davis (1975) also listed a fifth, unnamed species from the Cape Flats, which he thought showed close morphological affinity to *G. paeba,* but which is here treated as conspecific with *G. paeba.* Because the latter species is by far the most widespread of the genus and also as a consequence of certain incongruent results in the morphometric analyses of this species, the karyotypes of each of the four subspecies of *G. paeba* listed by Davis (1975) were examined individually.

MATERIAL AND METHODS

Standard karyotypes were prepared in the field, employing the *in vivo* bone marrow technique described by Patton (1967) and Robbins and Baker (1978). Determinations of diploid number (2N) and autosomal arm number (AA) were based on counts of a minimum of ten mitotic spreads per specimen. Nomenclature of chromosome morphology follows that of Patton (1967). Voucher specimens were prepared as conventional museum skins and skulls. These, as well as the microslides, are deposited in the Transvaal Museum (TM), Pretoria; Carnegie Museum of Natural History (CM), Pittsburgh; Kaffrarian Museum (KM), King William's Town; and State Museum (SMW), Windhoek. See lists of specimens examined for localities and museum holdings.

RESULTS

The karyological properties of the four species examined in this study are discussed below. The material examined for each species is listed.

Gerbillurus paeba (A. Smith, 1836)

2N = 36, AA = 68. Fig. 1

The autosomal complement consists of 17 pairs of metacentric or submetacentric autosomes ranging in size from the very largest to the

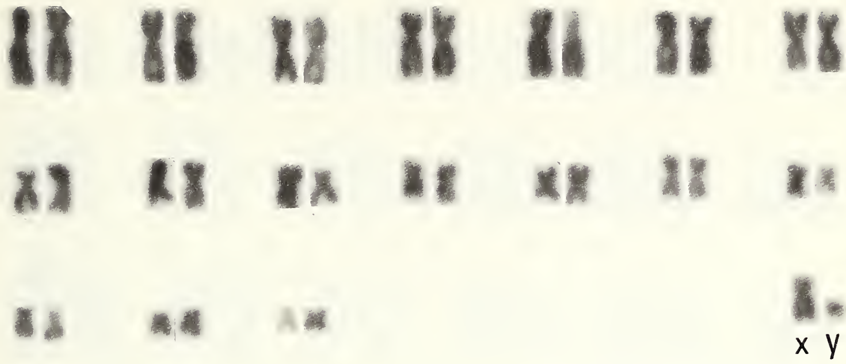

Fig. 1.—The standard karyotype for *Gerbillurus paeba* ♂ (TM 28910), 2N = 36, AA = 68.

smallest (exclusive of the Y sex chromosome) elements in a complete spread. The X chromosome is a medium-sized submetacentric, whereas the Y chromosome is a very small acrocentric. No marker chromosomes could be distinguished. Our findings agree with that of Matthey (1958), who recorded 2N = 36 for *G. paeba.*

Specimens examined (84).—SOUTH AFRICA: Cape Province, 6.5 km S, 50.3 km W Alexandria, 2 ♂♂, 1 ♀ (KM); Augrabies Falls National Park, 1 ♂ (CM); Dankbaar, Kalahari Gemsbok National Park, 1 ♀ (TM); Karoo National Park, 9 km NW Beaufort West, 1 ♀ (TM); Farm Kersbos, 10 km NNE Bitterfontein, 3 ♂♂, 3 ♀♀ (TM); Farm Kleintuin, 6 km NW Williston, 1 ♂, 1 ♀ (CM); Farm Skipperskloof, 6 km NW Williston, 1 ♂, 3 ♀♀ (CM); Mitchell's Plain, 25 km SE Cape Town, 9 ♂♂, 8 ♀♀ (CM); Transvaal Province, Farm Evergreen, Alldays, 1 ♀ (TM). SOUTH WEST AFRICA/NAMIBIA: Farm Kanaan 104, 5 ♂♂, 12 ♀♀ (12 CM, 5 TM); Ganab, Namib Desert Park, 2 ♂♂, 3 ♀♀ (TM); Namib Desert Ecological Research Station, Gobabeb, 8 ♂♂, 14 ♀♀ (TM); Homeb, 25 km upriver from Gobabeb, 1 ♀ (SMW); Huab River at Jack Scott Bridge, 1 ♂ (SMW); Tumasberg, Namib Desert Park, 2 ♀♀ (SMW).

Gerbillurus tytonis (Bauer and Niethammer, 1960)
2N = 36, AA = 68. Fig. 2

The standard karyotype of this species is indistinguishable from that of *G. paeba* described above.

Specimens examined (26).—SOUTH WEST AFRICA/NAMIBIA: Namib Desert Ecological Research Station, Gobabeb, 3 ♂♂, 4 ♀♀ (TM); Homeb, 25 km upriver from Gobabeb, 2 ♂♂, 3 ♀♀ (SMW); Farm Kanaan 104, 7 ♂♂, 5 ♀♀ (9 CM, 3 TM); Narra Valley, 10 km W Gobabeb, 2 ♂♂ (TM).

Gerbillurus vallinus (Thomas, 1918)
2N = 60, AA = 80. Fig. 3

The autosomal chromosomes consist of five pairs of metacentrics, six pairs of submetacentrics, and 18 pairs of acrocentrics. The X chro-

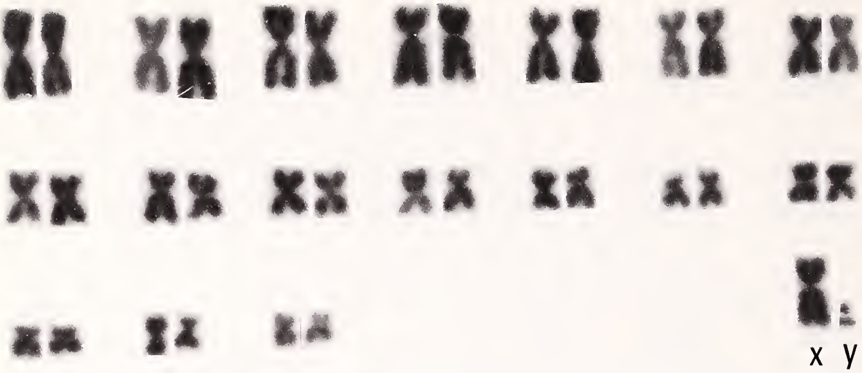

Fig. 2.—The standard karyotype for *Gerbillurus tytonis* ♂ (SMW 7620), 2N = 36, AA = 68.

mosome is metacentric and the largest chromosome. The Y is a small acrocentric chromosome.

This species differs significantly in its karyotypical properties from *G. paeba* and *G. tytonis* with respect to its higher diploid and autosomal arm numbers.

The two samples obtained are essentially topotypes for the nominate subspecies in South Africa and for *G. v. seeheimi* in Namibia.

Specimens examined (13).—SOUTH AFRICA: Cape Province, Farm Visservil, 25 km SW Kenhardt, 2 ♂♂, 4 ♀♀ (TM). SOUTH WEST AFRICA/NAMIBIA: Farm Rheinfels 125, 35 km SSW Keetmanshoop, 5 ♂♂, 2 ♀♀ (TM).

Gerbillurus setzeri (Schlitter, 1973)

2N = 60, AA = 76. Fig. 4

Autosomal chromosomes consist of nine pairs of metacentrics and submetacentrics and 20 pairs of acrocentrics. Thus, apart from autosomal arm number, this species also differs in chromosome morphology from *G. vallinus*. As in the other *Gerbillurus* species, the X sex chromosome is a submetacentric, although in this species and in *G. vallinus* it is the largest element present. This, together with a similar 2N, set these two species apart from *G. paeba* and *G. tytonis*. The Y sex chromosome is a small acrocentric, similar to the other three *Gerbillurus* species.

Specimens examined (11).—SOUTH WEST AFRICA/NAMIBIA: Brandberg West Mine, 1 ♂ (SMW); 13 km SSE Doros, 2 ♂♂ (SMW); Namib Desert Ecological Research Station, Gobabeb, 3 ♀♀ (TM); 33 km E Hentiesbaai, 2 ♂♂ (SMW); Homeb, 25 km upriver from Gobabeb, 1 ♂, 1 ♀ (TM, SMW); Ugab River mouth, 1 ♀ (TM).

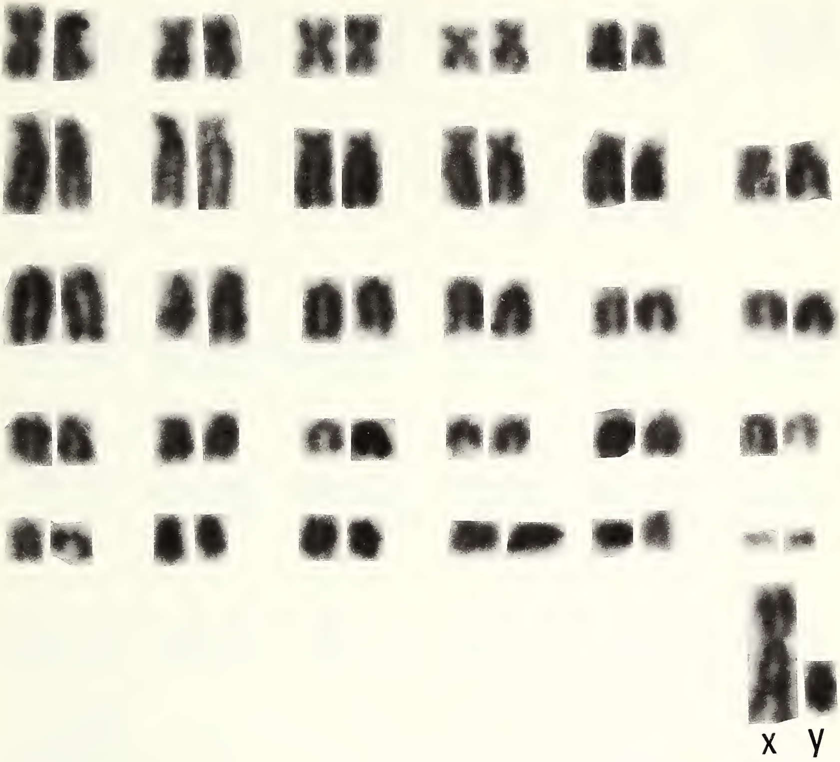

Fig. 3.—The standard karyotype for *Gerbillurus vallinus* ♂ (TM 32456) 2N = 60, AA = 80.

DISCUSSION

No differences in the karyotypes of *G. paeba* were found in 84 specimens examined from localities selected throughout the broad geographic range of this species in South Africa and Namibia. Specimens of all four subspecies (*G. p. coombsi* from the Soutpansberg district, *G. p. exilis* from the Port Elizabeth district, *G. p. infernus* from the Skeleton Coast of the Namib Desert, and *G. p. paeba* from the remainder of the South African range of the species) were examined and found to be all karyotypically similar. In addition, specimens of the *Gerbillurus* from the Cape Flats, which were listed by Davis (1975) as a potentially unnamed distinct species, also possess karyotypes identical to those found in other *G. paeba*. Because the karyotypic data are the same and the skulls of these specimens are morphologically similar

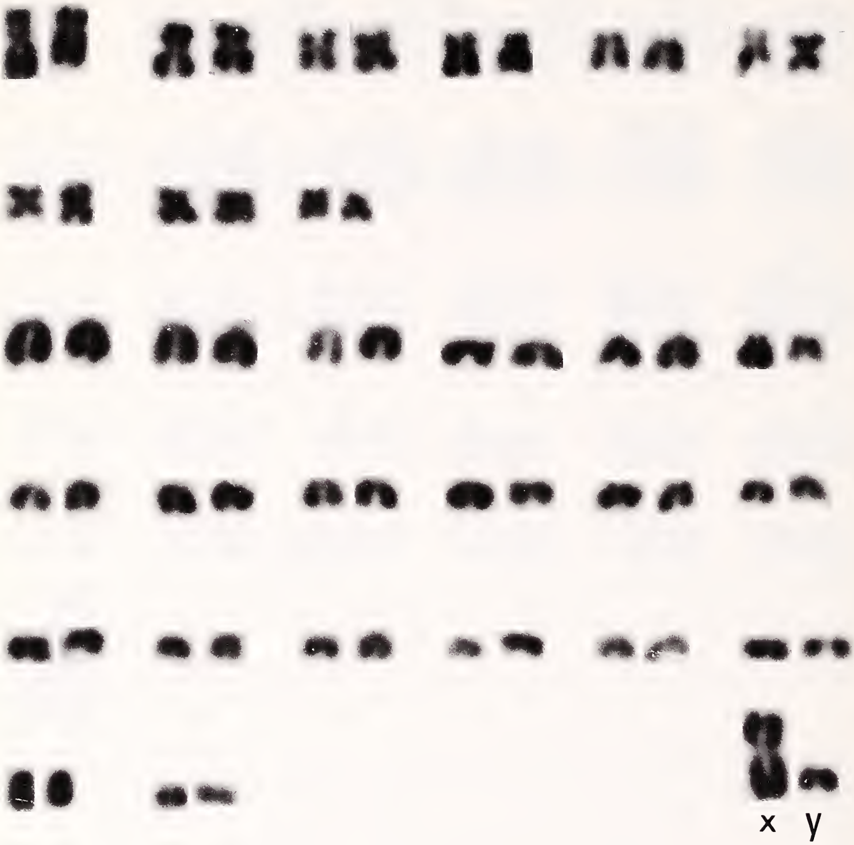

Fig. 4.—The standard karyotype for *Gerbillurus setzeri* ♂ (SMW 7619), 2N = 60, AA = 78.

to *G. paeba,* we provisionally place the Cape Flats specimens in *G. paeba* and assign them to *G. p. mulleri,* originally described from Eendekuil in the western Cape Province north of Cape Town.

Both Schlitter (1973) and Davis (1975) recognize two species groups among southern African *Gerbillurus,* that is, the *paeba* group consisting of *G. paeba* as well as the unnamed taxon of Davis from the Cape Flats, and the *vallinus* group of *G. tytonis, G. vallinus,* and *G. setzeri.* Subsequently, Pavlinov (1982) has described the subgenus *Progerbillurus* to include the *G. paeba* group as it is currently understood and Petter (1983) described *Paratatera* for *G. tytonis.* We concur that the *G. paeba* group deserved to be separated as a distinct subgenus based on morphological differences. However, based on the morphological evidence given by Petter (1983), we doubt the need for a separate subgenus to include *G. tytonis.*

Based on the standard karyotypes, there seems to be a closer relationship between *G. paeba* and *G. tytonis* than is evident from the morphological similarities. Similarly, *G. vallinus* and *G. setzeri* seems to form a closely related species group, although here minor interspecific differences in gross chromosome morphology indicate that the phylogenetic relationship of these two species is not as close as in the case of the other two species. These two species groups differ from each other in diploid number, number of autosomal arms and the relative size of the X sex chromosomes. Thus *Gerbillurus* (*Progerbillurus*) and *Gerbillurus* (*Paratatera*) are more similar karyologically than morphologically, whereas the species of *Gerbillurus* (*Gerbillurus*) form a distinct group karyologically. However, using chromosomal banding, Haiduk et al. (1981) and Wassif (1981) showed that chromosomal relationships of African megachiroptera and North African *Gerbillus* and *Dipodillus* based on standard karyotypes underestimate chromosomal variation.

Within the sequence *G. paeba* to *G. tytonis* to *G. vallinus* to *G. setzeri,* several morphological characters can be demonstrated to form an increasing size cline—skull length and breadth, posterior palatine foraminae, bullae size, body mass, tail length, and pilosity. Chromosomal characteristics reveal a similar increasing trend in 2N and autosomal arm numbers. However, as yet we can present no evidence that these trends reflect evolutionary sequence, and if so in which direction evolution is progressing. The debate whether derived forms exhibit a higher or lower 2N through chromosomal fission or fusion respectively, continues unresolved, and in this particular case fails to shed any light on the question of evolutionary direction. A *Gerbillurus* karyotype of 2N = 36 can be explained to have given origin to a 2N = 60 as is described above, through alternating processes of Robertsonian translocations and pericentric inversions. Conversely, however, the possible derivation of the 2N = 36 karyotype from a 2N = 60 can also be explained in the same fashion. Further studies on chromosome banding may throw some light on chromosomal evolution in *Gerbillurus.*

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GAZETTEER

Alexandria, 6.5 km S, 50.3 km W, Cape Province	33°42′S; 25°52′E
Augrabies Falls National Park, Cape Province	28°35′S; 20°21′E

Brandberg West Mine, SWA/Namibia	21°01′S; 14°04′E
Dankbaar, Kalahari Gemsbok National Park, Cape Province	25°03′S; 20°08′E
Doros, 13 km SSE, SWA/Namibia	20°50′S; 14°18′E
Evergreen Farm, District Alldays, Transvaal Province	22°43′S; 29°06′E
Ganab, Namib Park, SWA/Namibia	23°03′S; 15°08′E
Hentiesbaai, 33 km E, SWA/Namibia	22°10′S; 14°37′E
Homeb, 25 km upriver Gobabeb, Namib Park, SWA/Namibia	23°39′S; 15°10′E
Huab River at Jack Scott Bridge, Namib, SWA/Namibia	20°52′S; 13°31′E
Kanaan 104 Farm, Luderitz District, SWA/Namibia	25°53′S; 16°07′E
Karoo National Park, 9 km NW Beaufort West, Cape Province	32°20′S; 22°33′E
Kersbos Farm, 10 km NNE Bitterfontein, Cape Province	30°57′S; 18°12′E
Kleintuin Farm, 6 km NW Williston, Cape Province	31°20′S; 20°55′E
Mitchell's Plain, 25 km SE Cape Town, Cape Province	*ca* 33°52′S; 18°23′E
Namib Desert Ecological Research Station, Gobabeb, Namib Park, SWA/Namibia	23°30′S; 15°03′E
Narra Valley, 10 km W Gobabeb, Namib Park, SWA/Namibia	23°30′S; 15°03′E
Rheinfels 125 Farm, 35 km SSW Keetmanshoop, SWA/Namibia	26°55′S; 17°56′E
Skipperskloof Farm, 6 km NW Williston, Cape Province	31°20′S; 20°55′E
Tumasberg, Namib Park, SWA/Namibia	23°10′S; 15°31′E
Ugab River mouth, SWA/Namibia	21°12′S; 13°38′E
Visservil Farm, 25 km SW Kenhardt, Cape Province	29°23′S; 20°54′E

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